4 THE HABITAT

4.1 INTRODUCTION

As mentioned in Sections 1.3 and 3.4.6e, the Chough is believed to depend for its survival on low-intensity pastoral-based agriculture in combination with maritime cliffs. It is the most distinctive faunal link to utilise both these biomes via an imprecise transitional semi-natural zone, and it is a species which probably requires elements of all three within its yearly cycle. It seems able to exploit marginal areas, seasonal abundancies and restricted patches or foci of resources. An early precursor to the main study (Meyer 1990, see Appendix IV) proved useful in alerting me to the fact that Choughs required more than merely 'sheep-grazed pasture'. It has become apparent that the 'functional unit system' concept, as devised by Tamisier (1979) for waterfowl, and applied to Choughs by Bignal *et al*. (1989), is a useful tool in understanding the components necessary to sustain area viability for a particular species. Briefly, it takes into account the complete mix of biotopes used by all integral members of a species (not just the breeding population) within a range in order to accommodate all physical, social and behavioural needs, not merely those used at any one particular time.

While some general classification is useful, care must be exercised in the definition of the three biomes mentioned above: for example, 'cliffs' is a term often vaguely applied to any cliff region, and sometimes used to include all three, whereas, in reality, a great part will have been shaped and managed by man, *e.g.* cliffslopes grazed by sheep or introduced rabbits. Such broad categories, while useful as a starting point, especially when dealing with a species which associates with man, are, on own, inadequate, for Choughs use elements which occur in two or more. A detailed botanical examination of precise feeding sites found a consistent selection of ecotones and edge effects which confounded National Vegetation Classification (NVC, Rodwell 1982) (4.4), which advises that samples, to be representative, need to be placed well away from boundaries. The broad habitat variables used in this study are given in Table 2.2. Selection by Choughs is affected to a certain extent by local climatic and seasonal variables (Bullock 1980).

This chapter includes three assessments of Chough habitat: present-day (4.2), past (4.5) and changes over time (4.6). It deals with Chough selection within present-day range by study area and season in Section 4.3. Each part has its own introduction, methodology and results. The botanical enquiry (4.4) is a direct consequence of observations made in connection with Section 4.3.

4.2 PRESENT-DAY BACKGROUND HABITAT ASSESSMENT

4.2.1 INTRODUCTION

The basic assessment was introduced in Chapter 2.2, where the breakdown of km^2 selected and the rationale behind their survey were described. The assessment was designed to be compatible with a similar Scottish project (Bignal *et al.* 1988).

4.2.2 METHODS

The sequence of procedures was:
1. Selection of squares. 184 $1km^2$ arrayed on the OS grid, were selected to provide a 12% sample of land physiography and cover (see Appendix II for grid coordinates). Due to the Chough's natural habitat, coastal resolution was increased to *ca.* 25% by incremental selection of additional squares (see Table 2.1 and Figures 2.2 - 2.5). The main aim was to describe the land-cover types (natural,

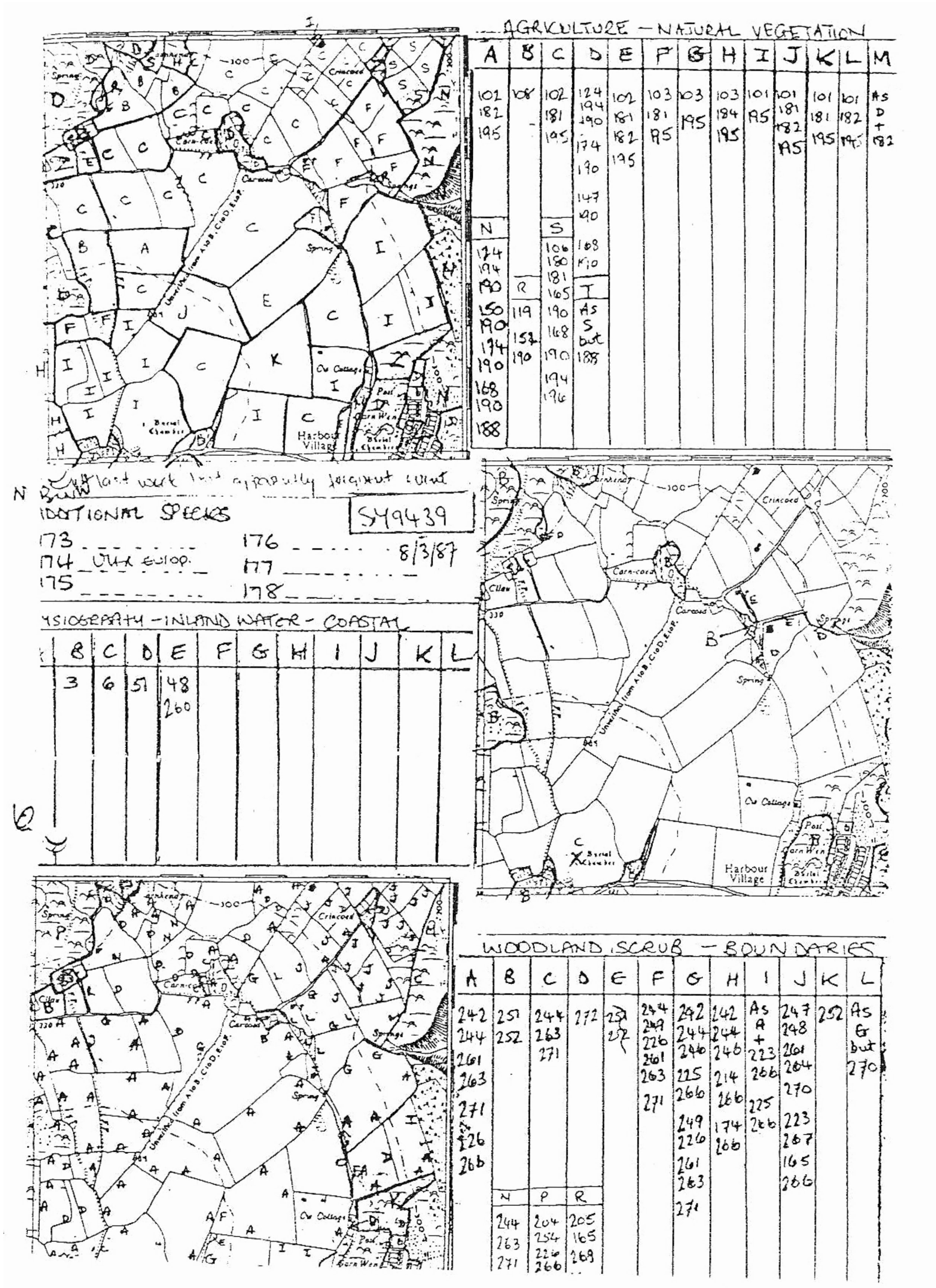


Figure 4.1a
Examples of completed 1km^2 field survey sheet: (a) inland.
Numbers in columns refer to cover types, usage, features and dimensions etc (see Chapter

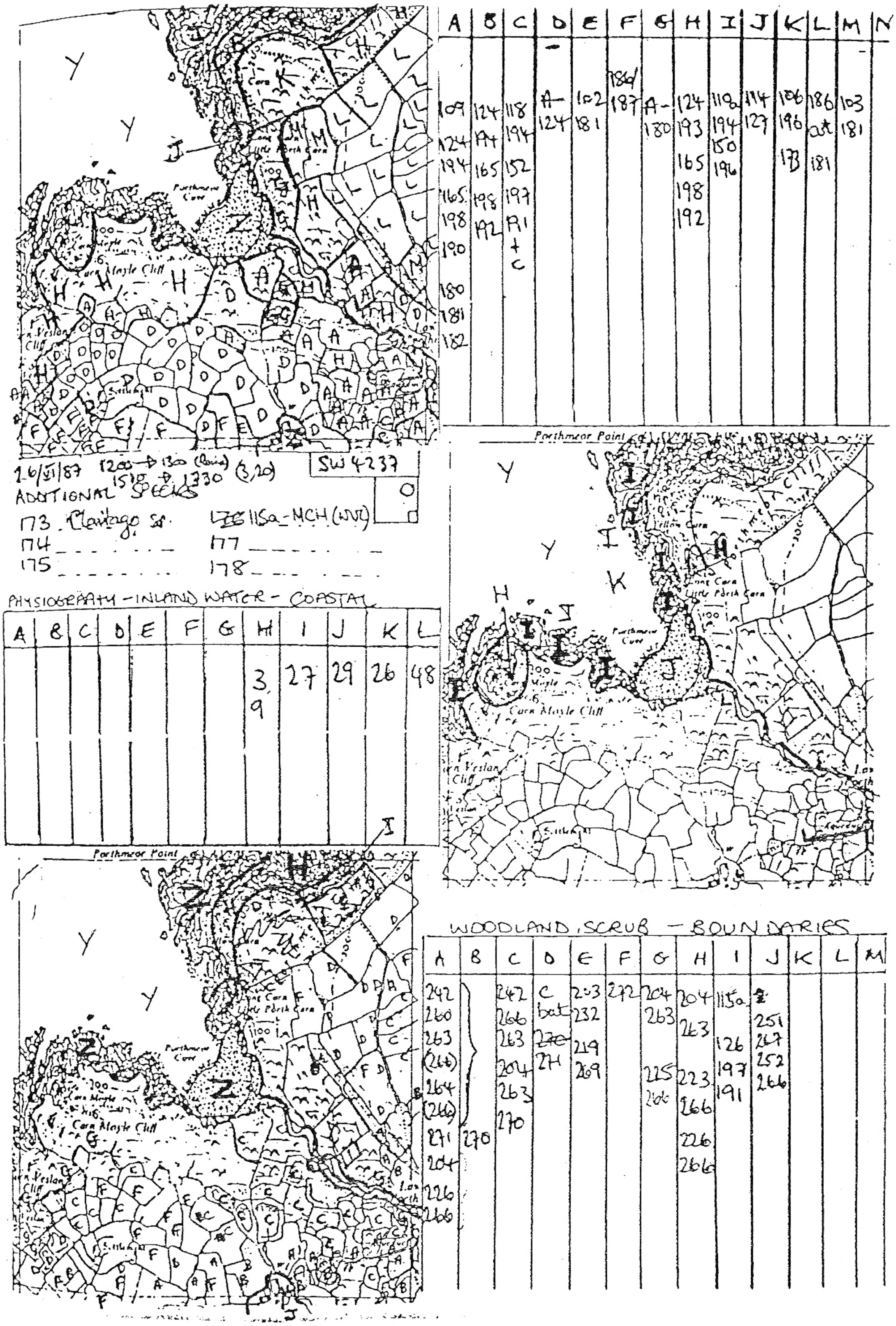


Figure 4.1b
Examples of completed 1km² field survey sheet: (b) coastal.
Numbers in columns refer to cover types, usage, features and dimensions etc (see Chapter

semi-natural and agricultural) in a way compatible with NCC habitat mapping systems, and to enable the data to be used as a base for future monitoring of habitat change.

2. Field mapping. Each $1km^2$ was surveyed and mapped for features associated with agriculture and (semi-)natural vegetation as described in Section 2.2. The boundaries of distinct patches, characterised by a particular variable or set of variables, were outlined on photocopied 1:10,000 maps and labelled (see Figure 4.1a,b); the variables are after Bignal *et al.* (1988a) but more detailed NVC classification was followed for maritime cliff communities (Table 4.1).

The system was devised to be sensitive to transitional stages: *i.e.* natural vegetation partially converted to agriculture, and vegetation modified by pastoralism. This was necessary to ensure that ecological variation was described and not lost by the application of inappropriate predetermined categories.

Table 4.1 Maritime influenced communities (after NVC, Rodwell 1982) used as the basis for habitat assessment (see Tables 4.2 - 4.4 for extra descriptions)

Code	Description
MC1	*Crithmum – Spergularia* maritime rock-crevice
MC4	Brassica maritime cliff-ledge
MC5	*Armeria - Cerastium* maritime therophyte
MC6	*Atriplex - Beta* sea-bird cliff
MC8	*Festuca - Armeria* maritime grassland
MC9	*Festuca - Holcus* maritime grassland
MC10	*Festuca - Plantago* maritime grassland
MC11	*Festuca - Daucus* maritime grassland
MC12	*Festuca - Hyacinthoides* maritime grassland
MG1	*Arrhenatheretum* grassland
U46	*Festuca - Agrostis* grassland
MCH	Maritime heath

3. Analytical methods. Completed field sheets were rasterized either by the use of automated digitising equipment or by manually transforming the discrete patches into arrays of letters by overlaying each completed field map with a 25x25 $4mm^2$ grid marked on a transparent acetate. Each square was scrutinised and subdivided by eye into quarters, giving 2,500 20x20m subsquares of information (called pixels) per map (Figure 4.2). The integrity of the original variables was maintained and formed into appropriate combinations of pixels per row to allow analysis of the data set. Each pixel type was assigned an individual letter to correspond with the environmental patch (Figure 4.3). Various analyses were then possible using either the original arrays of unique variables or derived combinations. Letters were used in alphabetical order in the field for each map and usually had no special significance or dependence on those used in other maps. For example, 'S' on one map might denote '100% improved pasture/<5cm tall/grazed by cattle' whereas on another square, 'S' might represent 'marsh'. It was necessary, however, for onward analysis, to ascribe letters which were consistent across all squares in order to conduct patch and map-square analyses:

Patch analysis. The field data were organised as described to produce a combination of patches which were then recoded to comply with a set consistent for all $1km^2$. A 'patch' therefore equalled a set of contiguous homogeneous pixels (20x20m mapped unit) bounded by a different set or sets

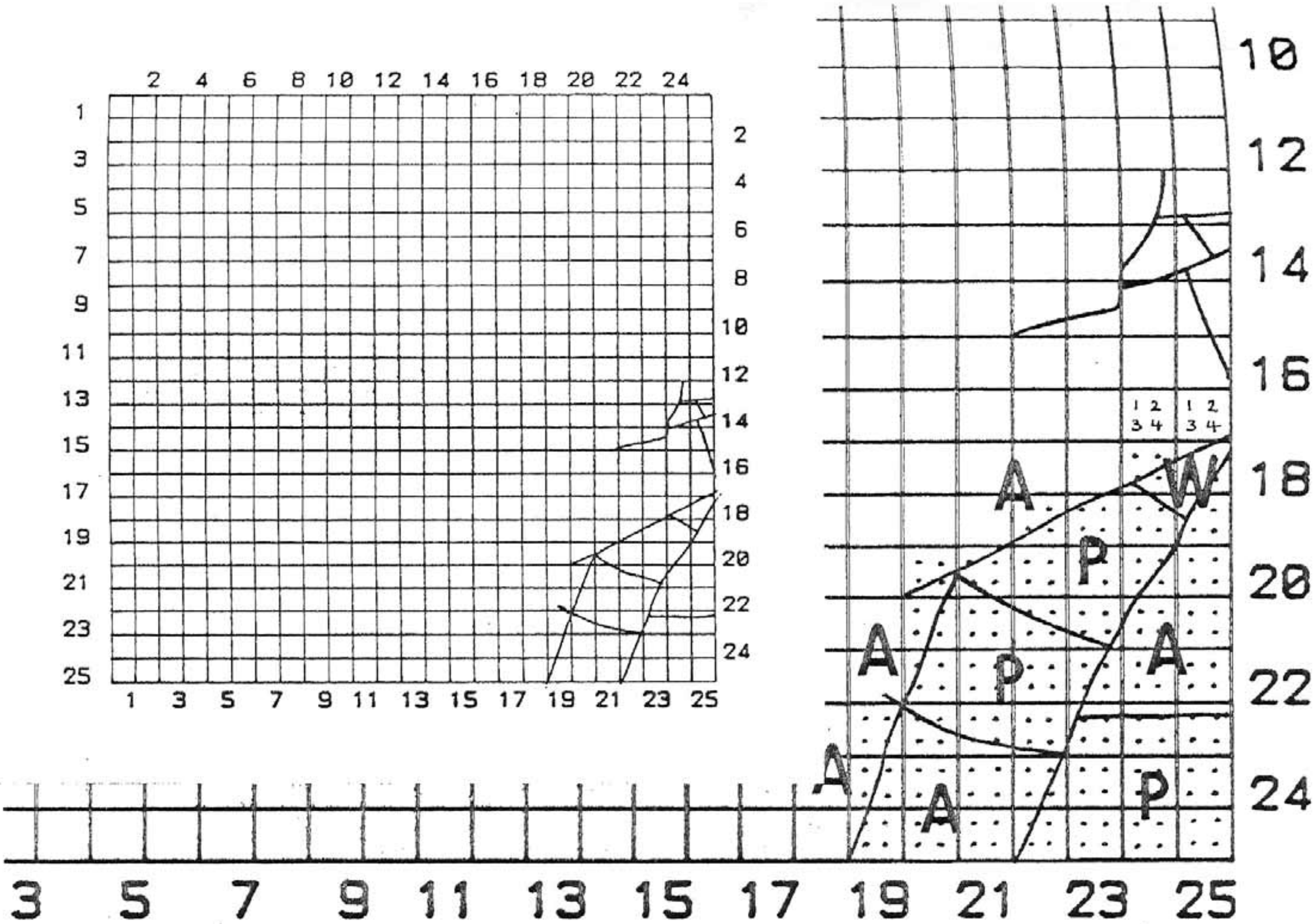


Figure 4.2
Diagram of acetate grid overlay and pixel counting rationale (row 17). Identified squares in bottom right corner would compute to:

Row 18	A*3W*4A	(A=4, W=4)	8 pixels
Row 19	A*3P*9WA*3	(A=6, P=9, W=1)	16 pixels
Row 20	A*5P*14A*5	(A=10, P=14)	24 pixels
Row 21	APAP*13A*8	(A=10, P=14)	24 pixels
Row 22	AP*12APA*9	(A=11, P=13)	24 pixels
Row 23	A*5PA*2P*2AP*17	(A+8, P=20)	28 pixels
Row 24	A*15P*13	(A=15, P=13)	28 pixels
Row 25	A*13P*15	(A=13, P=15)	28 pixels

* multipled by

Letters describe patch variable, *e.g.* A=arable, P=pasture etc or the limit of the map. Data handling involved taking the environmental data from the coded fieldsheets and entering them into a computer.

Map-square analysis. This was based on the descriptions of the 1km^2 by frequencies of different pixel types. Each pixel within the square was ascribed the letter of the patch-type to which it belonged. The squares could then be described by the quantity of pixels belonging to each patch-type (see Figure 4.3).

The data describing the observed patches were taken from each fieldsheet (see Figure 4.1). They were entered into computer as a subsidiary of the NCC land use project (Bignal *et al.* 1988a) at the Department of Biology in the Paisley College of Technology under the supervision of Professor D. Curtis and C. Moos. The TWINSPAN Cornel Ecology Program (Hill 1979) at the Institute for Terrestrial Ecology, Merlewood, Cumbria was used to classify squares and define habitat on the basis of pixel frequencies, and produce a dichotomous classification (Figures 4.4 - 4.6). TWINSPAN identifies indicator habitat-types and differential species, which are the attributes distinguishing the groups and governing the division at each ordinal level; all other variables are excluded.

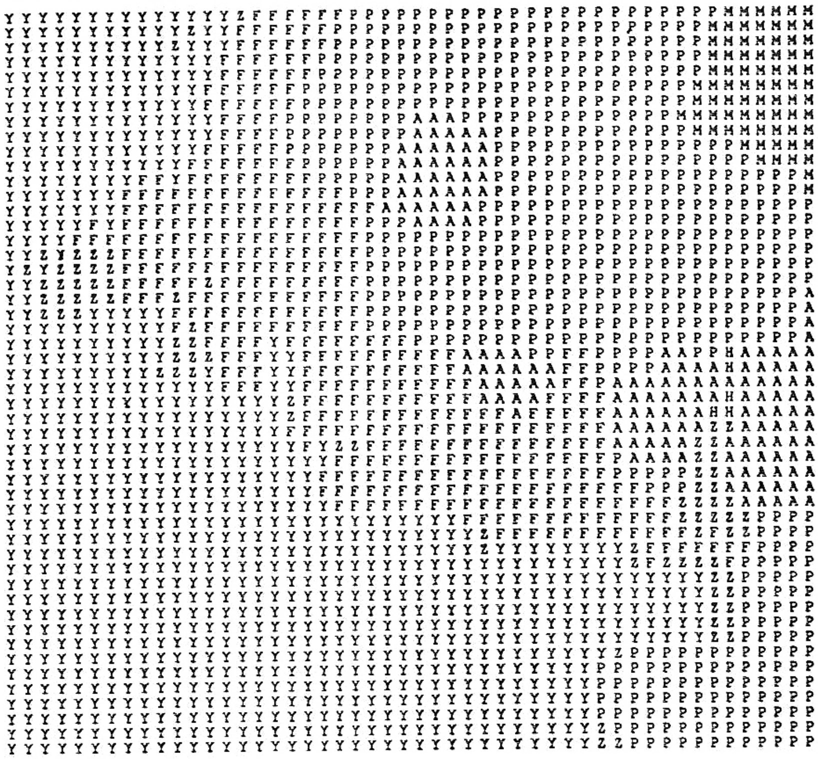
Subsequent observational fieldwork on the Chough showed that certain factors within the natural, often steep, cliff habitat influence the usage of the semi-natural and agricultural cliff-top habitat (see Section 4.3). The prescribed criteria were deficient in three main respects: (i) a minimum mappable unit of 20m^2 was not sufficiently sensitive to detect the smaller patches of complex mosaics used by Choughs within these natural habitats (see Section 4.4); (ii) the contour effect which, without correction, under-represents cover scores as assessed from 2-dimensional maps, *i.e.* the steeper the gradient, the closer together the contour lines, and the poorer the map resolution, until on a vertical cliff, map resolution is zero - a serious problem with a cliff-living species; and (iii) the intensive nature of the habitat survey prevented more than anecdotal recording of Chough usage within the sample during the study period. These problems were redressed in the assessment of habitat within the observational study areas (see Section 4.3.3b, Table 4.11). There is an opportunity for follow-up work specifically designed to relate the results of the original habitat survey to Chough usage.

4.2.3 RESULTS

The original TWINSPAN classification of all mapped patches (n=2176) is shown in Figure 4.4. As an example and for illustrative purposes, no selections or weighting were applied at this stage and yet the results show a good dichotomy between typical modern agriculture and habitats with attributes which are considered, on the basis of the literature and subsequent fieldwork, to be advantageous to Choughs. At level 6, 989 patches are selected, identified by the positive (for Choughs) attributes 'old-/improved pasture - cattle-grazed'. At the next level, on the left side, 266 patches are selected with the positive attributes of *Festuca* maritime grassland; however, the height profile (10-30cm) suggests disadvantageous under-grazing. At the final level (8), four end-groups of varying degrees of potency for Choughs are indicated; these are differentiated by, on the right side: (i) 'old-improved pasture - hay' (358); (ii) 'sheep-grazing' (63); and (iii) 'cattle-grazed - low profile permanent pasture' (14); whereas on the left side, 2 patches, indicated by *Ammophila arenaria* (Marram grass), are selected out, leaving the under-grazed maritime grassland as a <u>potentially</u> favourable habitat. Therefore 435 patch-types with positive attributes are selected, with a further 264 of high potentially.

