ISSUES IN CORVID BEHAVIOUR AND ECOLOGY

Richard Keith Waite

Thesis for Doctor of Philosophy Degree

1982

Department of Psychology,
University of Keele,
Keele,
Staffs.,
ST5 5EG,
Britain.
BEST COPY AVAILABLE.

VARIABLE PRINT QUALITY
Why...do rooks manœuvre in such immense numbers, and crows fly only in pairs? The simple truth is that birds, like men, have a history. They are unconscious of it, but its accomplished facts affect them still and shape the course of their existence. Without doubt, if we could trace that history back there are good and sufficient reasons why.....

Richard Jeffries (1879) Wildlife in a Southern County
## Contents

Abstract
Acknowledgements
General Introduction 1
Methods 4

Part One - Behaviour of Four Corvid Species in Sympatry
Chapter 1 - Introduction 54
Chapter 2 - The Birds 65
Chapter 3 - The Resource Base in Winter 72
Chapter 4 - Resource Utilisation by Four Corvid Species 93
Chapter 5 - Overlap and Partitioning of Resource Utilisation 111
Chapter 6 - Effects of Other Corvid Species on Prey Intake Rates 130
Chapter 7 - Competition and Coexistence: predictions and observations about short-term behavioural options 148

Part Two - Rook Flocks and Food Finding: tests of functional hypotheses
Chapter 1 - Introduction 203
Chapter 2 - Grouping by Birds: a review of functional interpretations 204
Chapter 3 - Local Enhancement for Food Finding by Rooks Foraging on Grassland in Winter 315
Chapter 4 - Rook Flocks and Food Finding: test by field experiment 361

References

Appendix 1 - Summary tables of invertebrate densities and dispersions
Appendix 2 - Dispersion of invertebrates within fixed grid samples
Appendix 3 - Analysis of variance summary tables
Appendix 4 - Copy of Waite (1981)
Appendix 5 - Rook breeding biology and earthworm abundance; rook and carrion crow mortality
Appendix 6 - Morphology of four corvid species
Appendix 7 - Summary tables of foraging rates of four corvid species on grassland in winter
Appendix 8 - Data not included in the thesis
Appendix 9 - Listing of null community test program
Abstract

In part one, the winter use of habitats available to four corvids (carrion crow, jackdaw, magpie and rook), sympatric in the mixed agricultural landscape of Keele, Staffordshire, is examined. Grassland, especially permanent pasture, was the dominant crop, and a majority of each species was found there. Selection between the different habitats available occurred. Carrion crows and magpies were found mostly on permanent pasture or grazed temporary leys, while jackdaws and rooks occurred mostly on permanent pasture. Rooks foraged mostly for below-surface invertebrates, especially earthworms. Jackdaws took small invertebrates from the surface, and beneath surface litter and dung. Carrion crows took mainly medium invertebrates and large earthworms above the soil surface, and medium invertebrates from dung. Magpies took both small and medium invertebrates above the soil surface, and from litter or dung.

The overlap of the four species in space, time, foraging microhabitat and prey types taken is examined. Discriminant function analysis showed that each species was significantly separated from every other on at least one of the functions derived, but magpies were found to occupy little unique niche space. Based on the observed overlaps and some negative or facilitative effects of other species' absence or presence on short-term prey intake rate, predictions are made about the possible behavioural mechanisms which might occur to reduce the impact of these effects. Computer simulation indicated that in general overlap between the four species was less than would occur by a chance utilisation of the available resources, suggesting that the species did differ in their use of the habitats sufficiently to cause some partitioning of resources. In addition certain species avoided foraging on a site when other species were present. Some interspecific aggression was seen, mainly by carrion crows against the other species. Data suggested that this was probably due to the presence of other birds disturbing large earthworms down their burrows, thus making them unavailable to foraging carrion crows, rather than to true 'interference' competition directed against species competing for the same resources.

In part two, functional interpretations of avian grouping are reviewed, and field observations of rook flocks foraging for earthworms described. The data suggested that social attraction to larger flocks increased the efficiency with which patches of earthworms were located, since larger flocks built up on the denser prey
patches. This effect may also have occurred within flocks foraging on a single field.