The same treatment was applied to the Welsh and Cornish data independently; the results are shown in Figures 4.5a-b. By these means, 742 patches are indicated which carry good Chough attributes, 507 in Wales and 235 in Cornwall. In Wales (Figure 4.5a), an additional 48 have quite

S M 8839A agriculture



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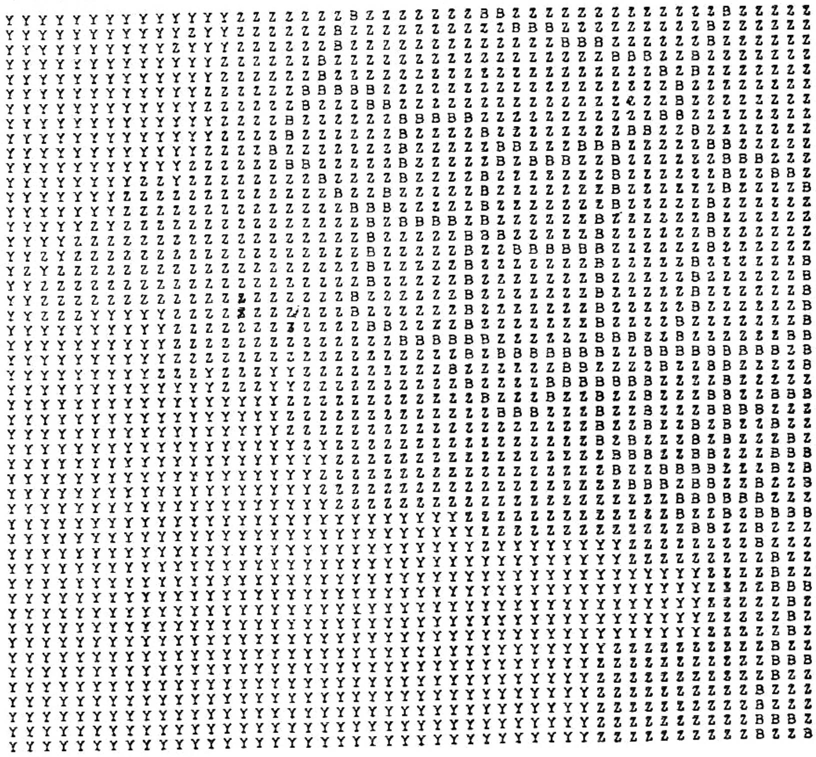

Figure 4.3
Rasterized 1km² map after environmental patches have been assigned individual letter arrays. Top, agricultural patches; bottom, boundaries; on both maps 'Y' = sea, other codes signfy patch variables. Boundaries: 'B' = boundary, 'Z' = other

high potentiality as indicated by the inclusion of sheep-grazing and old-improved pasture but this group also contains the indicators 'improved reseeded pasture' which seem less advantageous, at least in southern Britain (4.3). The '110' group is primarily maritime grass with heathland components but of a high vegetation profile and will contain many of the patches in the 266 mentioned above. The primary group in Wales is the '397' group, best summarised as low profile (<10cm) variably aged grassland, grazed by all the commoner domestic stock: cattle, sheep and horses.

The Cornish data analysis (Figure 4.5b) does not reveal short or even medium-short vegetation as differentially important. The largest group numerically is the '364' group indicated by tall bracken, indicative of 35.1% of all mapped patches. The equivalent group within the Welsh matrix is the '333' group which, as can be seen at level 6, contains the patches differentiated by tall bracken (this represents 29.3% of all patches). The primary ends groups in Cornwall, identified by TWINSPAN, and dichotomised by a high eigenvalue (>0.700), are the '162' group and, especially, the '73' group, which is exclusively maritime. The '242' group indicates intensive farming, and yet in Wales these elements are found in the '489' group at level 6 which also contains the Chough-positive '397' end group, suggesting that the mix of habitats in Wales is more varied.

It is important to remember that the data presented here are from the entire region, and therefore contain data from a high proportion of inland 1km^2 (see Figures 2.2 - 2.5), well outside current Chough range. It was decided not to attempt a classification based on a somewhat arbitrary selection of coastal squares but to create a dichotomy based essentially on the natural and semi-natural attributes indicated in Figure 4.4 since these already contain typical coastal characteristics. The result is shown in Figure 4.6; the emboldened end groups are those which have a high Chough value. The lower eigenvalues are well within validity limits (C. Moos pers. comm.). One hundred and thirty two patches (40%) are differentiated by a vegetation profile of <10cm; the balance is, not unexpectedly, comprised mainly of scrub, heath and longer grassland of variable but generally longer height.

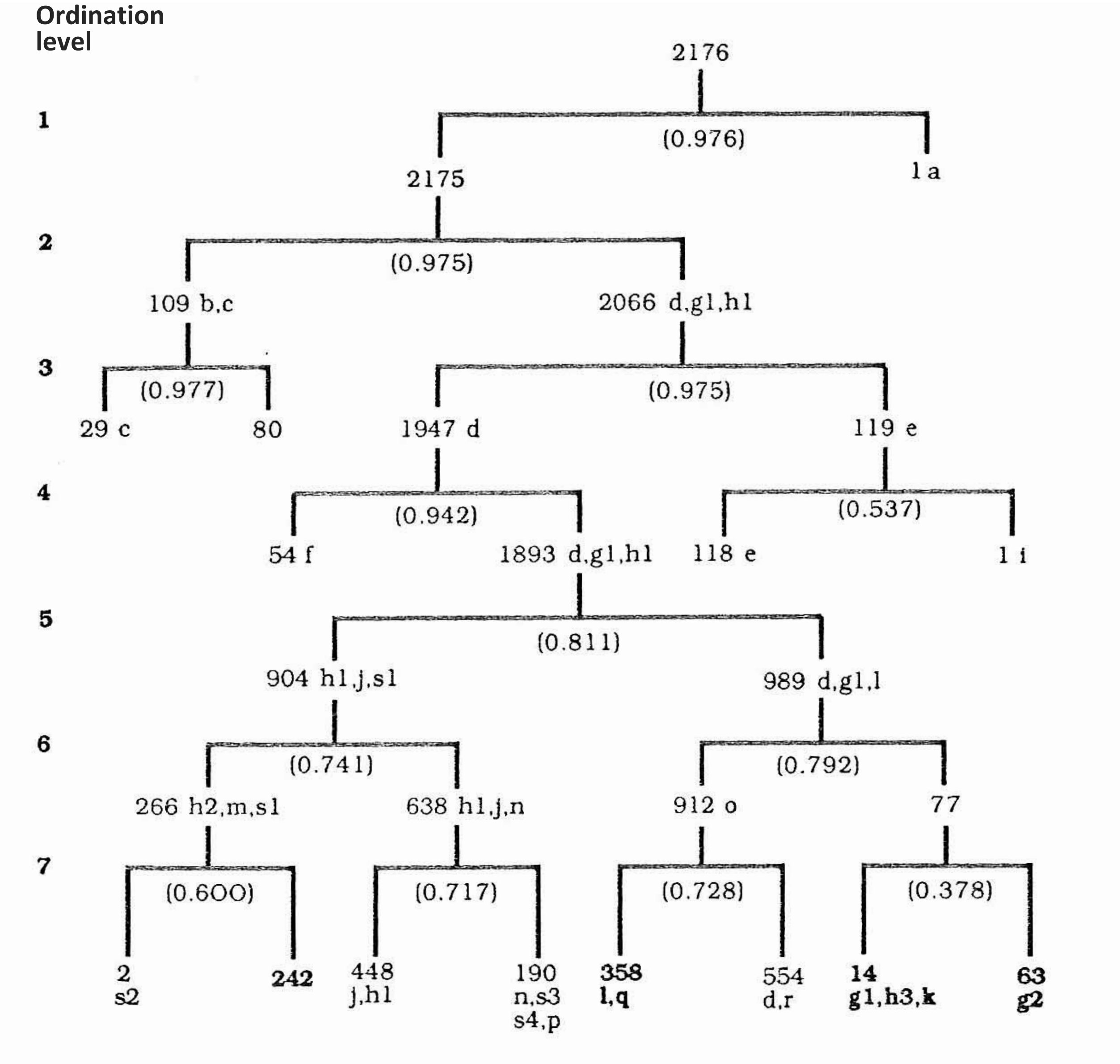

Figure 4.4
Hierarchical TWINSPAN habitat classification, Wales and Cornwall. Emboldened end groups contain possible attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level: greater value (0.001 - 1.0) + greater sample size (n=patches) = better dichotomy

Key (bold indicates possible Chough attributes included in end groups)

a	reclaimed land
b	root crop
c	other crop
d	improved pasture
e	cereal
f	ploughed
g1	cattled-grazed
g2	sheep-grazed
h1	vegetation <1m tall
h2	vegetation <30cm tall
h3	vegetation <10cm tall
i	burnt
j	*Pteridium* (bracken)
l	Old/permanent pasture
l	Old improved pasture
m	MC8 (see Table 4.1)
n	marsh
o	reseeded ley
p	flush
q	hay
r	silage
s1	*Ammophila arenaria*
s2	*Juncus* spp
s4	*Iris pseudocorus*

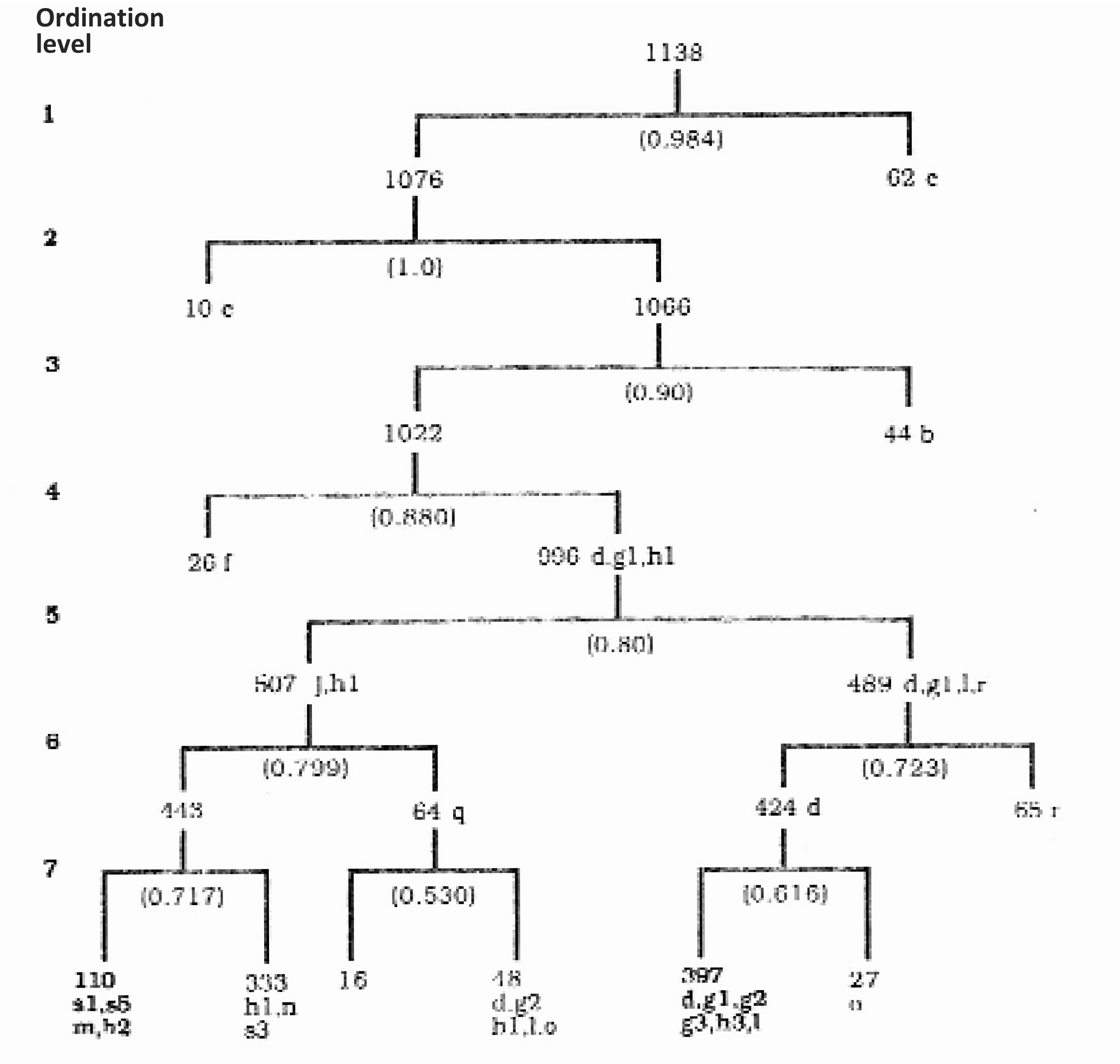

Figure 4.5a
Hierarchical TWINSPAN habitat classification, Wales only.
Emboldened end groups contain advantageous attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level.

Key (bold indicates favourable Chough attributes included in end groups)

b	root crop
c	other crop
d	improved pasture
e	cereal
f	ploughed
g1	cattled-grazed
g2	sheep-grazed
g3	horse-grazed
h1	vegetation <1m tall
h2	vegetation <30cm tall
h3	vegetation <10cm tall
j	*Pteridium* stands
l	Old improved pasture
m	MC8 (see Table 4.1)
n	marsh
o	reseeded ley
q	hay
r	silage
s1	*Festuca*
s3	*Juncus*
s5	*Calluna vulgaris*

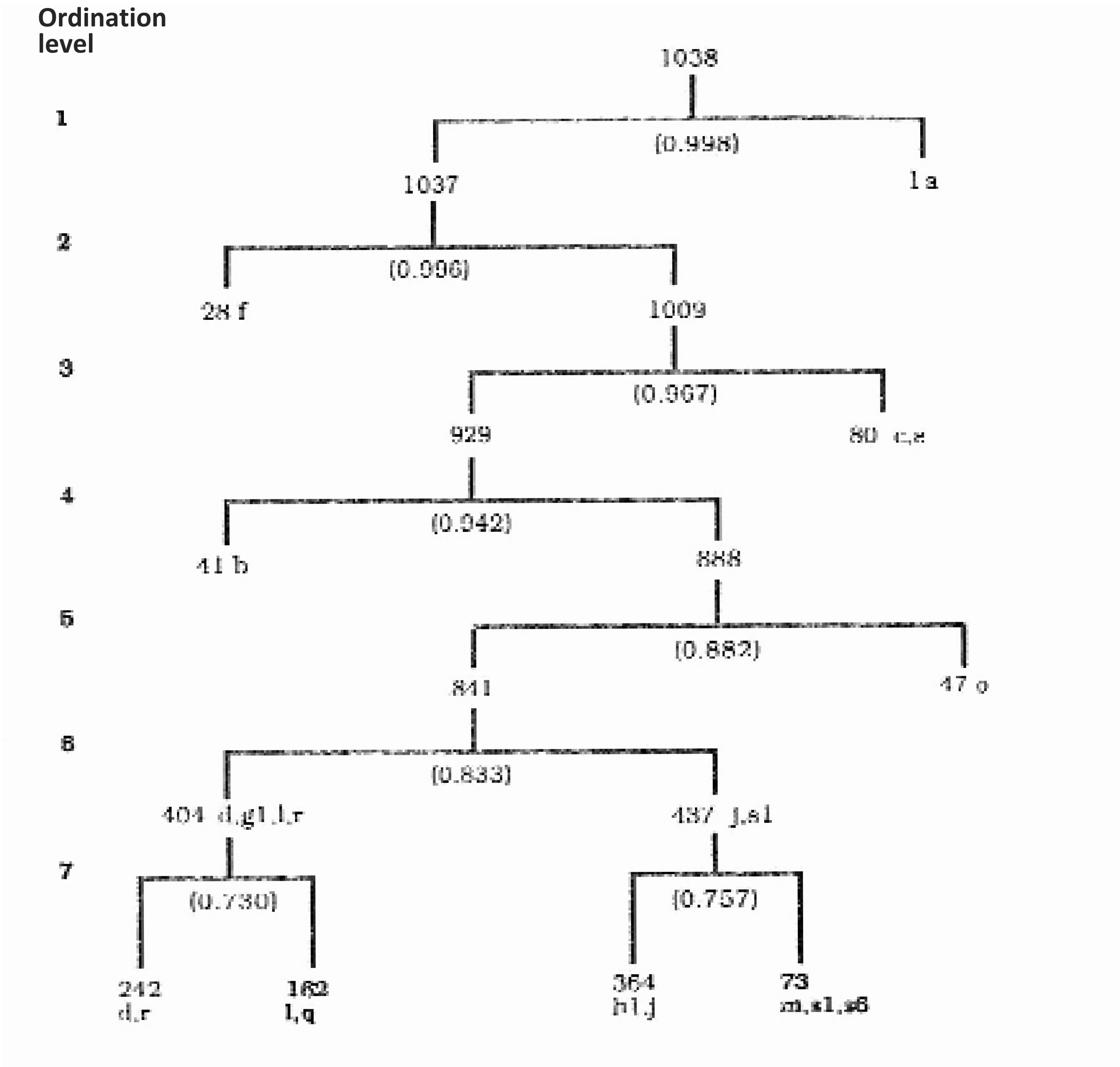

Figure 4.5b
Hierarchical TWINSPAN habitat classification, Wales and Cornwall. Emboldened end groups contain possible attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level: greater value (0.001 - 1.0) + greater sample size (n=patches) = better dichotomy

Key (bold indicates possible Chough attributes included in end groups)

a	reclaimed land
b	root crop
c	other crop
d	improved pasture
e	cereal
f	ploughed
g1	cattled-grazed
h1	vegetation <1m tall
j	*Pteridium* stands
l	Old improved pasture
m	MC8 (see Table 4.1)
o	reseeded ley
q	hay
r	silage
s1	*Festuca*
s6	*Armeria maritima*

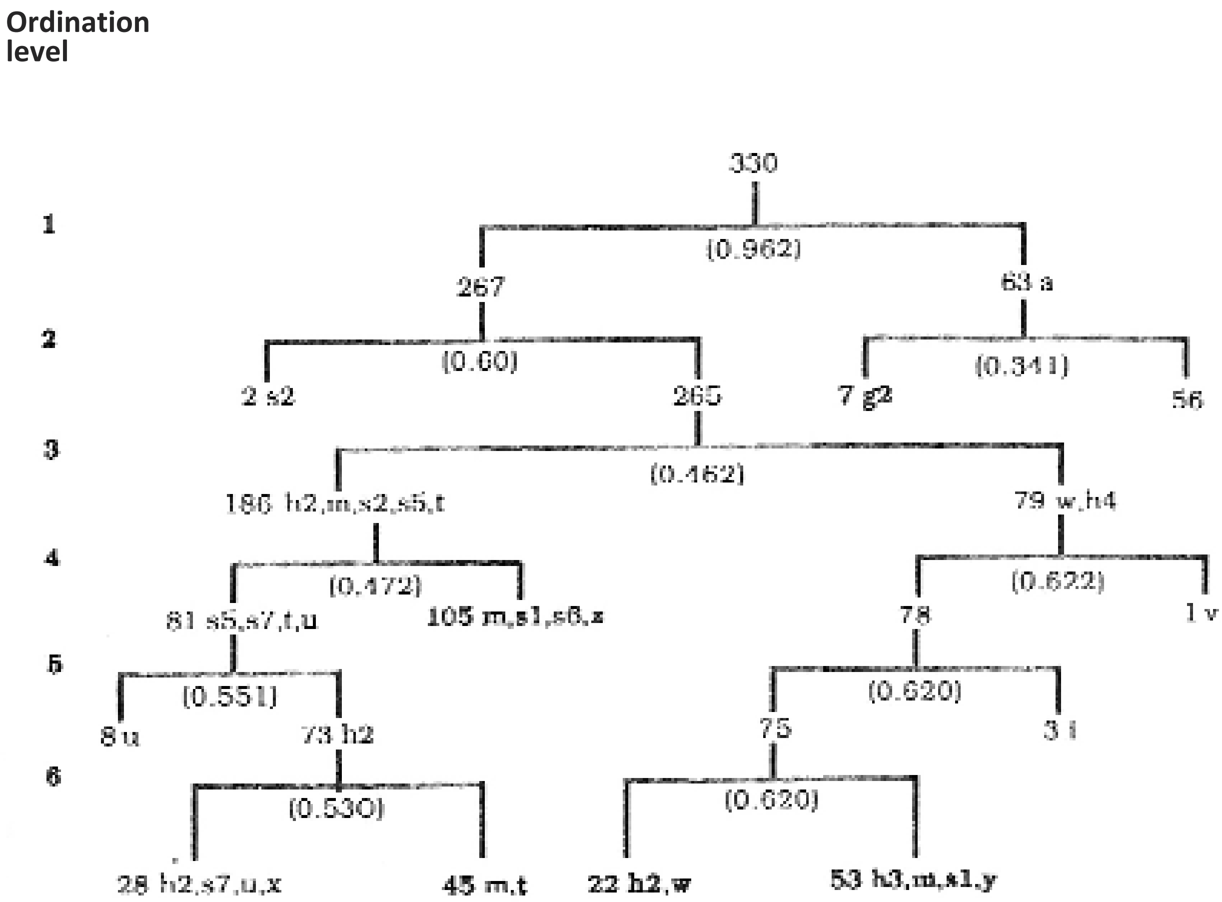

Figure 4.6
Hierarchical TWINSPAN habitat classification of natural and semi-natural habitat types, Wales and Cornwall. Emboldened end groups contain advantageous attributes for Choughs. Numbers in brackets are 'eigenvalues' (Hill 1973) which dichotomise the ordination level.

<u>Key</u> (bold indicates possible Chough attributes included in end groups)

a	reclaimed land	s6	*Armeria maritima*
g2	sheep-grazed	s7	*Erica cinerea*
h1	vegetation <1m tall	t	MCH (see table 4.1)
h2	vegetation <30cm tall	u	maritime scrub
h3	vegetation <10cm tall	v	aquatic macrophytes
i	burnt	w	species-rich grass
m	MC8 (see Table 4.1)	x	moor grass
s1	*Festuca*	y	rough grazing
s2	*Ammophila arenaria*	z	therophytes
s5	*Calluna vulgaris*		

4.3 SELECTION OF HABITAT BY CHOUGHS

4.3.1 INTRODUCTION

When members of a species select one habitat to exploit in preference to another nearby, an understanding of the factors which effected the selection is instructive about the particular species' ecological requirements. Appropriate habitat selection processes are likely to reduce the effects of competition. Within sympatric congeners, the degree of adaptive radiation of bill morphology, for example, is known to be sensitive to low abundancy food supplies (Schoener 1965). It is also possible to gain an insight into a particular species' niche by examples of convergency; for example, the decurved beak of the Curlew, not unlike the Chough's, has been shown to facilitate the shallow probing of subterranean invertebrate passages (Davidson *et al*. 1986; see Section 1.3.1). The tit family (Paridae) has provided much of the evidence for selective habitat use in birds (*e.g.* Kluijver 1951, Kluijver & Tinbergen 1953, Gibb 1954, Lack 1966, Royama 1970, Krebs 1971, van Balen 1973, and Krebs *et al.* 1977). For example, tits in the Old World, and chickadees in the New World, which exploit coniferous woodland in preference to deciduous woodland, tend to have finer and more sharply pointed bills with which to gather the particular invertebrate prey found at the base of conifer needles (Lack 1971).

As with the Curlew, the Chough is specialised in the mandibulation of invertebrate prey in subterranean passages and generally probes and 'investigates' for food. 'Good' Chough habitat might be summarised as 'invertebrate-friendly' and 'invertebrate-accessible': these are usually natural or semi-natural systems. However, of course, not all natural habitats within their current range are utilised by Choughs: if maritime scrub succeeds the abandonment of grazed clifflands, it would be the <u>previous</u> state that benefited Choughs (*i.e*. pastoralism), the natural succession representing a deterioration in the suitability of habitat for Choughs. It was necessary, therefore, in this study, to relate assessment criteria directly to known Chough usage. This was achieved by including on the benefit, or plus, side of the equation any habitat which Choughs use regularly and on the negative side any which they do not. The resulting categorisation could then be examined to see where a particular human activity lay, vis-a-vis benefit to Choughs; *i.e.* on which side of the equation did it fall. Maritime scrub may be regarded as man-influenced secondary habitat or non-Chough-friendly natural habitat but it is equally negative. Grassland morphology depends on extrinsic, climatic and biotic factors, and usage by man, such as his stocking, mowing and ploughing regimes, the application of chemicals etc. (Moore 1966), and just by his sheer physical presence (Liddle 1975). A history of rough grazing or low-input cultivation or pastoralism would be indicated by 'permanent', 'old', 'semi-' or 'un-improved' grassland, *i.e.* beneficial influence by man. There are likely to be 'grey areas' at the threshold from low- to high-intensity agriculture, where Chough usage changes or falls off. Also, it must be remembered that all areas accessible to man are vulnerable to reversion or drastic change. Such change, *e.g.* ploughing, is usually damaging but not inevitably so: scrub cleared perhaps by burning, can suddenly release habitat for Chough exploitation (Haycock & Bullock 1982); Owen (1985) recorded that all heathland feeding incidents in one year of his study in Ceredigion (north of study area W1) were in a single mown area (n=34hr). Similarly, rotation from arable to improved grass could provide a valuable winter dung resource. Only inaccessible islets and the steeper cliffs are generally beyond man's direct long-term influence.

Animals influence each other in selection of localised food resources,and they may remain in a known area rather than increase energy expenditure by searching for alternative sites (Norberg 1977). Optimal foraging has been most studied with intraspecific groups or solitary predators (see, *e.g.* Perrins & Birkhead 1983). Cost of feeding is altered by the spatial distribution of prey and its visibility, but it is usually implicitly assumed that flock-size of predators (even if n=1) is near optimal.

If so, various benefits must accrue to the co-operating individuals of flock-species that are lacking when the flock is at sub-optimal size. Ward & Zahavi (1973) advanced the theory that communal roosts act as 'information-centres' for food-finding, and Still (1989) discussed the hypothesis in relation to Choughs on Islay, where the species is not declining, and is considered to be at least stable or probably expanding at an historically high level (Easterbee & Bignal 1989). She concluded that it was important for Choughs to roost in high numbers near good feeding areas.

It is not known whether the Chough population in West Wales is stable; an apparent low-level stability (Bullock *et al.* 1985) could be disguising an ageing population or one bolstered by recruitment from elsewhere (*e.g.* Bardsey). The survival of breeding birds will exceed that of the population as a whole if opportunity to breed is related to social status and competitive ability (Perrins 1971); non-breeding birds might be forced to live in sub-optimum habitats. Whether stable or not, density and range is at a level well below that seen on Islay; observed flock size never exceeded 20 in the study-range of 950ha, compared to a maximum of 120 on Islay (*ca.* 30,000 ha of Chough range, after Bignal *et al.* 1988). Occasional larger flocks (>30) are seen however (J. Donovan pers. comm.). There were no large communal roosts to serve as information-centres in my study areas; all roosting appeared to be in small familial groups, but birds were not marked. If Dyfed is currently at carrying capacity, then a measure of actual Chough usage is perhaps of more value than a hypothetical comparison against idealised optimum conditions. For these reasons, the habitat usage data is presented in both aggregated (over all time) and disaggregated format (mean time per day) for different habitats and study areas (4.3.2). In Section 4.3.3b, usage in the study areas is measured against availability and by season; and the habitats for this purpose, unlike in Section 4.2, are described exclusively with the Chough in mind.

4.3.2 METHODS

It has been stated (4.1) that Choughs exploit marginal resources; they are characteristically able to find and exploit small pockets of suitable habitat within broader tracts of less favoured terrain. I was interested in a finer definition of habitat (its component structure) than that employed by Bullock (1980), Roberts (1983) and Owen (1985), but it was not possible to assess accurately the available area of each habitat component because of the scattered, overlapping, temporally variable and often minimal extent of some, *e.g*. exposed substrate (4.3.4). It is, though, possible to state, for example, that some (semi-)natural habitats have exposed substrate as a <u>constant feature</u> (*i.e.* therophyte communities - winter sensitive annuals). So, of course, do drilled and reseeded leys but these are transitory features of an intensive (non-invertebrate friendly) agriculture, and are not, therefore, (semi-) natural.

Time spent foraging in different habitats was used to measure habitat selection (4.3.3). While aggregated time across all observation periods was empirically valuable in demonstrating the kinds of habitats most utilised by the Choughs under observation, a potential statistical problem was engendered by the lack of independence between individuals within groups of feeding Choughs, and between the individual time units, *i.e.* minutes. This was overcome to some extent by calculating the mean proportion of time per group per pursuit period spent in each habitat type, thereby taking each observational period as an independent sample. Aggregated time was used as a means of identifying and assessing components, which could then be subjected to more rigorous analyses.

The main biomes used by Choughs formed the fieldwork base for land-type classification. They were:

1. Maritime cliffs: natural. Inaccessible to casual visitation by man and his livestock; includes areas dominated by rock, islets and steep slopes; often subject to severe exposure and salt deposition (Malloch 1972) which gives rise to unique botanical communities characterised by erosion zones and sparse open communities of therophytes (Rodwell 1982).

2. Agricultural: man-made. The largest and most homogeneous category. Land usually enclosed and under permanent but not necessarily rotational management. Arable land is mainly cereal crops, occasionally roots and brassicas. Buildings and other artefacts did not occur significantly in the study areas (1.35% of study range, see Table 4.11).

3. Transitional: man-influenced or semi-natural. Difficult to demarcate since farmland often blends into cliffland through a series of ecotones. These may be used by man at a low-level or only intermittently. Man influences habitats indirectly as well: one example is rabbit-grazed maritime grassland (rabbits are not indigenous British fauna but are now naturalized). Is such a habitat man-influenced? In order to arrive at a sensible and valid set of criteria, applicable to all likely eventualities, it was decided to begin by differentiating at a point between man-made intensive agricultural land, which is known to be little used by Choughs, and semi-natural land subject to lower levels of manipulation, *e.g.* permanent pasture, trampled natural vegetation etc. (man-influenced). For the main purposes of this study, therefore, (1) and (3) are combined into 'cliffs/non-intensive agriculture'. Grassland can be complex and is found in (1), (2) and (3) (see Tables 4.2 & 4.3). The main differentiating criterion for this study was permanency (*i.e.* 5-7 years was regarded as 'permanent pasture') and absence of top-dressing (*i.e*. biocides and fertilsers).

Since Chough activity concentrates very largely on foraging, accounting for well over 90% of active time (see Chapter 6), a detailed refinement of these broad classes was necessary in order to establish as precisely as possible exact habitat requirements. Of the 24 major categories or components selected (see Table 2.2), 21 are not dependent on intensive farming methods. Of the remainder, a further 3/8 of the specified types are not necessarily so; only categories 15 and 22a-c are usually the result of a more intensive agriculture.

All observed feeding sites were inspected, where accessible, after the birds' departure (or examined with a telescope if not accessible) for their patch physiography and vegetation characteristics. During pursuit periods (2.5.2), they were marked for later attention. Usually it was possible to ascertain the precise location of a feeding point by the presence of field signs (probe holes, disturbed ground, faeces, etc.). Field notes recorded such physiographical detail as botanical communities, and grazing regime where present.

An assessment of usage lumped over time 'FCMs' (Feeding Chough Minutes) was obtained by multiplying FC by M, where FC is the number of feeding Choughs, and M, the minutes spent feeding. This method was used to gain a broad overview of Chough habitat selection since it could include all incidental feeding observations, together with those recorded by volunteers. Mean proportion of feeding time (PFT) spent by individuals observed in different habitats during dedicated pursuit days was used as the basis for more rigorous statistical analyses which allocated each feeding event into an exclusive category (4.3.3). FCMs were related to availability by dividing by the amount of habitat available. Owen (1985) employed the equivalent of FCMs in his study at Lochtyn, to the north of Mwnt in Ceredigion, but used only 6 habitat variables (*rock dominant, short grass, long grass, thrift, sheep bare* and *heath*).

Feeding sites may be described in a variety of ways, the value of any being determined by the inquiry in hand. For example, one bout, selected at random, took place on a (i) *cliff* (ii) *-top* (iii) *path* comprised of (iv) *short* (v) *herb-rich* (vi) *maritime-grass* which had been (vii) *sheep-grazed*, shown by the evidence of (viii) *old dung*. It is the <u>combination</u> of two or more of these 8 features that

Table 4.2 Categories of maritime and sub-maritime grassland communities after NVC (National Vegetation Classification). A suite of closed swards with Red fescue *Festuca rubra* generally abundant, and understood in terms of species balance (see also Table 4.3)

Category	Description
MC5 *A. maritima* *Cerastium diffusum* maritime therophyte community	Constant spp. *F. rubra*, *Plantago coronatus*, *Sedum* sp. Characteristic of excessively-draining, often very shallow soils at all levels on rocky, where skeletal mixtures of mineral/organic matter acumulate, or near rock outcrops where deeper soils thin out. Generally out of reach of stock and ungrazed, even where there is no clifftop enclosure.
MC8 *Festuca rubra* - *Armeria maritima* maritime grassland	A generally closed sward, dominated by *F. rubra*, which often forms a thick mattress. *A. maritima* often abundant as scattered bulky cushions. The most maritime of the grasslands. Generally occurs on steep to moderate slopes up to *ca.* 50m a.s.l., but can also occur on level areas, *i.e.* Gateholm Island (Marloes study area); receives a lot of salt-spray.
MC9 *Festuca rubra* *Holcus lanatus* maritime grassland	Extra constant spp. *Plantago lanceolatus*, *A. maritima*. Closed fairly low-growing but often rather rank/tussocky. Usually dominated by *F. rubra*
MC10 *Festuca rubra* - *Plantago* spp. sub maritime grassland syn. 'Plantago sward'	Constant sp. *Agrostis stolonifera*. Closed very short and distinctive tight clifftop sward, generally dominated by *F. rubra* and *Plantago* spp., especially *P. maritima*, some *A. stolonifera*. A grazed equivalent of MC9 and possibly also MC8
MC11 *Festuca rubra* - *Daucus carota* sub-maritime grasland community	Constant sp. *Dactylis glomerata*. A fairly short and rather tussocky sward, of which *F. rubra* is the dominant grass. Most common on chalk and limestone cliffs of south coast W to Dorset and S Wales; isolated occurrences in SW England
MC12 *F. rubra* - *Hyacinthoides non-scripta* maritime bluebell community	Para-maritime: constant sp. *Holcus lanatus*. scattered *Rumex acetosa* and ocasionally *Daucus carota*. Occurs at same level as maritime heath grading from MC9 below.
MG1 *Arrhenatheretum elatioris* grassland	Sometimes encountered on maritime cliffs where well drained soils occur with slight maritime influence, often grades seaward into MC9
U46 *Festuca* - *Agrostis* grassland	Short tight sward dominated by *F. ovina* & *F. rubra* and *Agrostis capillaris*, often encountered on clifftops with neutral to acid grassland. Might be derived from maritime heath by heavy grazing

Table 4.3 Categories of maritime rock crevice and cliff ledge communities (after NVC) observed to support Chough feeding events

Category	Description
MC1 *Crithmum maritimum* - *Spergularia rupicola*	The typical rock crevice sub-community normally lacks *Inula crithmoides*.
MC2 *Armeria maritima* *Ligusticum scoticum*	Constant sp. *Festuca rubra*. Low growing, very open, rooted in rock crevices, strongly influenced by substrate. No species truly dominant. Not in Wales or Cornwall.
MC4 *Brassica oleracea*	Cliff ledge community. The *Beta vulgaris* ssp. *maritima* sub-community includes this type plus *F. rubra*, *Dactylis glomerata*, *Daucus carota* ssp. *gummifer* and *Brassica oleracea*

Table 4.4 Agricultural grasslands

Category	Description
RS Reseed (ley)	Grass sown in current or previous year
IP Improved pasture	< 5 years old. Short term grassland or ley, shown by evidence of ploughing, bare soil between grass plants (dominated by single sp.), scarcity of broad-leaved species (< 5-10/sq. m)
S-IP Old- or semi-improved pasture	Older IP - longer term grassland usually in enclosed land with a higher density of grass and herb species (*ca.* > 10sp/sq. m)
OP Old or permanent pasture	Unimproved pasture, no evidence of ploughing, generally species- and herb-rich

provide the attraction to Choughs. This form of presentation, though, provides a way of assessing the selection by Choughs of particular components or broader habitats but care should be exercised in their inter-relation, and for this reason they are not ranked. To overcome the problem of inter-relation, componental use was arranged hierarchically in order to establish the location of each within a broader context.

To relate usage or selection to availability (4.3.4), it was necessary to use habitat categories which were sufficiently broad to (i) be measured reasonably accurately and consistently, and (ii) form an identifiable standard of use outwith the study range. It would also be valuable to be able to relate this study to the results from other Chough autecological studies (*e.g.* Bullock 1980, Warnes 1982, Roberts 1985). For these reasons, dung and the component elements described in Section 4.3.3 were excluded. All feeding observations were allocated a biome category (dung events were placed in the host pasture habitat). Areas of biotopes in the study areas were calculated with a Cherry digitizer bit-pad.

4.3.3 RESULTS

4.3.3a FEEDING TIME SPENT IN DIFFERENT HABITATS

An indication of the relative importance of different components which build the habitat structure is given in Table 4.5. It is important to remember, regarding these data, that the components are not necessarily mutually exclusive but this array provides a convenient means of showing variability in the usage of different habitat components. The variability is at least partly explained by variation in availability across the study areas (4.3.3b). If West Wales is regarded as a study region, of which the study areas form a representative sample, the combined (=regional) percentage provides a representative view of West Wales as a whole, against which habitat selection in the individual study areas can be compared.

The cliff complex is the main biome, accounting for a mean feeding time of nearly 75% (Figure

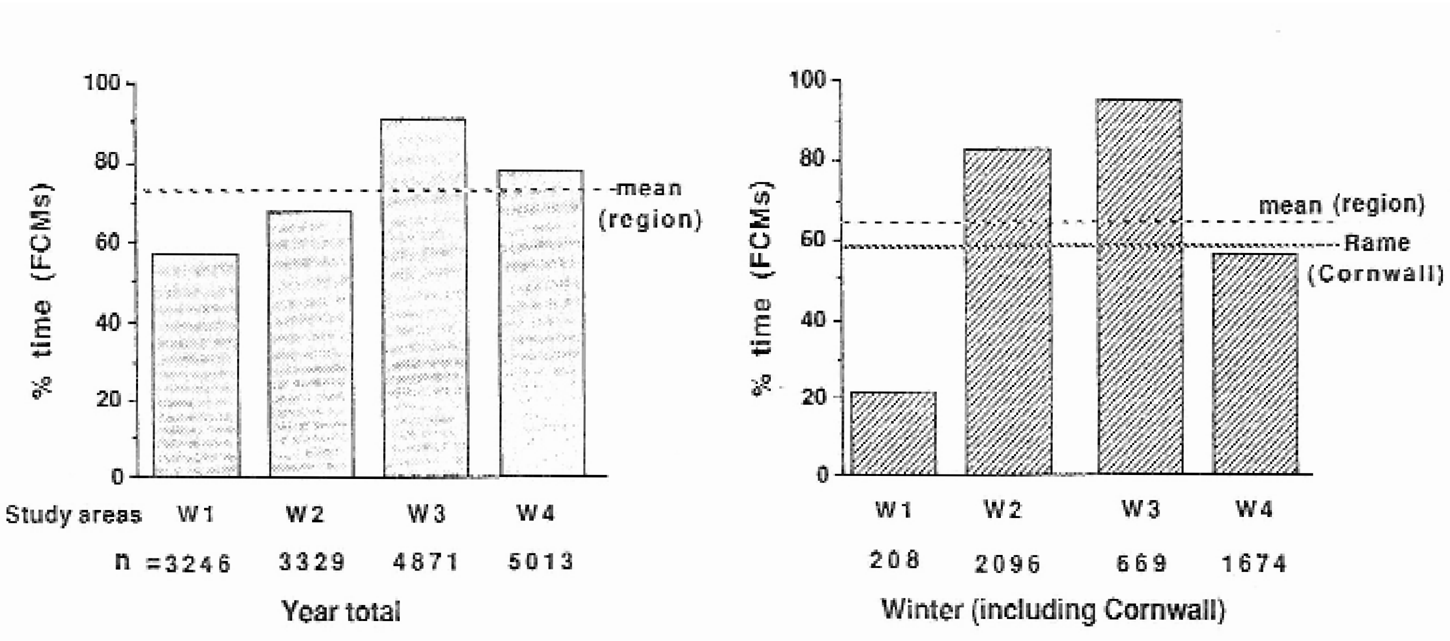

Figure 4.7
Percentage of Chough feeding time (FCMs) spent in cliffs and unimproved habitats. Yearly values on left and winter values on right, including, for comparitive purposes, the mean winter Cornish value from the Rame study (Appendix IV)

Table 4.5
Habitat components observed to be selected by Choughs in all Welsh study areas. Components are not mutually exclusive and may occur in more than one category. Category no's refer to Table 2.2. Study areas: W1 = Mwnt Ceames, W2 = Strumble, W3 = Newgale-Solva, W4 = Marloes

CATEGORY		%PCMs IN STUDY AREAS				
		W1	W2	W3	W4	Combined/ Regional
1	Cliffs (1a-e + 2 + unspecified)	57.1	50.5	58.2	71.3	64.5
	[Cliff complex (1 + semi natural)	57.8	68.4	92.9	78.0	74.3]
5	Exposed substrate	21.5	20.2	57.4	58.9	40.5
1c	Cliff-slope	24.4	30.9	50.95	35.1	35.2
3	Rock vegetation/earth interface	19.7	31.5	32.4	29.1	28.0
6	Maritime grassland	12.4	15.4	55.3	14.3	23.8
11	Man created habitat: hills etc.	12.0	4.9	46.9	21.5	21.4
1e	Cliff-crevice (> 50% rock)	7.4	3.9	9.9	24.1	21.1
17	Species-(herb-)rich	13.5	29.7	33.7	7.4	20.1
-	Short grass (< 25mm high)	15.1	13.8	17.4	11.5	17.75
2	Therophyte zone/sparse vegetation	8.0	2.75	24.0	26.15	15.9
18b	Sheep-grazed	20.6	32.85	3.1	7.3	15.4
7	Maritime heath	0.7	10.2	39.1	7.4	13.8
10	Path(-side)	7.5	6.8	34.4	3.9	12.8
21	Cereal grains	10.3	9.55	5.5	18.3	11.3
4	Shallow earth	14.6	1.0	3.1	18.3	9.95
1b	Cliff-edge	3.2	0.9	12.7	19.7	9.7
1a	Cliff top	4.5	0.2	9.0	20.5	9.3
-	Variable height grass	8.8	5.1	21.2	0.5	8.5
13	Permanent/old grassland	12.2	23.3	0.1	0.1	8.3
18d	Rabbit grazed	0	0	33.0	1.1	8.1
18a	Cattle-grazed	11.6	16.55	1.6	1.85	7.5
14	Old-(semi-)improved grassland	11.1	0	0.3	1.8	6.4
8	Seabird cliff flora	0.2	22.7	0	0	5.0
18c	Equine grazed	2.9	14.0	0	0	3.8
-	Medium height grass (25-50mm)	8.7	2.4	1.0	3.0	3.8
9	Rocky outcrops	0.8	7.2	5.9	0	3.2
22e	Ruderal/neglected agriculture	9.25	3.5	0.1	0	3.1
12	Wall/Hedgebank	3.6	8.8	0	0.03	2.9
20	Rough grazing	5.9	5.1	0.1	0	2.6
16	Stoney substrate	5.0	3.2	0.15	0	2.0
22c	Silage/hay aftermath	0	3.5	0	0.3	0.85
22?	Other agriculture	0	3.8	0	0	0.85
15	Drilled/reseeded/improved grass	0.2	0	0.4	1.8	0.8
19	Dung-feeding	1.9	0.3	0.5	0	0.7
-	Tall grass (> 50mm)	1.0	0	1.6	0.1	0.7
1d	Scree	0	0.1	1.35	0.1	0.4
18?	Unknown grazing	0.6	0	0	0	0.3
22d	Root crops/brassicas	0.1	0	0	0	0.02
	TOTAL PCMs	5618	4869	5240	6423	22150

4.7). Cliff-slopes with open and/or short vegetation caused by exposure and/or grazing pressure occupied at least 35% of FCMs. When grazed by domestic livestock, they form part of the semi-natural zone between inland agriculture and the natural cliffs (see Section 4.3.2). Choughs fed on sheep-grazed land for 15.4% of time, and on cattle-grazed land for 7.5%. In study areas W1 & W2, where there is an upland pastoral-based agriculture, these values increase to give 26.2% and 13.9% for sheep- and cattle-grazing respectively. At Strumble, grazing by all domestic livestock accounts for >60% of FCMs. Where plentiful and where the agriculture is more improved, as at Newgale-Solva, Choughs switch to rabbit-grazed swards (33% of FCMs *cf.* 3.7% and 1.6% for sheep- and cattle-grazed pasture respectively). Elsewhere, however, unlike the situation at Stackpole and on the islands of Skomer and Ramsey, where Chough populations might be faring slightly better, rabbits, and the effects of their grazing, were rarely apparent.

Time spent feeding within the cliff complex increases through the year from 64.7% in the winter to 87.2% in high summer (Table 4.6, Figure 4.7). During the winter at Mwnt-Cemaes, the cliffs were used for only 21.1% of feeding time, compared to 93.2% at Newgale-Solva; the regional mean of 64.7% is very close to that recorded in the preliminary Cornish study (*cf.* Figure 4.7; see Meyer 1990, Appendix IV). The onset of breeding at Mwnt-Cemaes resulted in a >40% increase in cliff usage; at Newgale-Solva and Marloes there were smaller increases, at Strumble there was a >30% decrease to 51.35%. The post-breeding season resulted in a consistently high cliff usage, ranging from 72.6% (Mwnt-Cemaes) to 96.1% (Marloes). For the year, there was a 35% difference in extremes: Newgale-Solva gave the highest cliff usage (92.9%: in no season was usage <90%), and Mwnt-Cemaes the lowest (57.8%).