A field experiment was conducted in which levels of prey density were manipulated. Wild rooks showed changes in behaviour in response to variation in prey densities which were consistent with the field observations. However, in addition to showing social attraction after an individual bird's 'giving-up time' on a patch had been exceeded, birds may also have monitored the size of other flocks available in the vicinity, and moved on before their 'giving-up time' was exceeded if a larger flock were foraging elsewhere. Since larger flocks tended to occur on the densest prey patches, this mechanism may further increase the efficiency with which prey patches are located.
Acknowledgements

Dave Chantrey supervised the project. Dave, Marc Brazil, Paul Green, Jim Reid and Des Thompson commented on various manuscripts. Peter Matthias helped with the logic of some of the paths in chapter 2.4. Chris Blunsdon, Dave Chantrey and Graham Jennings helped with some of the programming, and Mike Burton with some of the maths. Thames Valley Water Authority, John and Rosamund Hegarty (Blore Heath) and numerous farmers around Keele allowed access to land. Mike Edge of the Geography Department at Keele provided meteorological data. The punch girls at Keele Computer Centre prepared most of the data. The Edward Grey Institute for Field Ornithology allowed use of the Alexander Library. Thanks also, of course, to the many people who helped and encouraged at Keele, Nottingham and elsewhere; and to anyone else who gave specific help who I have forgotten to mention.
General Introduction

The western palearctic Corvidae form an interesting group. Apart from the two jays (Garrulus glandarius and Perisoreus infaustus) and the nutcracker (Nucifraga caryocatactes) they all inhabit open country to a greater or lesser extent, and many are sympatric over much of their total range. Within Britain it is theoretically possible in some parts to see six out of the seven resident species (i.e. excluding the woodland-inhabiting Garrulus glandarius) foraging on the same field (Williamson 1960 has recorded this in the Isle of Man). In the mixed agricultural landscape of so much of lowland southern Britain four species are sympatric — the carrion crow (Corvus corone), the rook (C. frugilegus), the jackdaw (C. monedula) and the magpie (Pica pica).

These four species are all 'omnivores' in the broad sense of the word, foraging in mainly open areas for invertebrates, grain, and to a limited extent live small vertebrates, carrion and miscellaneous vegetable matter (e.g. Holyoak 1968, Lack 1971). Yet these closely related species differ greatly in their social organisations, both in a gross difference of general degree of gregariousness, and in several more subtle ways.
This situation throws up many issues which, for the purposes of this thesis, have been reduced to two basic questions:

(a) What are the niche relationships of the four species?

(b) Why are there such differences in social organisation?

The thesis considers two main issues arising from these two questions. In part one, measurement of the winter niches of these four species is presented, based on quantification of gross (crop type) and fine (above-beneath soil surface, dung, stones or clods) habitat choice; of the use of space in time; and of a fairly crude estimate of prey type. An analysis of the possible relationships between the overlaps revealed and certain aspects of social organisation is made. In particular the effects of the niche relationships on short-term behaviour in terms of interspecific interference or exploitation competition are considered.

These observations suggested certain hypotheses concerning the function of different patterns of social organisation. One of these is tested in part two - a possible food-finding function of the rook flock is tested by field observation of wild birds foraging for a naturally-occurring prey. These observations identified prey density and dispersion as the likely key exogenous variables con-
trolling behaviour changes. A field experiment controlling levels of prey density artificially was therefore conducted to test this.
Methods

M.1 Study Areas

Most observations were made on farmland surrounding Keele, North Staffordshire. Some subsidiary observations were carried out at Blore Heath, near Market Drayton, Shropshire, and at Farmoor, Oxfordshire (inset to figure M.1a).

Keele is situated on the Trent–Hersey watershed a few miles west of Stoke-on-Trent (figure M.1a). The landscape is gently undulating on gley soil with a base of (and occasional outcrops of) red sandstone. Its position on the watershed means that only a few small streams run through the area. The gley soils keep the ground moist or waterlogged for much of the year but can become hard and dry in summer (see further chapter 1.3). There are small areas of copse and buildings at Keele, giving the landscape the 'patchwork' appearance common to much of lowland southern Britain (figure M.1b).

M.2 Dates

Most data were recorded between January 1979 and March 1981, though related work was carried out beginning in
Figure M.1

Maps of Study Areas

(a) Position of three study sites within Britain and position of the main study area at Keele, north Staffordshire.

(b) Field units and 'patchwork' appearance of the Keele study area. Trees indicate copses, houses indicate built-up areas.
Main Study Area Centred Here
Methods


Although some data were recorded in all months, all behavioural data reported here, except where specifically stated otherwise, were recorded between November 1st and February 28/29th. This was done because the behaviour and ecology of each species varied seasonally. November-February was a reasonably homogeneous 'season' within the annual cycle for each species (justification for this may be found in chapter 1.3 and has already appeared in more detail in Waite 1976 and 1978; see also Peare et al. 1974). No new trends in the data recorded for this study have altered these conclusions. Data were recorded between 0900 and 1700 GMT in winter.