Table 4.6 Time in FCMs with (%) observed spent feeding on cliffs

	Season			
Study area	Winter	Breeding	Post-breeding	Year
W1/Mwnt-Cemaes	208 (21.1)	1930 (62.2)	1108 (72.6)	3246 (57.8)
W2/Strumble	2096 (81.8)	1118 (51.4)	115 (87.8)	3329 (68.4)
W3/Newgale-Solva	669 (93.2)	1649 (97.5)	2553 (90.2)	4871 (92.9)
W4/Marloes	1674 (57.5)	1891 (94.2)	1448 (96.1)	5013 (78.0)
Total FCMs on cliffs	4647 (64.7)	6588 (73.4)	5224 (87.2)	16459 (74.3)
Total FCMs	7177	8980	5993	22150

Figure 4.8 shows the biomes and principal habitat components which were allocated for each feeding observation, enabling the mean proportional observed feeding time (PFT) to be calculated.

Table 4.7 Mean proportion of feeding time (PFT) ±1 s.e. with median values per observational period (=N) spent in main biomes. Old grassland is here included as part of pastoral agriculture, see Table 4.8 for its inclusion as part of the cliff complex (see text for explanation)

Study area	Biome												
	Clitis			Transitional			Pastoral			Arable			
	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.39	.15	.07	.17	.05	.04	.38	.23	.06	.05	.00	.04	37
W2/Strumble	.59	.63	.10	.13	.00	.06	.21	.00	.08	.07	.00	.06	17
W3/Newgale-Solva	.58	.63	.10	.36	.37	.08	.02	.00	.87	.04	.00	.03	17
W4/Marloes	.76	.81	.06	.11	.00	.04	.02	.00	.02	.13	.00	.05	25
K	10.05			11.63			33.32			8.01			
d.f.	3			3			3			3			
P	<0.05			<0.01			<0.001			<0.05			
Season													
Winter	.50	.53	.09	.07	.00	.03	.20	.00	.08	.23	.01	.07	20
Breeding	.55	.63	.05	.21	.06	.04	.24	.00	.05	.00	.00	.00	53
Post-breeding	.60	.81	.09	.22	.00	.07	.07	.00	.04	.11	.00	.06	23
K	1.52			5.45			3.96			24.74			
d.f.	2			2			2			2			
P	N.S.			N.S.			N.S.			<0.001			
Region	.56	.65	.04	.18	.03	.03	.19	.00	.03	.07	.00	.02	96

Kruskal-Wallis 1-way ANOVA test

Table 4.7

Dendrogram of principal feeding components, arranged rectangularly by vertical biome section and by horizontal hierarchical strata. Values are proportions of all feeding time (mean PFT) recorded during time dedicated to bird observation, and give probable principal components (end valued boxes) together with associated components, represented either by open boxes or valued boxes, where these values represent the principal (or end) components of other feeding incidents. The dendrogram should be read vertically from end box values to trace associate components

NB. Open boxes represent associate components which have no end or principal component value of their own

Key:

Biome section (zones):
C/N Cliffs/natural; S-N Semi-natural; A Agricultural

Strata:
1 (Semi-)natural structure
2 (Semi-)natural vegetation type
3 Agricultural regimes
4 Seabird cliff flora (C/N); root crops/brassicas (A)
5 Dung
6 Path (-effect)
7 Rock-vegetation interface
8 Ruderal agriculture
9 Therophyte zone (effectively a sub-group of Stratum 10)
10 Exposed substrate

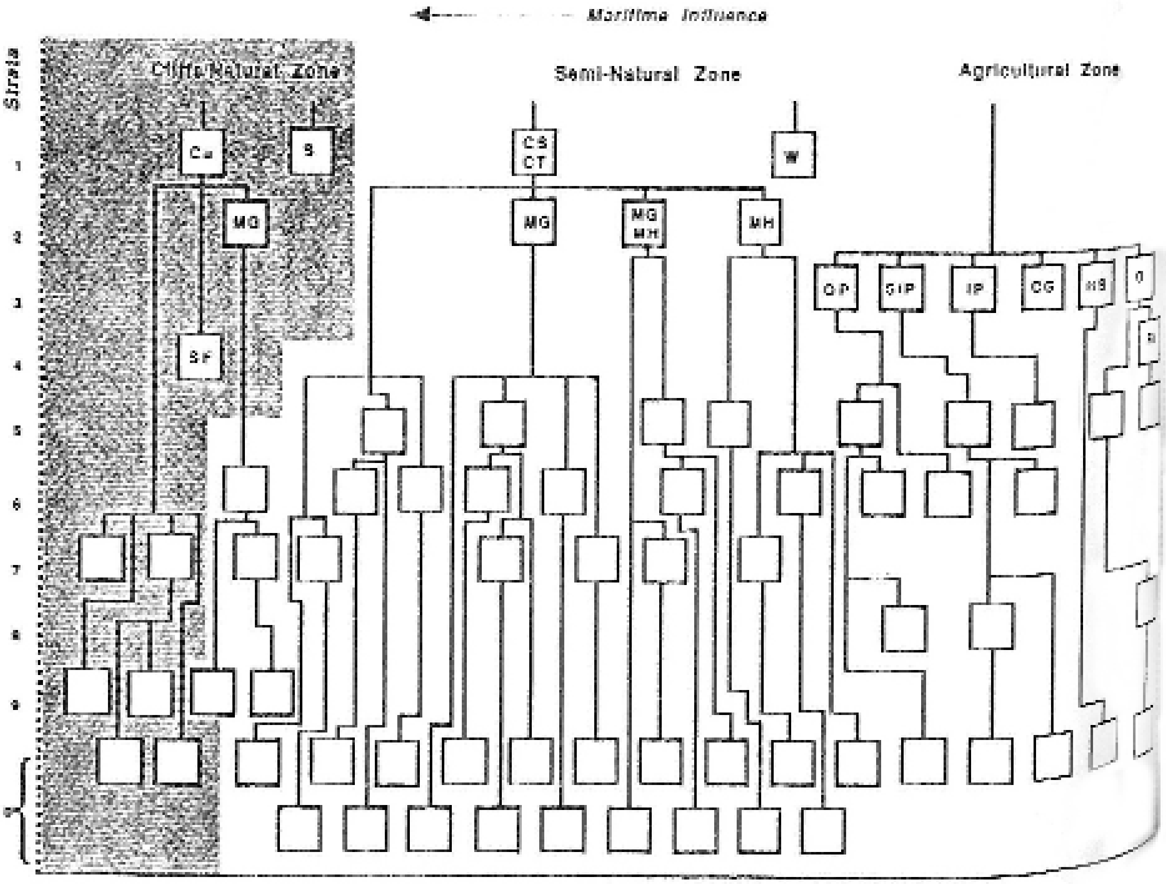

Figure 4.8
(Part 1)

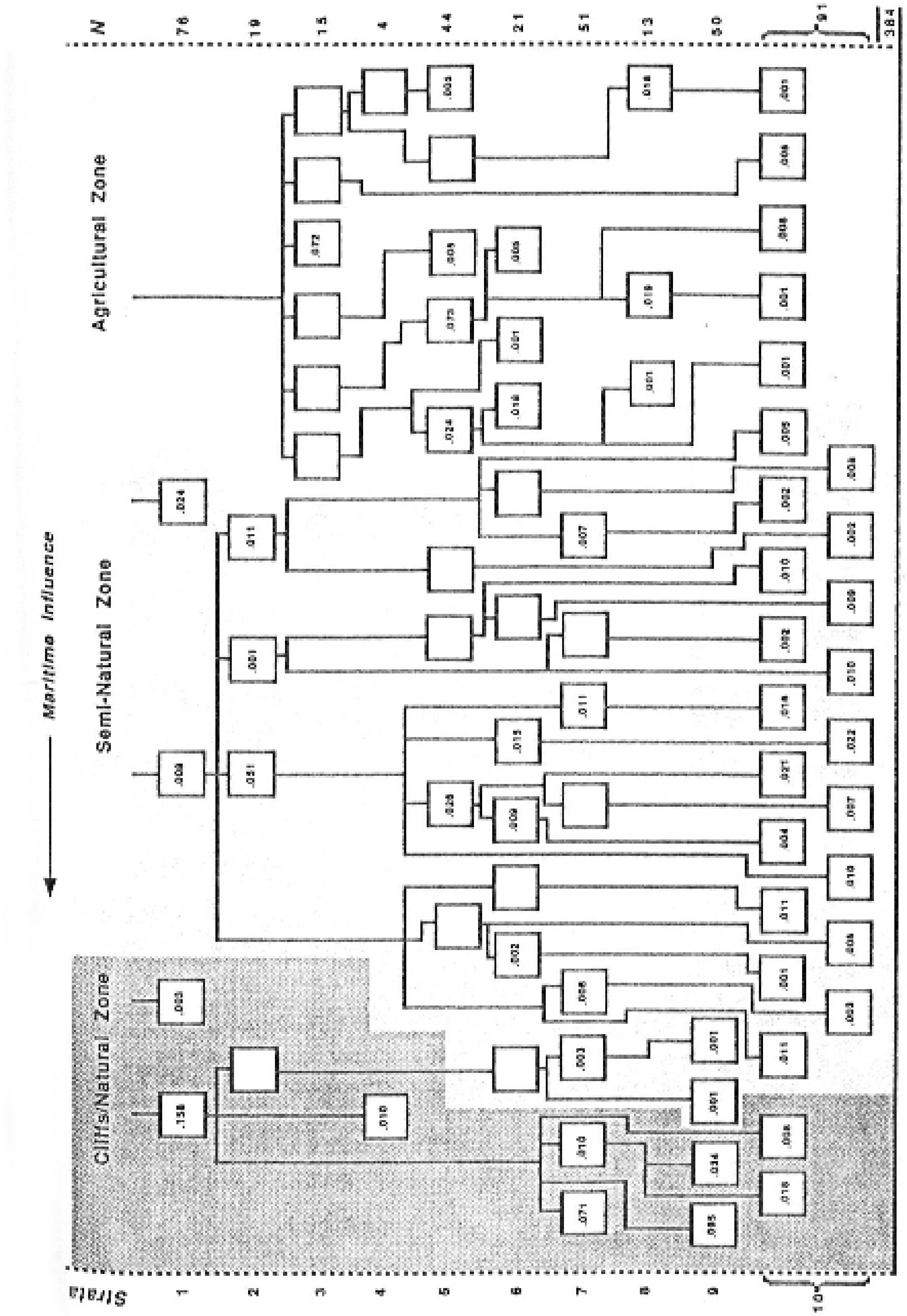

Figure 4.8
(Part 2)

The end categories represent possible principal components of the habitat; tracing the dendrogram up by strata shows associated components for all feeding events. The dendrogram may be read rectangularly, *i.e.* horizontally (by hierarchical strata) or vertically (by biome section); alternatively, other groups may be taken (*e.g.* as defined by human activity) which cut across the rectangularity, for example, the half-shaded boxes in Figure 4.9 show all natural complex or natural zone (PFT=.555).

The PFT based on daily means for the major biomes, with seasonal variation, is shown in Table 4.7, because the data are not normally distributed, median values are also given. There is a good level of agreement between PFT and FCM analyses; for example, cliffs/natural: PFT=.55, FCMs=64.5%; cliff complex (cliffs + transitional/semi-natural): PFT=.73, FCMs=74.3%. Table 4.6 shows that usage, except at Mwnt-Cemaes during the winter, of the natural maritime cliffs never fell below half; the Mwnt-Cemaes low is probably explained by sympathetic agriculture and management (4.3.4), and is responsible for depressing the regional winter value and consequently also the annual value. Regional winter values, excluding Mwnt-Cemaes, show 71.7% cliff usage, only 1.7% below the breeding season regional use.

In PFT analysis, cliff usage differs significantly (Table 4.7), increasing southwards from PFT .39 at Mwnt-Cemaes to .76 at Marloes. There was no significant seasonal variation in cliff usage, neither was there significant seasonal variation in the use of pastoral agriculture but there was a very highly significant difference in pastoral usage between study areas; the relatively low cliff usage at Mwnt-Cemaes being offset by a higher degree usage of pasture, giving a 50:50 ratio (Table 4.7). An opposite situation applied at Newgale-Solva and Marloes, where improved agriculture reduced the PFT spent on pasture (P<0.001) and resulted in increased feeding time on the cliffs, and, in the case of Marloes, on arable land. When the usage of arable is assessed seasonally, there was a very high significance between zero PFT in the breeding season to a winter high of .23 (P<0.001; Table 4.7). Seasonality did not significantly affect usage of the other biomes.

The transitional semi-natural zone was used significantly more at Newgale -Solva (PFT .36) than anywhere else, in fact, more than twice as much (P<0.01; Table 4.7). Maritime grass on cliffslopes when grazed can grade into old or permanent pasture (*e.g.* 'U46', Table 4.2), whereupon it may be regarded as semi-natural and could legitimately be categorised as 'cliffs', 'semi-natural' or 'pastoral agriculture'. Table 4.8 gives the PFT for 'old permanent grassland' when extracted from modern agriculture, and also when regarded as an element of the natural cliffs, and as a component of an extended (semi-)natural cliff complex (*e.g.* with walls and human-influenced natural communities). It is immediately apparent from Table 4.8, that usage of old (-improved) grassland is very significantly greater in W1 and W2 to the north, than in study areas W3 and W4 to the south where agriculture is intensively improved (P<0.001); the reduced availability (see Section 4.3.3b) of rough-grazed permanent grassland in these study areas resulted in virtually zero usage (but see Section 6.4). Although mean usage of pastoral elements increases during the breeding season (falling off sharply immediately afterwards), there were no significant differences between the seasons (Table 4.8). However, when grassland is regarded as part of the natural cliff complex, the differences between study areas begin to disappear, although there is an insignificant increase in selection of cliff habitat in the two southern, more agriculturally improved areas. Results presented later on (Chapter 6) regarding foraging success, suggest that, while it was tempting above to use the expression 'increased dependence' or 'increased reliance', in place of 'increased selection', to have done so might have been misleading; similarly I stated earlier that it was reduced availability' which caused zero usage; behavioural observations will cause reappraisal of such interpretations (as discussed in Section 4.3.4).

It is also apparent from Table 4.8, that the entire (semi-) natural cliff complex, including walls and

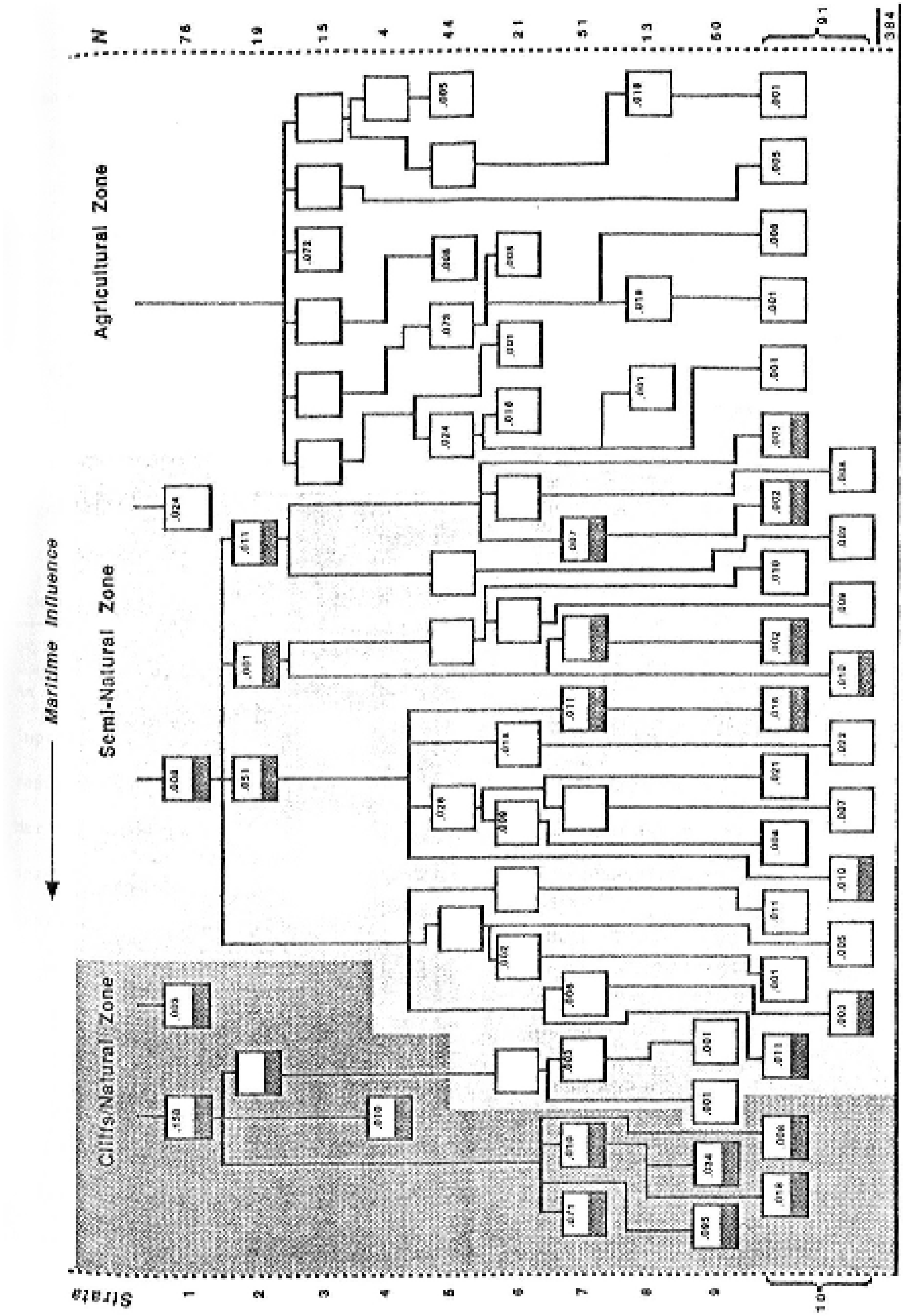

Figure 4.9

Figure 4.8 re-presented to show possibility of non-rectangular interpretation. In this case, the shaded boxes show an extended cliff complex: the non-human influenced zone

Table 4.8 The selection of semi-/old-improved pasture, old/permanent grassland, and transitional semi-natural habitats by Choughs within the cliff complex. Expressed as the mean proportion of feeding time (PFT) ±1 s.e. with median values per observational period (=N)

	Biome												
	Old- or semi-improved pasture			Old grassland alone			Old grassland as part of the cliff complex			Entire cliff complex: cliffs, old grassland, and other semi-natural habitats			
Study area	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.21	.01	.05	.18	.06	.05	.57	.61	.06	.74	.99	.06	37
W2/Strumble	.13	.00	.08	.09	.00	.04	.67	.68	.10	.80	1.0	.11	17
W3/Newgale-Solva	.02	.00	.01	.00	.00	.00	.58	.63	.10	.94	1.0	.03	17
W4/Marloes	.00	.00	.00	.00	.00	.00	.74	.81	.06	.87	1.0	.06	25
K	25.31			33.07			2.92			6.40			
d.f.	3			3			3			3			
P	<0.001			<0.001			N.S.			N.S.			
SEASON													
Winter	.08	.00	.05	.06	.00	.03	.56	.64	.08	.59	.74	.09	20
Breeding	.15	.00	.04	.10	.00	.03	.65	.76	.05	.85	1.0	.04	53
Post-breeding	.03	.00	.03	.04	.00	.02	.65	.93	.09	.87	1.0	.06	23
K	5.18			1.00			1.62			13.40			
d.f.	2			2			2			2			
P	N.S.			N.S.			N.S.			0.001			
All	.11	.00	.03	.08	.00	.02	.64	.74	.04	.82	1.0	.03	96

Kruskal-Wallis 1-way ANOVA test

Table 4.8

other semi-natural habitats, is exploited to a significantly very much greater extent outside the winter period (P=0.001), rising from PFT .59 in the winter to .87 after the breeding season. Seasonal sample sizes for individual study areas were small, but only during the breeding season was there significant differences between the study areas in the mean proportion of time spent feeding on the cliffs, increasing very significantly southwards, *i.e.* towards W4:

W4/Marloes	PFT=1.0,	median=1.0,	±1s.e.=.04,	n=12
W3/Newgale-Solva	PFT=.97,	median=1.0,	±1s.e.=.03,	n=10
W2/Strumble	PFT=.67,	median=.76,	±1s.e.=.11,	n=11
W1/Mwnt-Cemaes	PFT=.57,	median=.72,	±1s.e.=.09,	n=20
Kruskal-Wallis 1-way ANOVA:		K = 18.58, d.f.3, P<0.001		

Across the region, the (semi-)natural cliff complex represented a mean value of .82, the balance comprising arable (Table 4.7) and semi-improved agriculture (Table 4.8). Only at Mwnt-Cemaes did usage fall below 75% (.74), while at Newgale-Solva, it increased to .94. Figure 4.10 displays the increase in cliff usage in the study areas southwards (possibly representing increasing cliff quality) and the compensatory roles played by arable land, and the transitional categories of rough-grazed cliff grassland, other semi-natural habitats and old improved pasture.

The most important habitat components of feeding sites (shown in Table 4.5) were also tested for variance between study areas and seasons. The component appearing most frequently in Chough feeding sites was exposed earth: involving at least 8981 FCMs (40.5%), confirming Bullock's theory, tentatively advanced in his thesis (1980) that bare earth was especially important. It may be

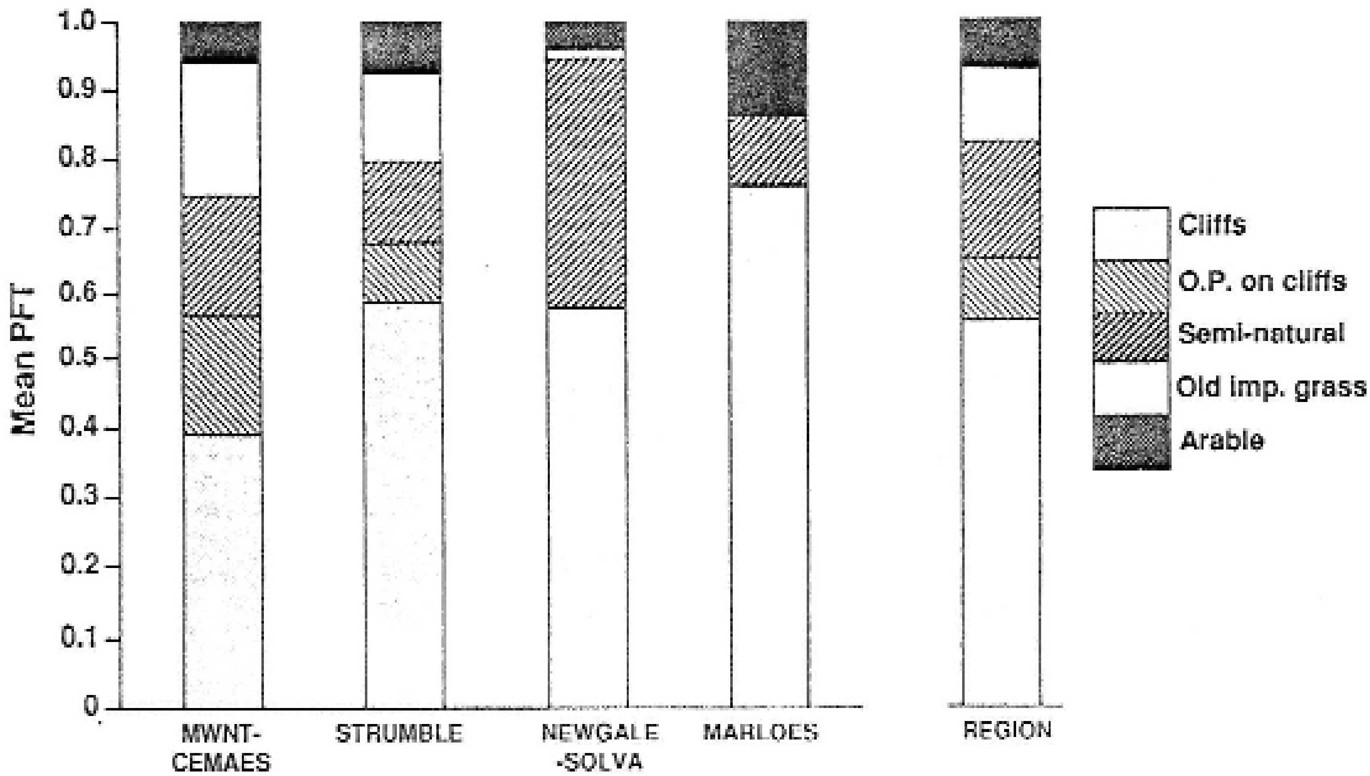

Figure 4.10
Time (mean PTF per observational period) spent in different habitat categories: cliffs, rough-grazed cliff grassland (O.P. on cliffs), semi-natural habitats, old-improved grassland, and arable. Data from Table 4.7 (cliffs, arable, semi-natural (transitional) habitats), and Table 4.8 (old pasture on cliffs (=rough grazing), and old-/semi-improved grasland)

theorised that this percentage is actually even higher because the exposed substrate element is partly linked to usage of the cliffs (accommodating the majority of feeding sites which could not be examined in detail). In study areas W3 & W4, where there was a common cliff usage of 64.8%, the exposed substrate value was 58.2%, in study areas W1 & W2, where cliff usage was reduced to 53.8%, usage of exposed substrate fell to 20.9% (Table 4.5). As the principal component (or end category), the regional mean PFT was .33, ranging from a low of .01 in the agricultural biome to .21 on the cliffs (Figure 4.11). There was a significant difference (Table 4.9) in overall usage of exposed substrate between study areas, caused by a high variance within the cliff biome (PFT .09 - .42; P<0,01), and, again overall, usage was significantly lowest in winter and highest in the breeding season (P<0.05). In Newgale-Solva and Marloes combined, the two areas where cliffs were most used (Table 4.6), the mean PFT was .34 (±1s.e. .05).

If habitats of unknown configuration are excluded from the analysis, the usage of exposed substrate could be expected to increase. It may be safely assumed that bare earth also supported feeding incidents in these habitats (primarily the inaccessible cliffs), and the maximum potential values are as shown in Figure 4.12. It is apparent that exposed substrate could well support more than three quarters of all feeding time within the natural cliff complex.

Short-grazed grassland, often said to be the main habitat requirement for Choughs, was involved in only 17.75% (3932) of FCMs regionally, and 43.6% of these were on open swards, *i.e.* mutually inclusive with bare earth (Table 4.5): thin/sparse grass and so-called 'sheep-bare' (Owen 1985). Approximately 15% of FCMs were associated with sheep-grazing, and 12% of FCMs (2653) were 'sheep-bare' linking exposed earth with sheep-grazed grass <25mm high; this represents 77.8% of all time associated with sheep-grazing, and 29.5% of all time associated with exposed earth. Feeding bouts involving exposed earth and sheep-grazed vegetation >25mm high or of variable height occurred in a further 450 FCMs. Over 20% of FCMs occurred on species-rich grassland (not necessarily sheep-grazed). The exposed earth specifically associated with therophyte communities supported almost 16% of FCMs (3524) (see also Section 4.4). Maritime grassland was associated with 23.8%, and 28% were concentrated at rock/earth-vegetation interfaces which provides a fissure exploitable by both Choughs and invertebrates (Table 4.5).

Habitat shaped by mound-building ants was present and identifiable in all study areas. *Lasius flavus*, in particular, is able to alter substantially the physical constituents and topography of grassland, and once established can even survive the spread of vegetation (Wallwork 1976). Since the ants themselves were the attractant rather than the habitat type *per se*, it was decided to include certain ant biotopes as categories of Chough feeding habitats.

Ants were preyed upon by Choughs in all study areas (5.3.1). Habitat shaped by ants had a mean usage of >20%, concentrated into the two warm weather seasons. The values presented in Table 4.5, suggest that ants are less preferred in pastoral areas: study areas W1 & W2 = 12% and 4.9% cf. study areas W3 & W4 = 46.9% and 21.5% respectively, but this could also reflect the spatial distribution of the ants themselves (4.3.4) and inter-specific behavioural differences (*e.g.* not all ants build mounds). Even though ant-formed habitats were utilised in all study areas analysis showed significant variance both by site, with ant habitats being used most in Newgale-Solva, and by season (Table 4.10); the latter due to the increased summer activity. Observations indicate that, if available, Choughs can prey on ants at all times of the year.

Dung is an important resource *at times*; more than one quarter of all PFT (.26, median .00,±1 s.e. .04, n = 96) was associated with dung, although very little actual dung-feeding was observed: only for 120 (2.7%) of 3613 dung associated FCMs (Table 4.5). The majority of time was spent in dung-rich habitats, with the birds possibly feeding on dung fauna made available by the grazed

Table 4.9 Usage of exposed substrate in principal biomes. Expressed as the mean proportion of feeding time (PFT) ± 1 s.e. with median values per observational period (=N)

	Biome												
	Cliffs			Semi-natural			Agricultural			All			
Study area	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	PFT	med.	s.e.	N
W1/Mwnt-Cemaes	.17	.04	.04	.10	.00	.02	.02	.00	.02	.29	.17	.05	37
W2/Strumble	.09	.00	.03	.11	.00	.04	.00	.00	.00	.20	.00	.06	17
W3/Newgale-Solva	.42	.43	.08	.17	.00	.07	.00	.00	.00	.59	.49	.08	17
W4/Marloes	.25	.26	.05	.09	.00	.04	.02	.00	.02	.32	.32	.06	25
K	15.39			4.33			1.51			12.52			
d.f.	3			3			3			3			
P	<0.01			N.S.			N.S.			<0.01			
SEASON													
Winter	.14	.00	.06	.04	.00	.02	.02	.00	.02	.20	.00	.06	20
Breeding	.24	.18	.03	.18	.00	.04	.02	.00	.01	.44	.29	.05	53
Post-breeding	.25	.10	.07	.13	.00	.06	.00	.00	.00	.38	.22	.07	23
K	6.09			9.29			2.43			9.99			
d.f.	2			2			2			2			
P	<0.05			<0.01			N.S.			<0.01			
Region	.21	.10	.03	.11	.00	.02	.01	.00	.01	.33	.21	.03	96

Kruskal-Wallis 1 way ANOVA test

Table 4.19

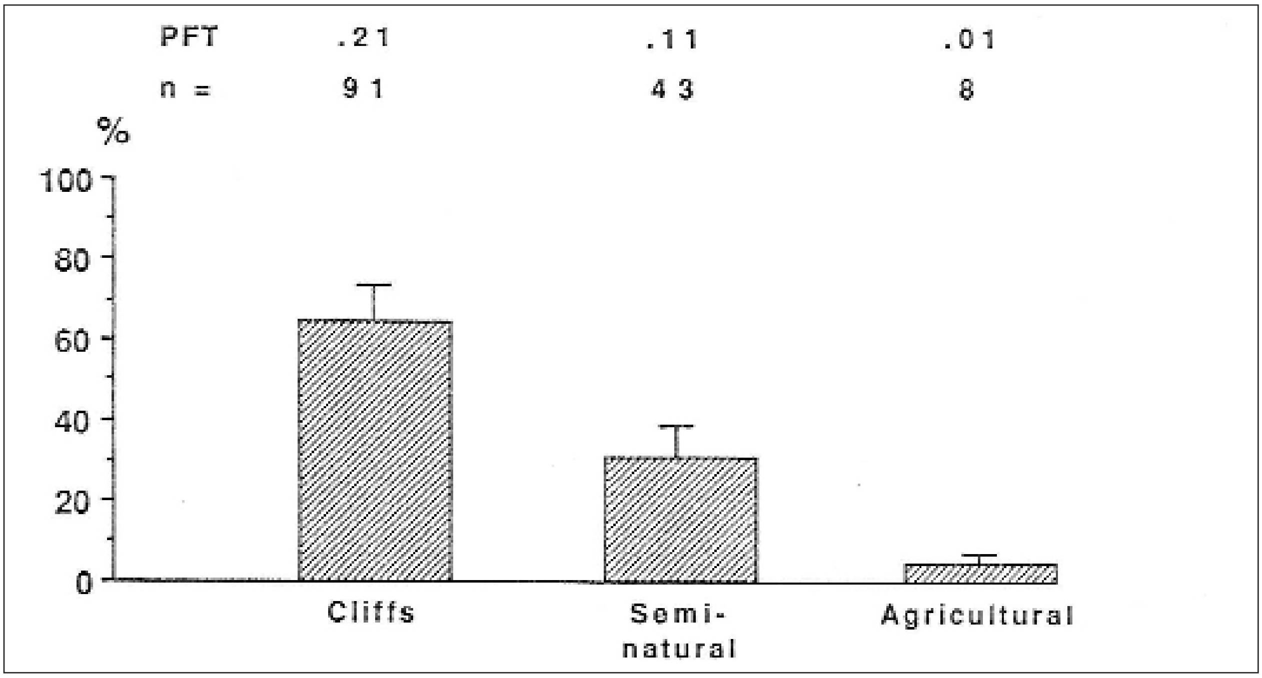

Figure 4.11
Usage of exposed substrate. Percentage of PFT (overall x .33) ±l s. e. spent in the principal biomes; N = observational periods

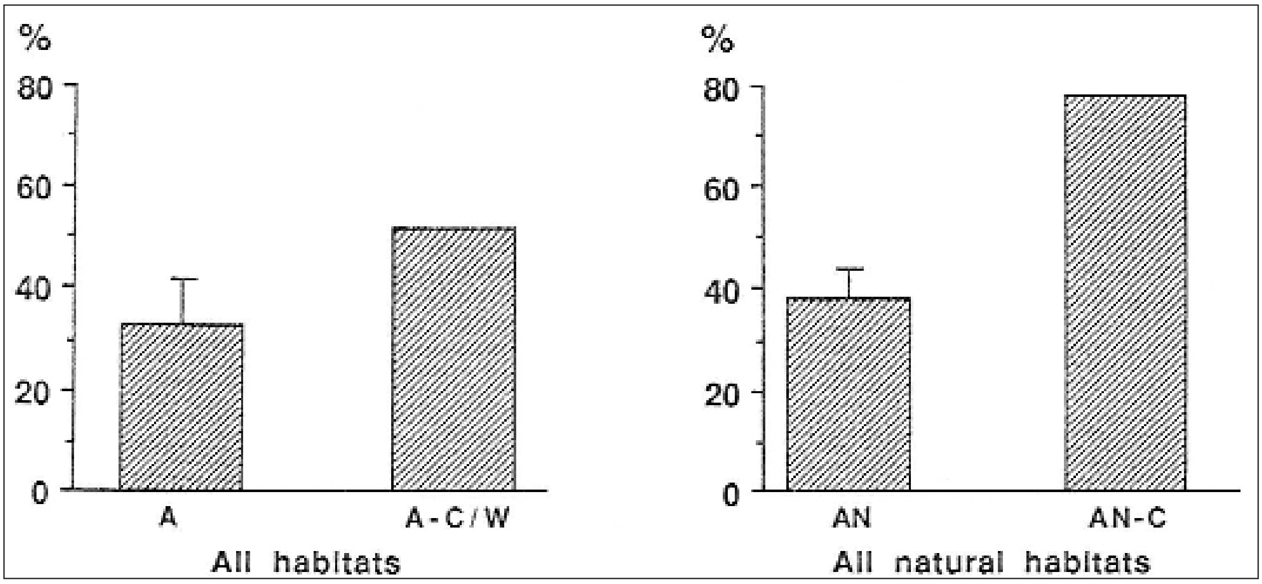

Figure 4.12
Usage of exposed substrate (% of mean PFT per observational period, ± s. e., N = 96) and hypothesised maximum values if habitats of unknown configurations supported exposed substrate feeding (based on data given in figure 4.8 and Table 4.9)

Key:

A	all exposed substrate (overall minimum value)
A+C/W	all biomes excluding unspecified records, *i.e.* unspecified clifflands and walls (giving overall maximum *potential)*
AN	all natural habitats (minimum value)
AN+C	all natural habitats excluding unspecified clifflands (giving maximum *potential* within natural biome)

Table 4.10 Mean proportion of time (PFT) ± 1 s.e. with median values per observational period (=N) spent feeding in ant-created habitats

Study area	PFT	med.	s.e.	N	*K*	d.f.	*P*
W1/Mwnt Cemaes	.14	.00	.05	37			
W2/Strumble	.12	.00	.05	17			
W3/Newgale-Solva	.42	.49	.08	17			
W4/Marloes	.23	.04	.06	25	12.56	3	.0057
Season							
Winter	.03	.00	.03	20			
Breeding	.22	.02	.04	53			
Post-breeding	.34	.22	.08	23	13.86	2	.0010
Region	.21	.00	.03	96			

Kruskal-Wallis 1-way ANOVA test

Table 4.10

conditions. In a later chapter, the importance of dung fauna is discussed. On aggregated FCM data from Table 4.5, dung-feeding was commonest in the north (89%), with 72% at Mwnt-Cemaes; as a mean proportion of feeding time per day, feeding associated with dung resulted in:

W1/Mwnt-Cemaes	PFT=.43,	median=.29,	±1s.e.=.06,	n=37
W2/Strumble	PFT=.26,	median=.00,	±1s.e.=.09,	n=17
W3/Newgale-Solva	PFT=.24,	median=.00,	±1s.e.=.08,	n=17
W4/Marloes	PFT=.04,	median=.00,	±1s.e.=.04,	n=25

Kruskal-Wallis 1-way ANOVA showed a very high significance between the northern and southern study areas: K=27.31, d.f. 3, P<0.001. There was no significant seasonal difference (K=2.52, d.f. 2). Environments enriched rabbit dung are included; however there is very little similarity between the invertebrate fauna of rabbit dung and that of, say, cow dung, and this will affect and, to some extent, govern Chough diet.

4.3.3b THE EFFECT OF HABITAT AVAILABILITY

It is self-evident that the availability of habitat will affect its selection. It was necessary to redefine habitat by biotope rather than the components given in the preceding section, which are not measurable accurately due to their small size (sometimes presumably visible only to Choughs), pocketed distribution, physiographical or temporal complexity or a combination of these factors. The areas of the defined biotopes comprising the study areas are given in Table 4.11. Cliffland values include some estimation due to complex coastal physiography. Cemaes Head and Newgale-Solva had 30-40% habitat yielding access to natural or semi-natural habitats.

In Cornwall, there was a weak negative correlation between availability and usage (r_S= -0.295, N.S; Meyer 1990, see Appendix IV). From data presented in Tables 4.12 and 4.13, usage is correlated with availability (see Figures 4.13 and 4.14). A relationship similar to the Cornish data is found: r_S= -0.125. At Mwnt-Cemaes, an increase in the availability of semi-natural grassland possibly causes a reciprocal increase in usage and a decrease in cliff usage, giving a weak correlation coefficient (P<0.10; Figure 4.13). At Strumble, the Choughs switch to an increased availability of old grassland. At Marloes, increased arable land, at the expense of old pasture, is exploited and reflected by an increase of cereal in the diet (Chapter 5). Most marked is the heavy usage made in all study areas of the small amount of available cliff habitat: over the region, this amounted to about 5% of cliff habitat supporting nearly 70% of Chough feeding-time (*cf.* Figure 4.10), and the importance of habitat quality, as opposed to quantity, introduced in the discussion below, is established in Chapter 6. The absence of significant correlations between availability and usage suggests that the Choughs are being selective in their choice of feeding habitat.

4.3.4. DISCUSSION

Variation in habitat selection across the region validated the decision to choose a range of study areas. The component data in Table 4.5 provide a means of stringing together habitat variables in order to help create suitable habitat-types in management programmes (Chapter 7). Figures 4.8 & 4.9 show how the major components combine in Chough foraging patterns.

Cliffs are shown to be of major importance (Table 4.7 and Figure 4.10), and depending on where the line is drawn between natural and semi-natural habitats, this can increase still further. For example, if rough grazing on cliffs is included within the cliff complex (valid in view of its extent on cliffs and headlands in historic time (3.4.6e)), the difference between the study areas shown in Table 4.7 loses its significance, and the mean PFT increases to .64 within a decreased range (.57 -

Table 4.11 Availability (ha) of habitat biotopes per study area and region. The Mwnt-Cemaes Study Area (W1) values are also given per sub-area: W1A=Mwnt, W1B=Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes

Sub-area of W1				Biotope	Study Area								Region	
W1A		W1B			W1		W2		W3		W4			
ha	%	ha	%		ha	%	ha	%	ha	%	ha	%	ha	%
2	2.0	6	4.0	Available cliff	8	3.0	10	4.0	8	6.0	28	9.0	54	6.0
7	8.0	9	6.0	Old grass/(semi-) natural, short/grazed	16	6.5	57	22.0	26	19.0	24	8.0	123	13.0
3	3.0	42	27.0	Old- (semi-) improved pasture	45	18.5	0	0	0	0	9	3.0	54	6.0
34	38.0	31	20.0	Improved pasture	65	26.5	64	25.0	27	19.0	84	27.0	240	25.0
9	10.0	9	6.0	Arable	18	7.5	4	1.5	22	16.0	67	22.0	111	12.0
29	33.0	49	31.5	Scrub/long vegetation	78	32.0	122	47.0	56	40.0	83	27.0	339	36.0
0	0	7	4.5	Other	7	3.0	1	0.	0	0	10	3.0	18	2.0
5	6.0	2	1.0	Homesteads	7	3.0	0	0	0	0	4	1.0	11	1.0
89		155		Total hectares	244		258		139		309		950	

Table 4.11

Table 4.12 Usage of habitat biotopes per study area and region. Time in FCMs and percentages per column. The Mwnt-Cemaes Study Area (W1) values are also given per sub-area on the left: W1A=Mwnt, W1B=Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes

Sub area of W1				Biotope	Study Area								Region	
W1A		W1B			W1		W2		W3		W4			
FCMs	%	FCMs	%		FCMs	%	FCMs	%	FCMs	%	FCMs	%	FCMs	%
315	65.6	3024	58.9	Available cliff	3339	59.4	2664	54.7	4218	80.5	4927	76.7	15148	68.4
32	6.7	627	12.2	Old grass/(semi-) natural, short/grazed	659	11.7	1568	32.2	610	11.6	87	1.3	2924	13.2
106	22.1	342	6.7	Old- (semi-) improved pasture	448	8.0	0	0	18	0.3	113	1.8	579	2.6
0	0	12	0.2	Improved pasture	12	0.2	0	0	21	0.4	113	1.8	146	0.6
0	0	578	11.3	Arable	578	10.3	465	9.6	286	5.5	1175	18.3	2504	11.3
27	5.6	31	0.4	Scrub/long vegetation	58	1.0	0	0	83	1.6	8	0.1	149	0.7
0	0	524	9.5	Other	524	9.5	172	3.5	4	0.1	0	0	700	3.2
480		5138		Total FCMs	5618		4869		5240		6423		22150	

Table 4.12

Table 4.13 Percentages of available habitat (AH) and usage (U) measured in FCMs, for the 4 Welsh study areas and region.
Key: W1=Mwnt-Cemaes, W2=Strumble, W3=Newgale-Solva, W4=Marloes
C = Available cliffs; OP = Old pasture; A = Arable (cereal grains); OIP = Old-improved pasture; R = Ruderal; S = Scrub; IP = Improved pasture; O = Other.
NB. Any % shortfall in habitat availability is accounted for by dwellings etc (*ie*. non-habitat).

	C		OP		A		OIP		R		S		IP		O	
Area	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U	AH	U
W1	3.0	59.4	6.5	11.7	7.5	10.3	18.5	8.0	2.8	9.5	32.2	1.5	26.4	0.2	0*	0.1
W2	3.9	54.7	21.7	32.2	1.6	9.6	0	0	0.4	3.5	47.1	0	25.3	0	0	0
W3	3.9	80.9	18.5	11.2	15.9	5.5	0*	0.3	0*	0.1	42.1	1.6	19.6	0.4	0	0
W4	8.9	76.7	7.8	1.3	21.7	18.3	3.1	1.8	0	0	27.1	0.1	26.8	1.8	3.2	0
All	5.3	68.5	12.8	13.1	11.7	11.3	5.7	2.6	0.8	3.1	36.1	0.7	25.2	0.7	1.1	0

NB. * = <0.1

Table 4.13

.74) (Table 4.8). When all semi-natural habitats are incorporated, the mean usage increases to .82, and it is possible to conclude that Choughs will use the transitional zone between the wild cliffs and the agricultural hinterland extensively when available, such as at Mwnt-Cemaes (Figure 4.10). Where this is not available to the same extent, such as at Marloes, there is an absolute requirement for high-grade cliffs. If these do exist, as indeed at Marloes, any agricultural short-comings are made irrelevant. The importance of the natural cliffs is underlined by investigations into foraging economics described in Chapter 6.

The importance of bare earth, within (semi-)natural vegetation mosaics, is clearly demonstrated. Table 4.9 shows how usage of this decreases from a mean PFT .21 in natural clifflands to .01 in agricultural land where the substrate is considerably more disturbed by human activity (mechanical and chemical) to the inevitable detriment of invertebrate communities (Wallwork 1976). The semi-natural zone (a 'mid-range' between natural and agricultural habitats), supports a midpoint PFT of .11 (*i.e.* between .21 and .01). There is a significant difference in usage of exposed substrate across the site range (P<0.01; Table 4.9), which was affected by availability and season, with usage lowest in the winter and increasing in the summer.

Usage of cliffland within the region is PFT .56 (Table 4.7). The lower usage at Mwnt-Cemaes (.39) is probably explained by a combination of relatively poor quality cliffs, and the special management within the Cemaes Head nature reserve and on the adjacent farmland in an initiative project designed by the NCC and Pembrokeshire Coast National Park explicitly to improve the habitat for Choughs. Elsewhere, usage of the cliffs *per se* ranges from mean PFT .58 to .76, which implies that unsuitable agriculture 'forces' an increased dependence on cliffs, although evidence presented in Chapter 6 suggests that high quality cliffland is preferentially selected over even Chough-friendly pastoral agriculture. The more improved the agriculture, the higher the dependence on cliffs (see also Chapter 5.4), resulting in the high value recorded at Marloes - the most agriculturally improved study area.

Table 4.14 Rank order of exclusive feeding habitat strata from Figure 4.8 with corresponding mean PFT

Rank	Stratum	PTF
1	Exposed substrate + therophyte communities	.331
2	Major unqualified biomes (mainly cliffs and walls)	.193
3	Dung	.133
4	Rock-vegetation interface	.108
5	Cereal grain	.072
6	Maritime grass and heath	.063
7	Paths	.050
8	Ruderal/atypical agriculture	.038
9	Seabird cliff vegetation	.010

Table 4.14 ranks the feeding habitats which were shown in hierarchical strata in Figure 4.8. The unspecified clifflands and walls (which provide a unique combination, in varying proportions, of natural, semi-natural and agricultural components within a discrete unit) are ranked 2, but the second most important specific <u>component</u> is dung; it may often be the primary attractant when found in combination with other components, and, therefore, its importance is probably greater than intimated by a mean PFT of .133 (*cf.* associated mean PFT=.26, see p. 90).

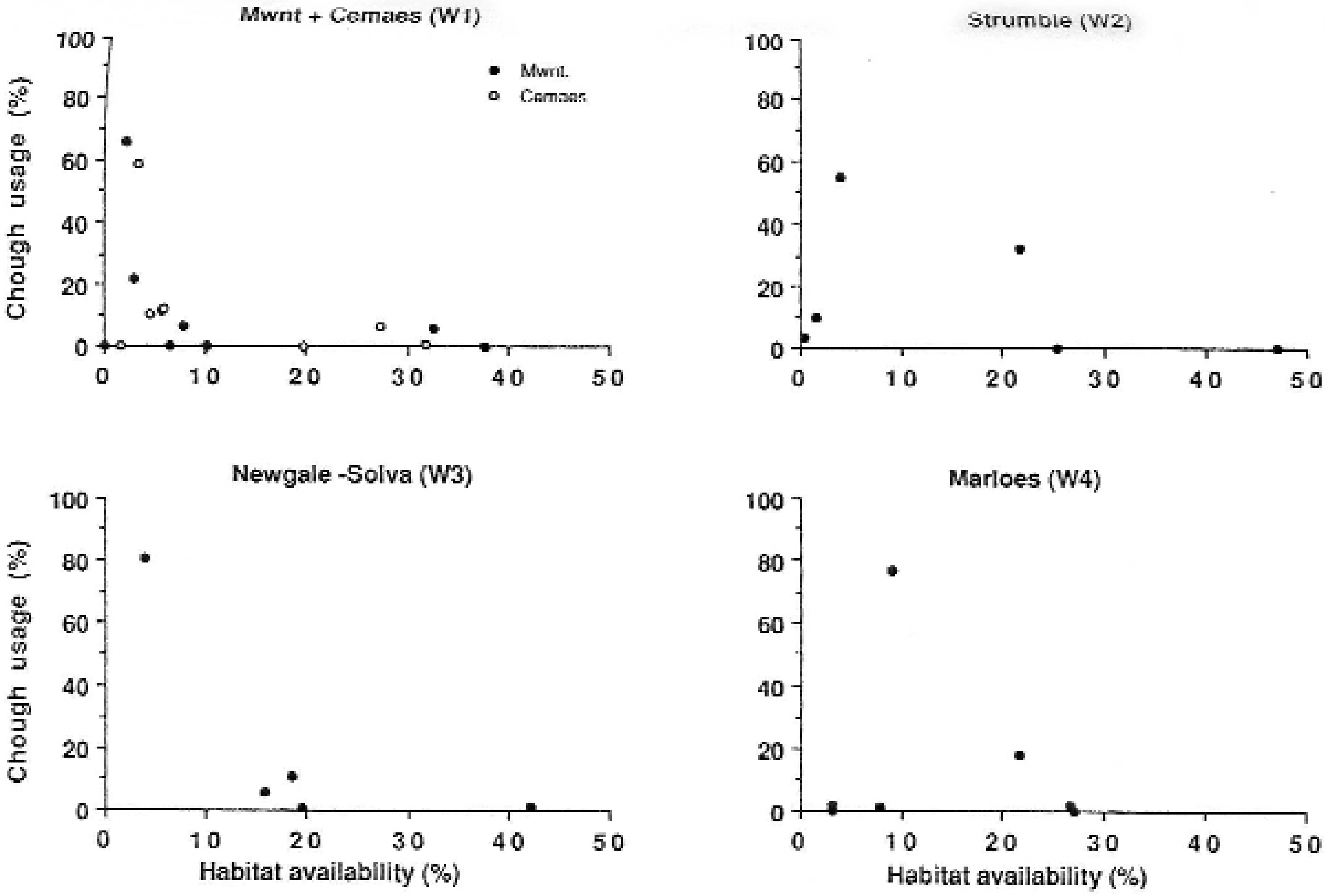

Figure 4.13
Relationship of usage by Choughs (%FCMs) and availability of habitats per study area. Area W1 (Mwnt - Cemaes) is shown with disaggregated values (see also Section 4.3.5).

Spearman rank correlation coefficients for study areas:
Mwnt - Cemaes r_s = -0.750, *P*<0.10, n=7
Strumble r_s = -0.686, N.S., n=6
Newgale - Solva r_s = -0.500, N.S., n=5
Marloes r_s = -0.098, N.S., n=7

Two of the commonest ant prey species, *Lasius flavus* and *L. niger*, generally inhabit exposed sites with sparse vegetation and little shade (Pontin 1961, 1963). Permanent pasture can encourage stable populations and, once established, *L. flavus*, by building mounds which rise above the level of the sward and altering the local topography, can even survive the cessation of grazing, but generally ants are reduced by the disturbance caused by large herbivores, and this is particularly true of *L. niger*, which builds loose mounds (Wallwork 1976). In Chapter 5, direct evidence of ant predation is examined but it is clear from the Choughs' selection of habitat that ants were heavily preyed on, confirming Cowdy's (1973) observations on Ramsey Island, especially at Newgale-Solva, where 46.9% of FCMs occurred in habitat influenced by mound-building species, all of these within the cliff region. Although, as would be expected from life-studies of ants, ant predation is highest in the summer, ants are taken throughout the year (Section 5.4).

The data presented in Table 4.5 and the multi-componental structure of Chough habitat, introduced in Section 4.3.1, reveal the physiography of Chough habitat. At Newgale-Solva, for example, it suggests quite accurately an environment characterised by grass-clothed cliffs, and retained in an open condition not by domestic livestock so much as by paths, rocky outcrops, rabbit-grazing, as well as ant activity.

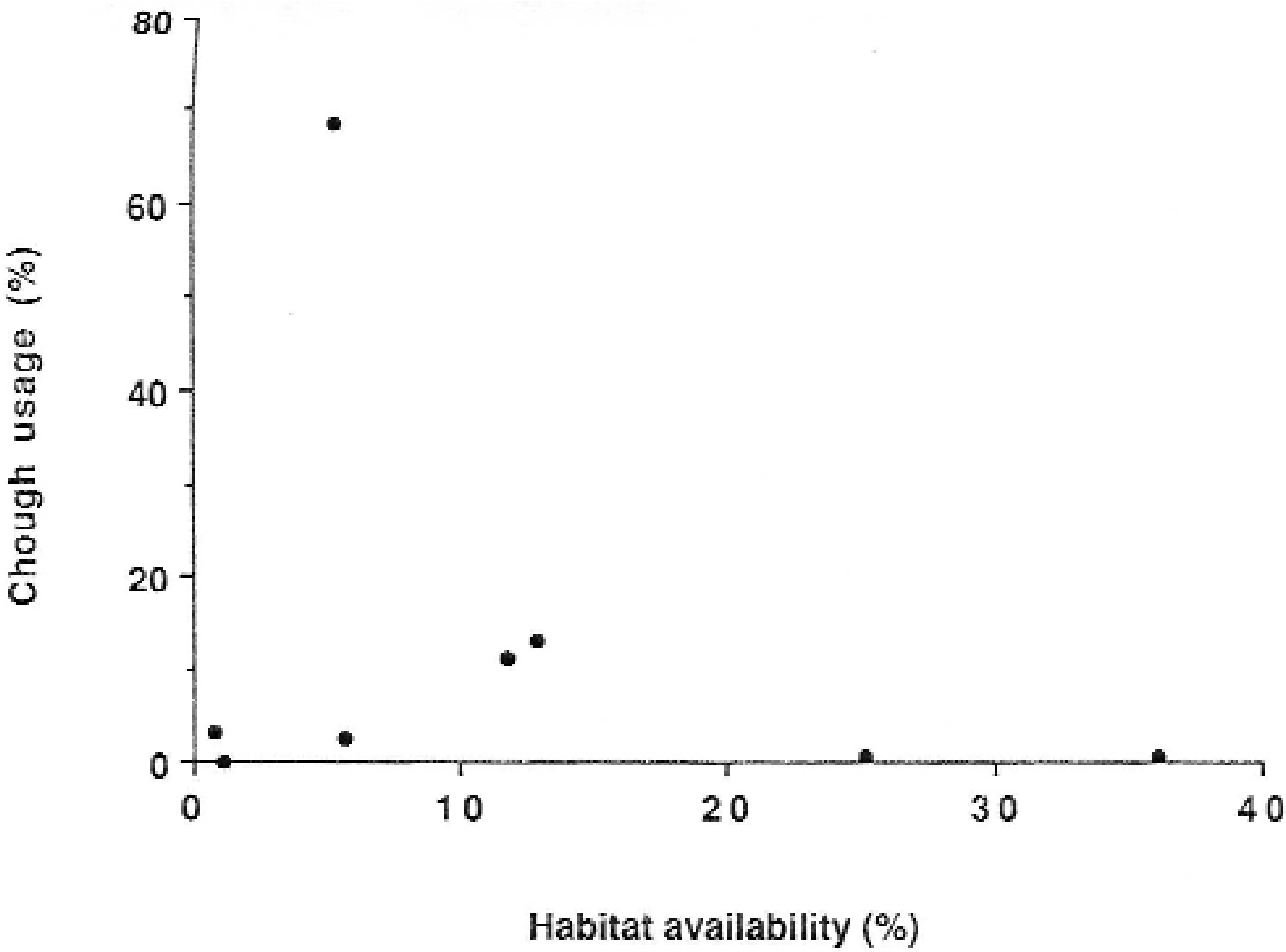

Figure 4.14
Relationship of usage by Choughs (%FCMs) and availability of habitats for aggregated study areas (=region)

4.4 THE BOTANY OF CHOUGH FEEDING SITES

4.4.1 INTRODUCTION

To define the structure of Chough feeding habitats even more precisely than was attempted in the component analysis based on the data given in Table 4.5, the accessible key Chough feeding sites were identified (those which supported >10 observed events) and a detailed botanical examination of these was undertaken in which species and cover composition were scored in order to relate the profiles to communities recognised within the National Vegetation Classification (NVC) (Rodwell 1982, Evans *et al.* 1989). It was hoped from this approach to produce botanical profiles which could be used as a guide to optimality of Chough feeding sites. Some quadrats were also surveyed in Cornwall for comparative purposes.

4.4.2 METHODS

In Wales, 58 key sites which were accessible and had supported >10 feeding events during regular bird observation, were identified (see Appendix VIII); of these, 52 were within the four main study areas (W1-W4), the remaining 6 were located at Stackpole NNR in south Pembrokeshire from information supplied by the NCC. Field botany is best understood in terms of plant communities (Tansley 1954), and it was intended to try and fit Chough feeding sites to the standard NVC, which is based on such communities. However, it was quickly apparent during survey work that Choughs do not select feeding sites from national botanical criteria! Many of the sites fell at the edges of recognised botanical communities or within ecotones. Interpretation by botanical community alone was, therefore, not sufficient, and recourse was made to species aggregations and their percentage cover ratios in order to construct profiles.

In July 1989, all species occurring within 2x2m quadrats, positioned at exact feeding points and initially ignoring botanical considerations, were assessed on the Domin range (Domin 1923, Shimwell 1971) of abundance (Table 4.15). Other 'cover types' were scored similarly: 'exposed substrate' (*i.e*. how much of the quadrat was 'covered' by bare earth); 'dung' identified to species; 'rock' (bedrock or large stones unable to be moved by birds); and 'stones' (loose/movable stones).

Table 4.15 The Domin scale for scoring abundancy or percentage cover in 2x2m quadrats

Scale	Estimated cover
10	91 - 100
9	76 - 90
8	51 - 75
7	34 - 50
6	26 - 33
5	11 - 25
4	4 - 11
3	1 - 4 (frequent but low cover)
2	1 - 4 (occasional)
1	1 - 4 (rare - 1 or 2 individuals)

The other variables recorded were: aspect, altitude, slope, soil-depth, and the homogeneous area of stand of which each quadrat was representative. As soon as possible afterwards (August 1989) in order to make the results as comparable as possible, 15 quadrats were also examined in Cornwall. At Rame (Chapter 8), a strategy similar to that employed in Wales was adopted; elsewhere, in the absence of present-day Chough evidence, representative samples in ex-Chough areas were taken, in stands which resembled the Welsh sites. These were: on the north coast, at Pentire Head (location #30 Figure 3.2; near the ancient Pentireglaze site (2.3.3) and at Beacon Cove (#27; the last Cornish site - see Figure 7.2); in West Penwith at Zennor (#19) and Gwennap Head (#14); and Predannack cliffs on the Lizard (#9; 2.3.3).

4.4.3 RESULTS

One hundred and nineteen plant species were recorded from 58 quadrats in Wales, and 44 from 15 quadrats in Cornwall. All those appearing in >10% (>5) of the Welsh quadrats are ranked in Table 4.16, with the 5 supplementary cover-types interpolated as appropriate. The dominant NVC type describing the Chough feeding sites is MC5 (*Armeria maritima - Cerastium diffusum* ssp. *diffusum* maritime therophyte community (Table 4.1); comparison of the distributions of this and present-day Chough distribution (Figure 4.15 *cf.* Figure 1.2) or, more closely still, distribution in recent historic times within Scotland, Wales and England, show remarkable affinity (the Isle of Man has not as yet received equivalent observer effort). It can be seen, from Table 4.16, that the two annual 'hair-grasses' (*Aira praecox* and *A. caryophyllea*) represent 58.6% and 39.7% presence in all quadrats. The *Aira praecox* sub-community of MC5, which is widespread particularly around the Mull of Galloway (NCC 1989), itself an important historic site for the Chough in Scotland until the early part of this century (Baxter & Rintoul 1953), was the dominant sub-type.

Table 4.17 gives the mean percentage cover ±1 s.e. per study area of the species and other variables listed in Table 4.16. The Domin scale is not a linear scale, and the percentage cover given represents a mean around which there might be 10-20% fluctuation depending on season and weather conditions etc. During this survey, drought conditions had applied for several weeks. Table 4.18 provides physiographical information on the Welsh quadrat sites. Figure 4.16 represents the aspect of each, and as can be seen no pattern emerged; in fact, the two majority aspects were diametrically opposed: SE (12) and NW (11).

A regional significance test (Mann-Whitney) was carried out on the mean percentage cover of the components, despite the different criteria necessary for selection of quadrats (4.4.2). Only 3 cover-types showed significant difference between the regions: *Festuca ovina*, *Agrostis stolonifera* and rabbit dung (Table 4.17); identification problems, due to the drought conditions, concerning the fescue grasses, could possible partly explain the very highly significant difference found in this case.

4.4.4 DISCUSSION

The extent of the vegetation stands which supported the surveyed sites were not normally distributed (Table 4.18), thus confirming the observation already made that Choughs exploit a wide range of habitat configurations: from small pockets to large zones and fields. The deciding factor is quality <u>not</u> integral size. Effects of altitude are expected to be overshadowed by those of maritime influence (Malloch 1972). This is in accord with NVC descriptions: MC5, in particular (*cf.* Table 4.2), is characteristic of excessively-draining, often very shallow soils at all levels on rocky cliffs; it is often ungrazed although the effects of hard grazing and burning will cause it to expand from its shallow-soiled refugia (S.B. Evans pers. comm.). Floristic variation of MC5 can be related to differences in maritime influence and in bedrock and soil type Rodwell 1982). The depth of soil

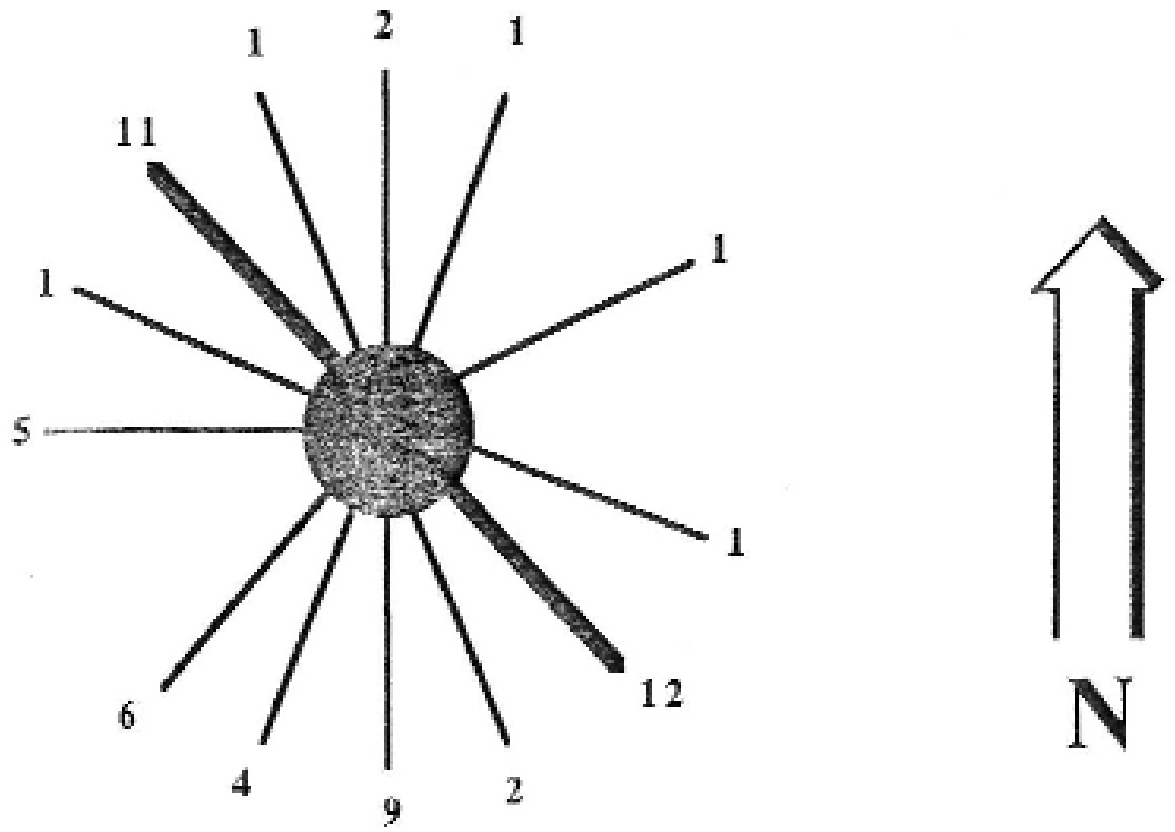

Figure 4.16
Frequency of aspects of sampled key breeding sites surveyed for their botany (N=36), 2 sites were on level ground, *i.e*. no aspect)

Table 4.18 Physiography of key feeding site quadrats in which vegetation was recorded

Variable	Measurement	x	±1s.e.	N
Altitude (a.s.l)	10 - 180m	66m	5.9m	58
Slope	0 - 80°	20°	2.8°	57
Soil-depth	.5 - >80mm	18mm	2.2mm	58
Stand area	1 - 2000m^2	284m^2	63.3m^2	45

Table 4.16 Plant species (+ 5 other cover types '*') with a frequency of >10% in Welsh study areas (including Stackpole 'W5' and Cornwall), ranked in order of Welsh regional frequency

Scientific name	Common name	No. times present W1	W2	W3	W4	W5	Region	Cornwall
*	Exposed substrate	15	9	12	10	6	52	14
Festuca rubra	Red fescue	8	8	10	7	3	36	8
Holcus lanatus	Yorkshire fog	14	6	5	7	4	36	8
Plantago lanceolata	Ribwort plantain	9	5	12	5	5	36	12
Hypochoeris radicata	Cat's-ear	9	6	6	9	5	35	7
Aira praecox	Early hair-grass	15	5	8	6	0	34	7
Lotus corniculatus	Common bird's-foot-trefoil	9	5	10	4	5	33	4
Plantago coronopus	Buck's-horn plantain	8	3	9	7	6	33	12
Armeria maritima	Thrift	8	3	8	8	3	30	13
Dactylis glomerata	Cock's-foot	8	6	9	6	1	30	12
Sedum anglicum	English stonecrop	9	6	7	6	0	28	11
Aira caryophyllea	Silver hair-grass	5	3	9	4	2	23	8
Scilla verna	Spring squill	4	5	5	5	3	22	1
Jasione montana	Sheep's-bit	7	4	5	5	0	21	3
*	Stones	3	2	8	5	3	21	9
Agrostis tenuis	Common bent	9	3	4	1	1	18	0
Plantago maritima	Sea plantain	7	3	3	3	2	17	1
Cerastium diffusum	Sea mouse-ear	2	0	8	6	0	16	1
Festuca ovina	Sheep's-fescue	3	6	2	5	0	16	7
Centaurium erythraea	Common centaury	2	0	6	4	3	15	2
Silene maritima	Sea campion	2	2	6	3	2	15	6
*	Rabbit dung	1	2	7	0	5	15	4
Cerastium holosteoides	Common mouse ear	6	4	2	2	0	14	0
*	Rock	2	5	1	2	4	14	7
Thymus drucei	Wild thyme	3	1	3	2	4	13	6
Trifolium repens	White colver	6	1	3	1	2	13	2
Anthoxanthum odoratum	Sweet vernal-grass	8	1	3	0	0	12	2
Bromus ferronii	Least soft brome	0	1	5	6	0	12	6
Leontodon taraxacoides	Lesser hawkbit	1	2	7	1	1	12	0
Calluna vulgaris	Heather	3	5	3	0	0	11	1
Rumex acetosa	Common sorrel	2	3	3	1	2	11	2
Poa annua	Annual meadow-grass	5	1	3	1	0	10	1
Anthyllis vulneraria	Kidney vetch	1	3	2	4	0	10	5
*	Sheep dung	4	2	2	0	2	10	3
Koeleria cristata	Crested hair-grass	1	1	4	3	0	9	2
Sieglingia decumbens	Heath-grass	3	3	3	0	0	9	0
Achillea millefolium	Yarrow	4	0	4	0	0	8	2
Daucus carota	Wild carrot	0	0	2	6	0	8	8
Festuca sp.	Fescue indet.	4	0	1	0	3	8	1
Galium saxatile	Heath bedstraw	3	3	2	0	0	8	0
Senecio jacobaea	Common ragwort	3	2	2	0	1	8	0
Spergularia rupicola	Rock sea-spurrey	4	1	1	2	0	8	3
Bellis perennis	Daisy	4	1	2	0	0	7	0
Lolium perenne	Perennial rye-grass	4	1	2	0	0	7	2
Rumex acetosella ssp.	Sheep's sorrel	4	2	1	0	0	7	0
Sagina procumbens	Procumbent pearlwort	6	1	0	0	0	7	0
Viola riviniana	Common dog-violet	1	2	2	2	0	7	0
Catapodium marinum	Sea fern-grass	0	1	2	3	0	6	0
Erica cinerea	Bell heather	1	3	2	0	0	6	0
Potentilla erecta	Tormentil	1	4	1	0	0	6	0
Agrostis stolonifera	Creeping bent	1	1	0	2	1	5	2
Galium verum	Lady's bedstraw	0	0	3	0	2	5	0
Prunella vulgaris	Selfheal	2	2	0	0	1	5	0
Teucrium scorodonia	Wood sage	4	1	0	0	0	5	0
Vulpia bromoides	Squirreltail fescue	2	0	3	0	0	5	0
No. of samples		17	11	14	10	6	58	15

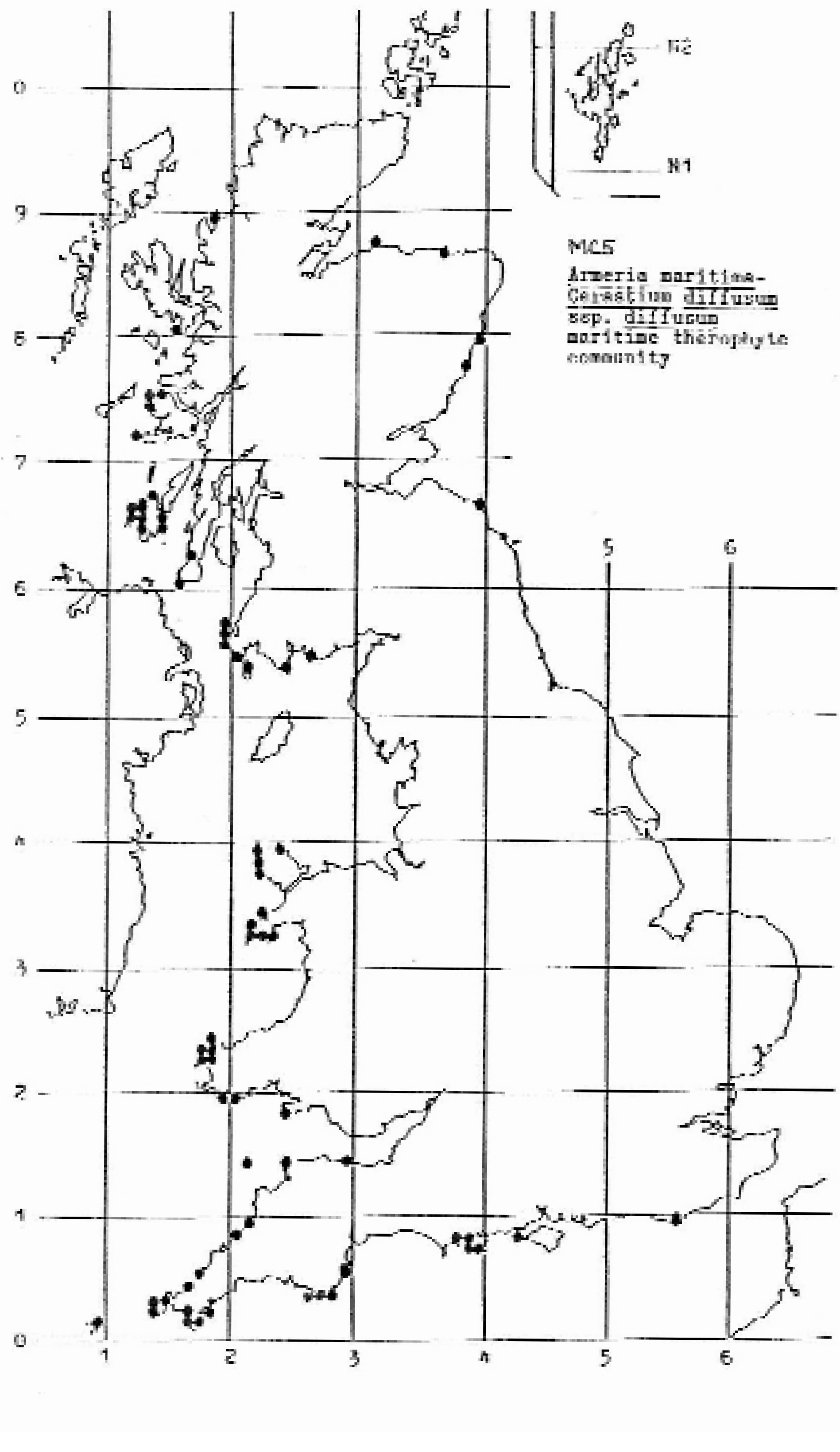

Figure 4.15
Distribution of the dominant National Vegetation Classification (NVC) type within British Chough range: *Armeria maritima - Cerastium diffusum* spp. *diffusum* maritime therophyte sub-community (*cf.* Figure 1.2)

Table 4.17 Mean percentage cover ±1 s.e. in Welsh study areas with [illegible], region aggregate, and Cornwall; Mann-Whitney regional z statistic (N.S. except ** P<0.01, * P<0.05)

Cover type	Mean percentage cover in all quadrats												
	W1	s.e.	W2	s.e.	W3	s.e.	W4	s.e.	Rgn	s.e.	Cnl	s.e.	z
Exposed substrate	13.9	4.6	14.3	7.7	17.2	5.1	12.2	4.4	14.1	2.6	23.4	5.4	1.8
Festuca rubra	8.2	3.1	9.3	3.8	22.6	8.2	17.7	7.4	15.5	3.2	18.1	7.6	0.3
Holcus lanatus	3.6	1.1	2.9	1.1	2.3	1.3	1.7	0.4	2.7	0.5	2.0	1.2	1.4
Plantago lanceolata	1.4	0.5	0.9	0.3	3.1	0.6	1.8	0.8	1.9	0.3	4.7	2.1	0.1
Hypochoeris radicata	3.4	2.4	1.2	0.4	0.8	0.3	3.2	0.9	2.1	0.8	0.9	0.3	0.9
Aira praecox	2.2	0.4	1.2	0.7	1.3	0.3	1.2	0.4	1.4	0.2	1.3	0.4	1.8
Lotus corniculatus	1.6	0.6	0.9	0.3	2.3	0.7	0.7	0.3	1.7	0.3	0.4	0.2	1.5
Plantago coronopus	2.1	0.7	0.5	0.3	3.7	1.3	12.2	5.0	4.8	1.3	6.7	1.5	1.5
Armeria maritima	1.4	0.5	1.3	0.8	2.4	0.9	1.5	0.4	1.9	0.4	8.2	3.1	1.4
Dactylis glomerata	1.8	1.0	1.3	0.4	1.4	0.4	6.3	3.2	2.2	0.7	4.3	1.3	1.3
Sedum anglicum	1.9	0.6	1.9	0.7	3.1	1.0	5.0	2.3	2.5	0.6	4.8	2.2	0.9
Aira caryophyllea	0.5	0.2	0.4	0.2	1.6	0.4	1.1	0.5	0.8	0.2	1.1	0.3	0
Scilla verna	0.9	0.5	0.9	0.4	0.9	0.4	0.6	0.2	0.9	0.2	0.1	0.1	0.2
Jasione montana	0.6	0.1	0.6	0.3	0.9	0.4	0.8	0.3	0.7	0.1	0.3	0.2	0.2
†Stones	2.6	2.5	0.4	0.9	3.0	1.4	3.9	2.9	2.7	1.0	3.6	1.6	0.3
Agrostis tenuis	9.4	3.2	6.1	5.2	3.4	3.0	0.2	0.2	4.9	1.7	0	-	-
Plantago maritima	5.3	3.3	4.0	2.2	6.1	5.9	0.9	0.8	4.8	1.9	0.1	0.1	1.0
Cerastium diffusum	0.3	0.2	0	-	1.4	0.4	1.3	0.4	0.7	0.1	0.2	0.2	0.9
Festuca ovina	0.3	0.2	3.7	1.7	0.8	0.6	5.4	2.3	1.9	0.6	12.8	4.5	3.2**
Centaurium erythraea	0.1	0.1	0	-	0.6	0.2	0.5	0.2	0.4	0.1	0.3	0.2	1.2
Silene maritima	1.2	1.1	0.8	0.7	0.8	0.3	0.4	0.2	0.9	0.4	3.3	2.0	0.9
†Rabbit dung	0.1	-	0.2	0.1	1.0	0.3	0	-	0.5	0.2	1.1	0.6	2.1*
Cerastium holosteoides	0.5	0.2	0.5	0.2	0.2	0.2	0.2	0.1	0.3	0.1	0	-	
†Rock	0.5	1.8	16.3	7.1	0.2	0.2	4.3	4.2	4.9	1.8	4.3	2.2	1.4
Thymus drucei	0.3	0.2	0.1	0.1	1.4	0.8	0.5	0.3	3.7	1.8	3.1	2.0	0.4
Trifolium repens	1.6	1.0	0.2	0.2	0.9	0.6	0.2	0.2	0.8	0.4	1.3	1.2	0.2
Anthoxanthum odoratum	3.5	1.5	0.3	0.3	0.9	0.6	0	-	1.3	0.5	0.3	0.2	0.7
Bromus ferronii	0	-	0.2	0.2	1.7	0.8	3.3	1.7	1.0	0.4	1.3	0.6	1.3
Leontodon taraxacoides	0.1	0.1	0.3	0.2	1.6	0.8	0.1	0.1	0.6	0.2	0	-	
Calluna vulgaris	1.4	1.1	7.6	4.4	0.4	0.2	0	-	1.9	1.0	0.1	0.1	1.7
Rumex acetosa	0.1	0.1	0.6	0.3	0.3	0.2	0.1	0.1	0.3	0.1	0.2	0.1	0.1
Poa annua	3.9	2.6	1.6	1.6	0.4	0.2	0.1	0.1	1.6	0.9	0.5	0.5	0.6
Anthyllis vulneraria	0.2	0.2	2.8	1.7	0.1	0.1	1.2	0.8	0.8	0.4	2.5	2.0	0.1
†Sheep dung	0.5	0.2	0.4	0.3	0.1	0.1	0		0.3	0.1	0.4	0.2	0.4
Koeleria cristata	0.1	0.1	0.3	0.3	0.8	0.6	0.6	0.3	0.4	0.2	0	-	-
Sieglingia decumbens	0.4	0.2	0.5	0.3	0.5	0.3	0	-	0.3	0.1	0	-	-
Achillea millefolium	0.4	0.2	0	-	0.7	0.3	0		0.3	0.1	0.1	0.1	1.7
Daucus carota	0	-	0	-	0.1	0.1	1.5	0.8	0.3	0.2	1.1	0.3	1.3
Festuca sp.	6.1	3.4	0	-	0.6	0.6	0	-	5.8	2.5	5.5	5.5	1.2
Galium saxatile	0.2	0.1	0.5	0.3	0.1	0.1	0		0.2	0.1	0	-	-
Senecio jacobaea	0.2	0.1	0.5	0.4	0.1	0.1	0	-	0.2	0.1	0	-	
Spergularia rupicola	1.1	0.6	0.7	0.7	0.1	0.1	0.5	0.3	0.6	0.2	0.3	0.2	1.5
Bellis perennis	0.4	0.2	0.2	0.2	0.4	0.3	0	-	0.2	0.1	0	-	-
Lolium perenne	5.0	3.5	0.7	0.7	0.7	0.6	0	-	3.8	1.1	2.4	1.6	1.2
Rumex acetosella ssp.	0.4	0.2	0.2	0.1	0.1	0.1	0	-	0.2	0.1	0	-	-
Sagina procumbens	0.5	0.2	0.1	0.1	0	-	0		0.2	0.1	0	-	-
Viola riviniana	0.6	0.1	0.2	0.1	0.1	0.1	0.3	0.2	0.1	0.1	0	-	-
Catapodium marinum	0	-	0.1	0.1	0.4	0.2	0.8	0.4	0.2	0.1	0	-	-
Erica cinerea	0.1	0.1	2.2	1.1	1.1	0.8	0	-	0.7	0.3	0	-	-
Potentilla erecta	0.1	0.1	0.6	0.3	0.1	0.1	0	-	0.2	0.1	0	-	
Agrostis stolonifera	0.1	0.1	0.2	0.2	0	-	0.5	0.3	0.3	0.2	2.4	1.6	2.0*
Galium verum	0	-	0		0.7	1.3	0		0.4	0.3	0	-	-
Prunella vulgaris	0.2	0.2	0.2	0.1	0	-	0	-	0.1	0.1	0	-	-
Teucrium scorodonia	0.2	0.1	0.1	0.1	0		0	-	0.1		0	-	-
Vulpia bromoides	0.1	0.1	0	-	1.0	0.6	0	-	0.3	0.2	0	-	

was overall very shallow (<2cm; Table 4.18). Nearly a quarter of the feeding-sites also included bare rock, which accounted for nearly 5% cover (Table 4.17).

The degree of slope of sampled sites was influenced by considerations of accessibility and safety, and, therefore, no special significance should be attributed to this part of the description in Table 4.18. Choughs are able to feed on vertical and even overhung cliffs (pers. obs.) and certainly had access not been a seriously limiting factor, more cliff sites, representative of MC1 and MC4 (Table 4.3), would have been sampled.

Many of the species listed in Table 4.16 are of constant or frequent occurrence within various sub-communities of MC8 - MC11 (Table 4.2), others are characteristic of pastoral agriculture and indicate its often close proximity. It is possible to conclude that the botanical communities which represent favourable conditions for Choughs in West Wales are: MC1, MC4, MC5, MC8, MC9, MC10, MC11 and U46. More precisely, the *Aira praecox* sub-community of MC5, represents the most favourable of all recognised communities. MC5 is an edge-type in itself which retains an open state (=sparse vegetation and exposed substrate) by abiotic factors and maritime influence as well as extending this into neighbouring communities by virtue of burning, hard-grazing and other effects of human agency. The over-riding impression gained from this survey was a concentration on ecotones and often difficult to categorise boundaries and peripheral niches and crevices (see frontispiece). *Aira praecox* was found growing in nearly 60% of the 58 quadrats surveyed, but represented a mean cover of less than 2% (Table 4.17), which confirms its status as an indicator species for the purposes of Chough biology. The main cover-types within this survey were *Festuca rubra* and exposed substrate; no other exceeded 5%.

4.5 HISTORICAL HABITAT ASSESSMENT

4.5.1 METHODS

The rationale behind this part of the study was introduced in Section 2.4. Ninety nine coastal 1km^2 from the arrays shown in Figures 2.2 - 2.5 and surveyed during the present-day habitat assessment (Section 2.2 and see Section 4.2) were located on the very large but variably scaled maps (held by the County Record Offices) drawn during the Tithe survey of the mid-C19, and the contemporary land use noted along with appropriate physiological data. The quality of surveying and recording in the 1840s varied considerably from area to area, and this resulted in some maps yielding little or no useful information; occasionally maps were damaged or had portions missing; two maps contained no field-by-field data at all. Where a parish boundary cut through a kilometre square, definitions of obviously homogeneous land types would sometimes vary.

As stated in Chapter 2.4, only rudimentary historical habitat information was available compared to that achieved during the current assessments (Sections 4.2 & 4.5). It fell into broad categories such as 'cliffs', 'rough pasture', 'common', 'arable', 'turbary' (communal turf- or peat-cutting ground), 'furze', 'waste', 'homestead' etc. Detailed information, *cf.* Figure 4.8, was not available. To overcome this problem, land-types were reduced to a classification consistent with known usage practices of the day, *e.g.* "furze and pasture" was classified as "rough grazing", as was "commons/moorland". A similar analytical approach as described in Section 4.2 for the background assessment was employed except that TWINSPAN was not involved.

On 10 maps, field data were not given or merely lumped as, for example, "arable and pasture alternately". Nevertheless, it was usually possible to measure the sizes of fields and, therefore, the extent of permanent boundaries (*i.e.* walls), and this explains the differing sample sizes in Table 4.19. The rectangular pixel configuration is more sympathetic to polygons than narrow linear areas, and, therefore, wall/boundary values are over-estimated unless corrected for. Typical Pembrokeshire and Cornish drystone walls are seldom wider than 2m at their base although their surface area is approximately 1.75 times greater; this area, if grazed or otherwise having negligible vegetation, is available to Choughs. Therefore, 1x2m of wall (0.5%/pixel) gives about 3.5 sq.m. (0.875%/pixel) of potential habitat. So, although a simple linear measurement will underestimate wall-surface area, uncorrected rasterized data will overestimate it, due to the fact that any pixel (400 sq.m.) showing wall would be read as solid wall, clearly nonsensical (see Figure 4.17). A straight linear 20x2m of wall (=10%/pixel) corrects to *ca.* 70 sq.m. of wall-surface area (=17.5%/pixel), but walls are often angled and abutted by other walls. When random samples of pixels containing walls were scaled-up, it was found that the values were exactly doubled giving a corrected mean wall-surface area per pixel of 35% (±s.e. 1.6%, n=10). To give an estimate of wall-surface area, irrespective of whether it is available to Choughs or not, 400 sq.m. of wall-pixel area is converted to the found average 35 sq.m. by the equation: WP(400)/11.429 - where WP is the number of wall-pixels; 11.429 is the factor by which 400 must be divided to give 35.

Tithe information is sketchy and has to be interpreted with care (Kain & Prince 1985). Arable land was the most valuable to commissioners, therefore, never under-recorded, although there was often disagreement between surveyors and farmers as to where the distinction lay between pasture and arable. Generally, 'arable' was defined as land ploughed over the previous 3 years or sometimes the previous 7 years (the period in which the act required tithe receipts to be averaged). Convertible husbandry was widely practiced in the C19 and created problems of interpretation which were exploited by both surveyors and farmers to their own advantage. The pastoral component on Tithe apportionments was often combined with meadowland and sometimes arable. The usual sequence of rotation was that seeds lay for 3 to 10 years before being ploughed. After the first year, when leys were mown for hay, they were pastured until deterioration necessitated ploughing, usually 5-8 years (Kain & Holt 1981).

Maps were digitized (see Section 2.4), and the rasters (rows of pixels) loaded onto the Prime mainframe computer at Paisley College of Technology. Summary statistics were generated for analysis on microcomputer by SPSS/PC+ (SPSS 1986). Nearly 40% of the total area (97km squares) analysed was accounted for by sea, and for the main analyses, this was excluded and the values corrected to give percentage cover of land surveyed.

Use of tithe data to estimate numbers of livestock must be exercised with great caution, although Cornwall provides some of the best available data (Kain & Prince 1985). Unfortunately, Pembrokeshire farmers often refused to co-operate with commissioners, barring their folds and dairies; the estimated data are not considered reliable (*ibid*.). Kain & Holt (1981) examined the reliable data for Cornwall, and these are later related to present stocking levels within the Cornish regional study area (4.6.2).

4.5.2 RESULTS

The proportions of habitat in Wales and Cornwall as recorded from the tithe survey of the 1840's are given in Table 4.19. For 87km^2 sufficient data existed to make some assessment of contemporary land use, and for an additional 10, measurements of boundaries were obtained. Of the 87 maps from which land-use data were obtainable, 38.9% was accounted for by sea, with very little variance between the two regional blocks (38.02% and 39.61%) indicating that no bias existed in the selection or in the degree of oceanicity between the two sample sets.

The largest proportion of agricultural land was down to arable (x-=37.9% over both regions ±1s.e. 3.1%). There was significantly more in Cornwall (double) than in Wales (P<0.001). There was also

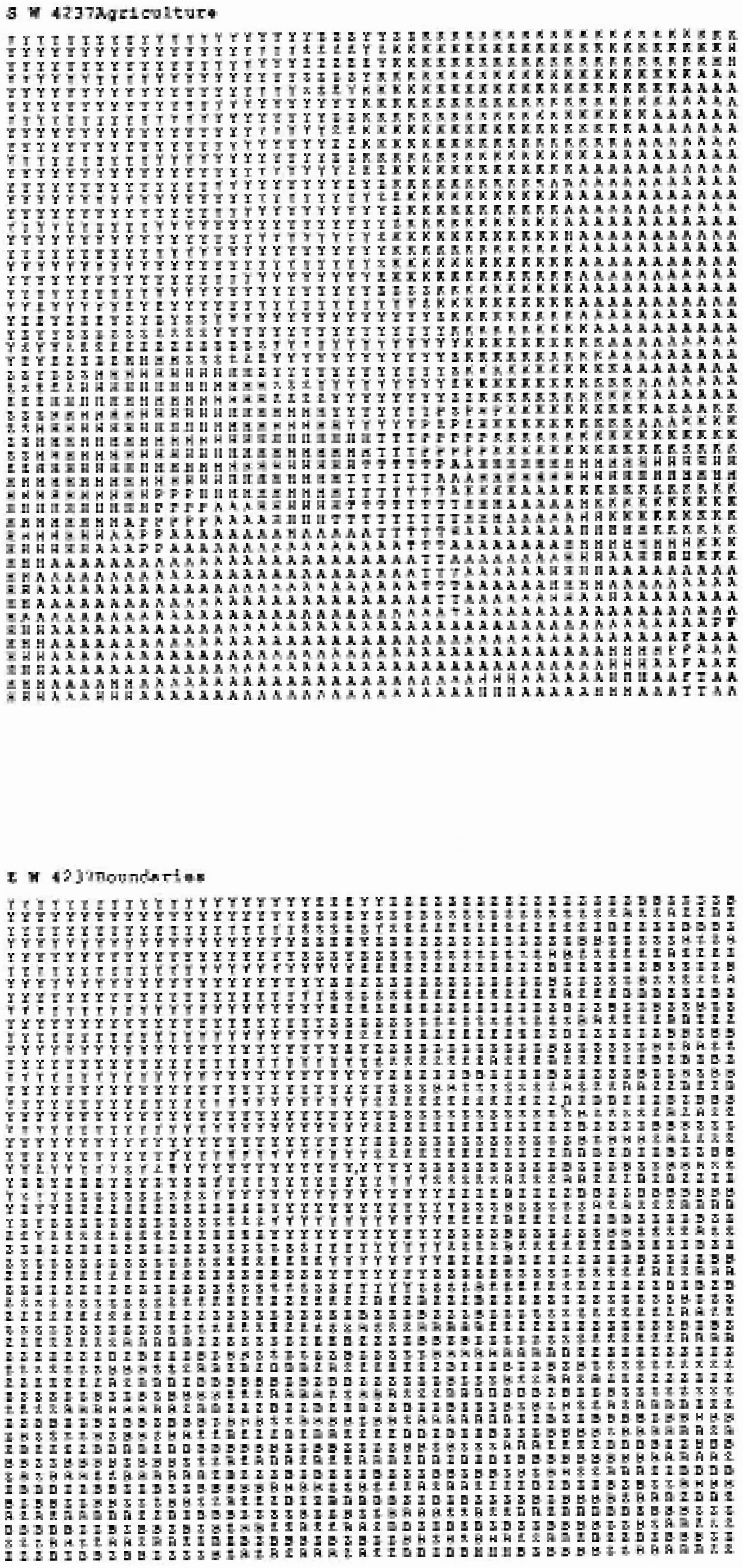

Figure 4.17
Example of rasterized $1km^2$ (SW4237, Zennor, West Penwith), showing tithed agriculture.
Top: A=Arable, Z=shoreline, Y=sea; and boundaries (uncorrected).
Below: B=boundaries, Z=agriculture, Y=sea. See also Figure 4.18

Table 4.19 Mean percentage composition ±1 s.e. of 1km coastal squares in West Wales and Cornwall mapped from tithe data (mid-C19) and measured in 20 m² pixels (2500=1km sq), corrected for exclusion of sea

Cover type	% in Wales		% in Cornwall		Mann-Whitney z value	P<
	Mean	s.e.	Mean	s.e.		
Sea	38.02	5.20	39.61	4.49	-.4322	N.S.
Excluding sea						
Arable	24.91	3.32	48.00	4.45	-3.408	0.001
Pasture	39.12	3.84	11.09	2.71	-5.523	0.001
Undefined/unknown	18.98	3.63	8.02	2.31	-3.415	0.001
Rough grazing	1.67	0.80	11.02	2.85	-3.350	0.001
Homesteads/crofts	2.22	0.60	3.11	1.07	-0.880	N.S.
Furze	3.50	2.00	4.86	2.31	-2.738	0.01
Turbary	0	0	5.55	1.92	-3.850	0.001
Meadow	5.17	1.23	0.03	0.02	-5.767	0.001
'Arable & pasture'	1.35	0.50	2.91	1.33	-1.279	N.S.
Waste	0.29	0.18	1.40	0.52	-3.348	0.001
'Clifflands'[1]	1.66	0.99	2.23	1.89	-1.371	N.S.
Orchard	0	0	0.53	0.34	-2.595	0.01
Rocks	0.18	0.16	0.22	0.12	-0.526	N.S.
Woods/plantations	0.04	0.02	0.01	0.01	-0.817	N.S.
Scrub	0.03	0.03	0	0	-0.198	N.S.
No. 1km sq's mapped	38		49			
Walls (corrected[2])	6.66	0.56	7.15	0.56	-0.505	N.S.
No. 1km sq's mapped	47		50			

1 possibly unused, agriculturally
2 for methods, see text (p.102)

more turbary, waste, rough grazing ($P<0.001$) and furze ($P<0.01$) in Cornwall. In Wales, the shortfall was made up by significantly more pasture (both regions x-=23.3% ±1s.e. 2.7%) and meadow ($P<0.001$), both being products of rotational leys. Unfortunately, there was also a far greater amount of indeterminate land ($P<0.001$) in Wales, and were this land use known, it would almost certainly increase some of the other Welsh proportions, including 'turbary', which was, otherwise, unrecorded in Wales. Orchards scored zero in Wales possibly due to other vagaries of classification (see below). There was no significant difference in the extent of walls between the two regions during the mid-C19: a mean wall-pixel value of nearly 20% (±1s.e. 1.1%) over both regions is corrected to *ca.* 7% estimated available area, as described above (4.5.1).

The zero score in Wales for orchards is probably explained by their being valued as much for pasture as for fruit produce, and they were frequently therefore included within the pasture acreage (Kain & Holt 1981). Notwithstanding the 11% balance of undefined land in Wales, the data support the statement in Section 3.4.6e that Cornwall until quite recent times was relatively backward in its agriculture with significantly more rough pasture of various kinds, certainly more than was to be found in Wales, where the agriculture was more improved with significantly greater areas of land down to meadow and pasture. 'Cliffs' (the slopes and horizontal tablelands) were utilised to a considerable extent for only about 2% was not apportioned with a more specific description. A similar percentage was accounted for by buildings and gardens.

4.6 CHANGES IN HABITAT OVER TIME

4.6.1 METHODS

Two methods were used to assess the broad changes in habitat, as they might have affected Choughs, over 150 years (1840-1990). One related the results described in the coastal km^2 analyses described in Sections 4.2 and 4.5; the second compared summaries of coastal parishes obtained from the Tithe Commission apportionments with June 1987 Ministry of Agriculture Fisheries & Food (MAFF) parish summaries. Due to discrepancies in methods of data collection (not designed for ecological purposes), inevitable limitations affected these analyses. It was only possible to undertake fairly crude correlation between them, yet it was hoped they might help to reveal some of the changes in land-use over that period of time.

Coastal parishes in Cornwall and Dyfed within the habitat blocks surveyed during the assessment described in Section 4.2, which provided land-use data over both periods (1830-40s & 1987) are listed in Tables 4.20 & 4.21. This amounted to 47 parishes (24 in Wales and 23 in Cornwall). One Welsh parish (Dale) was tithe documented as 121 acres (49ha), the current size is 459ha (MAFF 1987 June census) and has remained unchanged since feudal times (S. Morrell pers. comm.); to prevent confusion, Dale was omitted from individual parish comparisons. For a further 3 parishes in Wales and one in Cornwall, MAFF could not supply 1987 data. Since a regional overview rather than an individual parish position was required, inter-parish boundary changes, whether actual or effective, were ignored. A paired t-test showed there to be no systematic difference between the mid-C19 and 1987 parish areas (Table 4.22). The mean differences per area were: Wales 1.59%, Cornwall 7.24%; and combined: 4.35%. Changes in recording techniques might account for some

Table 4.20 Parishes in Wales surveyed for agricultural use in the mid-C19 and 1980s

Parish	TITHE SURVEY Date	Acreage	Comments
Angle	1841	1994	
Rhoscrowther	*ca*.1840	2227	
Roch	*ca*.1840	4300	
Waltonwest	*ca*.1840	1152	
Nolton	*ca*.1840	1475	
St. Elvis	1837	360	no 1987 data
Whitchurch in Dewsland	1838	3200	
Dale	1847	121	*con.* current data
St. Brides	1839	1703	
Brawdy	1842	5173	
Marloes	1842	2268	
St. Ishmael's	1839	3000	
Llanwnda	1843	4330	
Dinas	1841	2000	
Newport	1844	4372	
Neverne	1840	10290	
Fishguard	1839	3442	
Moylgrove	1847	2370	
St. Dogmael's	1838	5900	
Verwig	1838	3000	
Mwnt	1847	1100	no 1987 data
Aberporth	1838	2100	
Blaenporth	1837	3500	no 1987 data
Penbryn	1838	10000	
Llangranog	1840	4034	
Llandysiliogogo	1841	9182	
Llanllwchaearn	1846	2975	

Table 4.21 Parishes in Cornwall surveyed for agricultural use in the mid-C19 and 1980s

	TITHE SURVEY		
Parish	Date	Acreage	
St. Mawgan in Pydar	1842	6078	
Mullion	1843	5595	
Zennor	*ca*.1840	3184	
Rame	1844	1247	no 1987 data
Padstow	1840	3639	
St. Endellion	1842	3641	
St. Buryan	1844	5468	
St. Minver	1838	6300	
St. Teath	1841	4842	
Tintagel	1842	5173	
Marloes	*ca*.1840	3709	
Grade	1841	1946	
St. Keverne	1840	10158	
St. Anthony in Meneage	1840	1500	
St. Merryn	1841	3608	
St. Eval	1841	2673	
St. Just in Penwith	1845	6500	
Sennen	1838	2050	
Morvah	1839	1120	
St. Levan	*ca*.1840	2100	
Madron	1842	6000	
Towednack	1839	2800	
Gunwalloe	1839	1328	
Landewednack	1841	1929	
Magan in Meneage	1838	5210	

of the discrepancies.

Table 4.22 Mean recorded sizes (ha) ±1 s.e. of parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	paired t-value	
Wales	3934.22	547.80	3811.01	543.88	.53	N.S.
Cornwall	3972.96	459.00	3436.26	437.60	1.96	N.S.
Mean	3953.59	353.36	3623.67	346.47	1.83	N.S.
t-value	-.05 N.S.		.54 N.S.			

Proportions of pasture (representing advantageous year-round habitat) excluding modern improved pasture and arable (representing non- or only seasonally advantageous habitat), within parishes, were compared over time and between regions. Changes in woodland cover (negative habitat) were also measured. For the purposes of this study, all land recorded as having a pastoral function was included. Data were not available from this source on the spread of urbanisation nor on the indirect effects of an increasing human population, both of which are discussed in Chapter 3.

Data from the present day assessment undertaken by field surveys of 1km^2 described in Sections 2.4 & 4.2.2 were related to the assessment of the same kilometre squares from the tithe surveys of the 1840s (4.5.1).

4.6.2 RESULTS

Tables 4.19 and 4.23 - 4.26 give the proportions of pasture, arable and woodland in the coastal parishes of Wales and Cornwall respectively, and the changes since the 1840s as revealed by past and present agricultural surveys. With regard to arable land, while there was significantly more in Cornwall than in Wales during the mid-C19 (see Table 4.19), by recent times this difference had disappeared (Table 4.23). In Cornwall, there has been a great reduction in the amount of land down to arable in these coastal parishes ($P<0.001$), reducing to a negligible level the differences between the two regions; the mean proportions in Wales changed less significantly (.31 to .20, $P<0.01$).

The amount of old pasture has been significantly reduced in Wales but not in Cornwall: from there being very much more in Wales during the mid-C19 (Table 4.19), this disparity had largely disappeared by 1987 (Table 4.24). Whereas in Cornwall there had been less than half of the land down to pasture, in Wales the proportion was well over half. The change is due to generally increasing pastoralism in Cornwall. The inclusion of improved pasture within the modern values (Table 4.24) does not significantly affect the inter-region analysis, and with both pasture and arable land there is now no difference between the two regions. In Cornwall, however, more improved pasture in recent times resulted in a very great general increase in grassland since the tithe survey ($P<0.001$, Table 4.24). It has been mentioned already that improved pasture (in this case leys more recent than 6 years old) are not readily used by Choughs, at least in southern Britain. More important were clifflands; these were variously described as 'waste', 'turbary', 'furze', 'rocks' etc. They were extensively grazed and existed in Cornwall very much more significantly than in Wales (Table 4.25). While the extent of such clifflands will not have altered significantly between the two

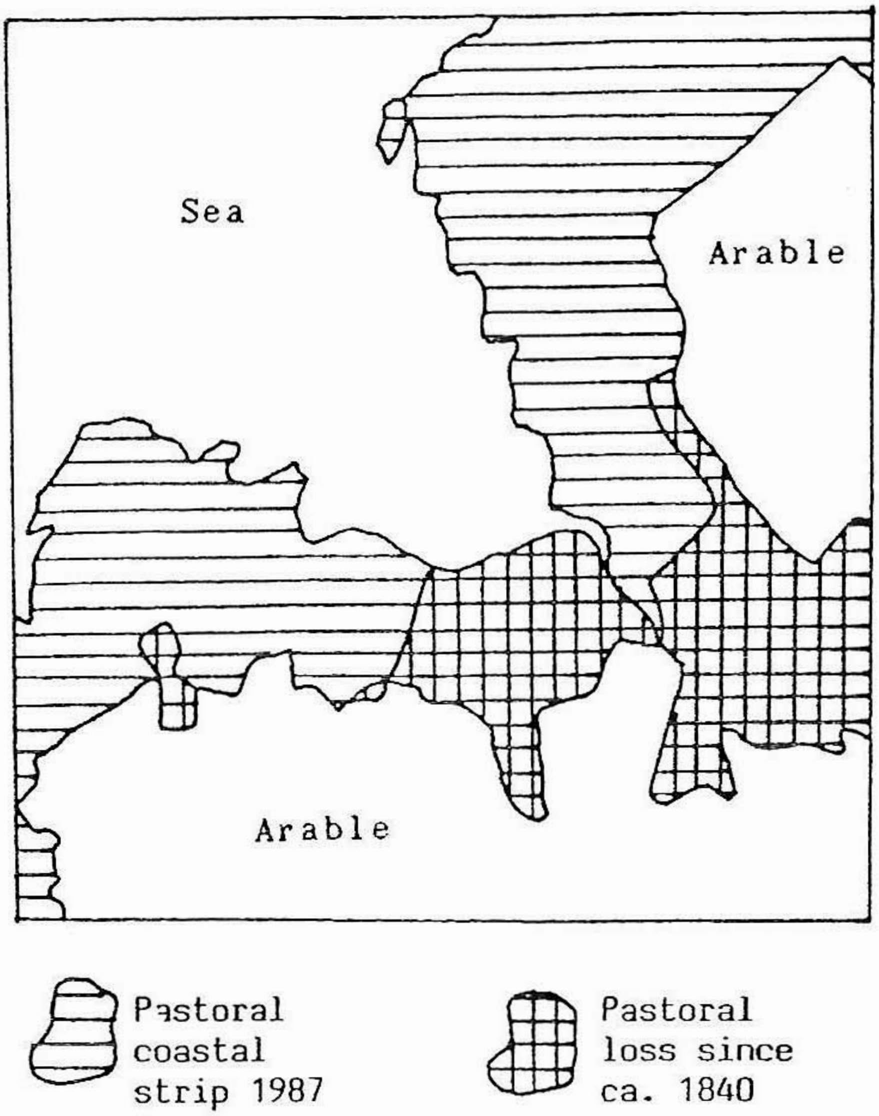

Figure 4.18
An example of the decline of coastal pastoral land between 1840 and 1990 within 1km2 (SW4237, Zennor, West Penwith) of Cornwall; see also Figure 4.17. NB. Most of what remains is degraded: non-grazed with tall scrub

regions during the intervening years, a general reduction in grazing from the high levels which existed, certainly in Cornwall, will have seriously reduced the amount of available Chough habitat (*e.g.*, see Figure 4.18).

Table 4.25 Total and mean proportions ±1 s.e. of uncultivated clifflands within the coastal parishes of Wales and Cornwall in the mid-C19

Region	Sum (ha.)	x	s.e.	No. parishes
Wales	7770	338	156	23
Cornwall	25908	1126	241	23
Mann-Whitney z-value	-3.690	*P*<0.001		

Coastal Cornwall was slightly more wooded than Wales in the mid-C19, however the proportion of woodland has increased significantly in the Welsh region over the subsequent 150 years, at the same time, a decrease in Cornwall has resulted in a significant difference now between the two regions (Table 4.26).

Kain & Holt (1981) presented the density of livestock per 100 acres for those Cornish parishes with reliable data; this was not possible for Pembrokeshire (4.5.1). The results from the June 1987 MAFF census are here presented as individuals per parish (Table 4.27) and also converted as in Kain & Holt (*ibid*.) to enable comparison, albeit very limited, over time. When assessed in raw form, there was no significant difference between the regions (although the higher numbers of sheep in Wales approached significance: *P*=0.057), but when converted to density per unit of land irrespective of parish size, significant differences emerged both with sheep and cattle, and it is seen that currently, on the coastlands, Cornwall supports significantly more cattle than Wales (*P*<0.05); Wales supports a very much greater density of sheep than Cornwall (*P*<0.01) (Table 4.27).

Table 4.26 Mean proportions ±1 s.e. of woodland in coastal parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	Wilcoxon Matched Pairs Z-value	n	P
Wales	.002	0	.017		-4.107	23	<0.001
Cornwall	.016	0	.009		-2.294	23	<0.05
Mann-Whitney z-value	-.290			-2.583			
P	N.S.			<0.01			

In a few parishes in the Cornish study region it was possible to get an insight (but no more) into

Table 4.27 Mean numbers of cattle and sheep per parish and per 100 acres in Welsh and Cornish study regions, June 1987 (after MAFF)

	Cattle			Sheep			
Region	$\bar{x}$/parish	$\bar{x}$/100a	s.e.	$\bar{x}$/parish	$\bar{x}$/100a	s.e.	Parish N
Wales	2040	51.4	2.4	4355	90.3	15.8	23
Cornwall	2017	59.8	2.5	1621	40.6	9.8	23
Mann-Whitney z value	-0.406	-2.340		-1.901	-2.582		
P	N.S.	<0.05		N.S.	<0.01		

Table 4.28 Mean density of cattle and sheep per 100 acres in Cornish parishes for which reliable data exists (n=7) over the two periods

	Cattle		Sheep	
Period	Density	s.e.	Density	s.e.
1840's	25.7	7.8	25.7	9.0
1987	63.6	3.7	17.6	11.0
Wilcoxon matched-pairs test Z-value	-2.366	P <0.05	-0.734	N.S.

the measure of changes in stocking levels over the last 150 years (Table 4.28; historical data after Kain & Holt 1981). There was a significant increase over time in the density of cattle ($P<0.05$) but non-significant decrease with respect to sheep.

4.6.3 DISCUSSION

The broad trends in coastal land-use, as they might affect Choughs during the 150 years between the tithe survey and recent MAFF June surveys, are shown in Tables 4.23 - 4.28. From these it can be seen that whereas during the mid-C19 there was significantly more rotational pasture in Wales than Cornwall, this discrepancy had largely disappeared by 1987 (Table 4.24). These results are due to variable increases in pastoralism in both regions, however quality of pasture is more important than quantity, and old pasture was significantly reduced in Wales although not significantly in Cornwall to a point where there was no significance in variability between the regions (*ibid.*). Details of C19 pasture are not known; no doubt the uncultivated so-called wastes, morasses, turbary, furze, rough pasture etc were crucial to Choughs, and it seems likely that due to the importance and extent of tin-mining in Cornwall and the consequent importance of the horse, pony and donkey as draught animals, these uncultivated coastal areas, which existed to a significantly greater extent in Cornwall than Wales (Table 4.25) were also harder grazed there. This would have had the effect of considerably extending naturally favourable botanical communities such as MC8 (4.4). It was clear from an intensive botanical inquiry of prime feeding sites that exposed earth, already identified as crucially important (see Figure 4.8 and Tables 4.5 & 4.9) was the most consistent high-scoring component (Table 4.17); the *Aira praecox* sub-community of MC5, characteristic of edge-types and ecotones, was by far the most important botanical indicator of Chough favourability. It is reasonable to assume that this and herb-rich swards generally would have been commensurately more frequent when stocking rates were much higher and there was no risk of pollution by, for example, invasive *Lolium* rye-grasses and chemical drift. Since ecotones and boundaries between botanical communities contain taxa (flora and fauna) of both adjoining communities plus specialised taxa restricted to the ecotone itself, the population densities of some species are greater here than in the two adjoining regions (Elton 1966), and when this 'edge-effect' incorporates open vegetation or interfaces which Choughs are able to exploit, a more optimal habitat is created. Choughs may therefore select ecotones because they provide unstable, open and accessible conditions, and because prey abundance is increased above that of the surrounding areas.

Analysis of map squares provided better coastal targeting and slightly more detailed data than were available in the parish summaries although the two surveys were complementary. By both methods, the extent of arable land during the mid-C19 was significantly greater in Cornwall than Wales, and the reduction in the former has been very great: from over 50% to less than 20%, compared to a reduction of little more than 10% in Wales (*cf.* Tables 4.19 & 4.22). A reduction in the proportion of arable land has been correlated with increasing Chough success (Williams 1989).

The amount of seeded C19 pasture was significantly greater in Wales than Cornwall (*cf.* Tables 4.19 & 4.23), the significance level, increasing in the field-by-field coastal analysis, suggesting that coastal fringes represent a more extreme example of the typical hinterland agriculture. The relative amounts of 'uncultivated cliffland', shown in Table 4.25, agree with the more detailed breakdown possible from the field survey (Table 4.19): the amounts of rough grazing, furze, turbary and waste were all significantly greater in Cornwall.

Paucity of reliable historical livestock data in the Pembrokeshire study region prevented a meaningful assessment of the changes over time, as was minimally possible for Cornwall. However, the extent of conversion of coastal arable land to intensively improved pasture in both regions (to

Table 4.23 Mean proportions ±1 s.e. of arable land in coastal parishes in Wales and Cornwall in the two periods

Region	C19	s.e.	1987	s.e.	Wilcoxon matched pairs Z-value	N	*P*
Wales	.31	.03	.20	.03	-2.585	23	<0.01
Cornwall	.52	.06	.19	.02	-3.984	23	<0.001
Mann-Whitney *z* value	-2.658		-.055				
P	<0.01		N.S.				

Table 4.24 Mean proportions ±1 s.e. of different pasture categories in coastal parishes in Wales and Cornwall in the two periods. Modern values are given both excluding and including intensively improved pasture ('1987 + improved')

Region	C19	s.e.	1987	s.e.	1987 + improved	s.e.	Wilcoxon matched pairs Z-value	N	*P*
Wales	.69	.03	.56	.04			-2.859	23	<0.01
					.77	.02	-2.129	23	<0.05
Cornwall	.45	.06	.52	.05			-.791	23	N.S.
					.76	.02	-3.498	23	<0.001
Mann-Whitney *z* value	-2.408		-.912		-.363				
P	<0.05		N.S.		N.S.				

a very highly significant level in Cornwall (*P*<0.001; *cf.* Tables 4.23 & 4.24) for the use principally of cattle in Cornwall, and presumably sheep in Wales), suggests that the changes in Wales have not been so great as in Cornwall, where agricultural development lagged behind the remainder of mainland Britain (Roberson 1941). A significant increase in the numbers of cattle in Cornwall since the 1840s has not been matched by the sheep population, which, in Wales, is at a level more than double that in Cornwall. Over the period 1875-1950 the numbers of sheep in Britain declined from *ca.* 28 millions to less than 21 millions, the decline wholly taking place in England; the sheep population in Wales and Scotland remaining stable or even increasing slightly (Hart 1953). In Cornwall, it was shown (Table 4.27) that sheep numbers had decreased, though not significantly in the few coastal parishes for which reliable data exists. The high numbers of cattle in Cornwall would certainly have helped create good Chough habitat although rough-grazing by cattle possibly needs to be mixed with or followed up by a regime of close-cropping either by sheep (or rabbits) in order to create the most favourable pastoral conditions for Choughs. The balance in Wales of more sheep/less cattle is probably preferential to that of less sheep/more cattle currently found in Cornwall. On the other hand, the quantity of un-/semi-improved pasture decreased significantly in Wales (*P*<0.01; Table 4.24) within the period under study while the amount available in Cornwall appears to be at a level slightly higher than in the 1840s. It is, however, reasonable to assume that the reduction of grazing pressure since those times, particularly that exerted by horses on the very clifflands of greatest interest (3.4.6e), although unfortunately no hard data exist, has caused a profound reduction on the quality of the pasture and rough grazing. Therefore, the differences in basic agricultural land-use patterns, which differed greatly in the past between Wales and Cornwall, have now all but disappeared. However, numbers of sheep are at a far lower density in Cornwall than Wales, and previous work by Roberts (1983) in Bardsey to the north, and by Bullock & del-Nevo (1983) in the Isle of Man, has shown that Chough occupancy correlates positively with sheep density. Historically, this could probably be extended to horses as well, and these have certainly decreased dramatically in Cornwall. The effects of a reduced grazing pressure result in a taller vegetation profile, and this was reflected in the Cornish background habitat assessment (4.2.3).