M.3 Corvid Species

Behavioural data were recorded from three congeners, the carrion crow (*Corvus corone*), the rook (*C. frugilegus*), and the jackdaw (*C. monedula*); and from the magpie (*Pica pica*).

M.4 Recording Behaviour

Observations were made on actively foraging birds only. Flock size and nearest-neighbour distances were recorded at the beginning and end of each separate
Methods

observation. An individual bird was chosen arbitrarily and a continuous commentary of feeding attempts, prey eaten, agonistic interactions and flights was spoken into a tape recorder, along with an instantaneous time sample with a five-second interval for certain behaviours (see list below). Mean length of records was 212.2 seconds (s.d. = 83.1); records lasting less than two minutes were discarded. Recording was stopped after 10 minutes if the subject bird was still visible; in practice there were very few records exceeding c. 6 minutes. Observations were made from field edges, using a vehicle as a hide, with a zoom telescope (25-60×60) mounted on a tripod, at ranges not exceeding c. 50 metres (depending on weather conditions).

M.5 Recording Meteorological Data

Daily recordings were made for the Meteorological Office by the meteorological officer of the Department of Geography at the University of Keele. The recording sites were positioned in the centre of the main study area. Further background data on the climate of Keele were available in Beaver & Shaw (1970). Meteorological data for Blore Heath and Farmoor were not sought.
M.6 Sampling Prey Densities and Dispersion

Only measurements of grassland invertebrates were made (sections 1.3.6 and 1.4.1 explain why). Due to a limit on time and equipment available, the sampling programme was designed to sample only earthworms (Lumbricidae) with known confidence. (*)

M.6.1 Sampling Method.

Samples were taken as a series of soil cores (7cm diameter by 7.5cm deep). Cores of this depth were taken since the birds were presumably unable to exploit prey below a few centimetres depth. Total bill length in the rook (the species with the longest bill of the four) is between 5.5 and 6cm (table 1.2.1); when digging birds can go somewhat deeper than this in the soil. Thus cores of 7.5cm depth probably covered all prey potentially available.

It is of course unknown how closely the samples reflected what was actually available to a foraging bird. The main prey type which cores will have underestimated were large lumbricids inhabiting permanent vertical burrows.

(*) A project investigating prey availability, prey fed to nestlings, and social organization of carrion crows and rooks included correct sampling procedures for other invertebrate groups, but was not completed within the thesis period due to the extent of the task (see appendix B).
down which they were able to escape as the core was taken. The cores were driven and removed as quickly as possible to alleviate this. Worms within permanent burrows did occur in the cores (4.04% of all worms sampled), often broken in two at the bottom or side of the core. The birds, of course, had a similar sampling problem - though they were no doubt more efficient at catching such prey than I (see section 1.4.5.2). Permanent burrows could be several feet in depth (Gerard 1967, Edwards & Lofty 1976).

However much this method introduced error, it was felt that cores were a better alternative than chemical extraction (the other commonly used method), since the latter techniques are known to bring worms up from depths at which they would undoubtedly be unavailable to foraging rooks (e.g. see Nordstrom & Rundgren 1972, Raw 1967a, Satchell 1967a, and summaries in Edwards & Lofty 1977 and Southwood 1978). Since Gerard (1967) has shown that in winter the majority of earthworms live beneath 7.5cm, such error would be unacceptable. Dunnet & Patterson (1968) drew similar conclusions when studying rooks foraging for earthworms in NE Scotland.

M.6.2 Sorting Method.

Cores were removed to the laboratory and handsorted. The number of different invertebrates and the live wet
weight of earthworms were recorded. Handsorting combined acceptable accuracy with the possibility of noting from which part of the core invertebrates were recovered (e.g. Edwards & Lofty 1977, Satchell 1971, and Southwood 1978 summarise the literature on comparative efficiencies of different sorting methods).

M.6.3 Sampling and Sorting Dung.

Samples from dung were taken by removing a core through the pat, and a separate core of normal depth from beneath the pat. The soil cores were handsorted in the usual way, whilst the dung was sorted by using a combination of handsorting and flotation in a 25% solution of magnesium sulphate (Laurence 1954). The absolute efficiency of this method is unknown, though Southwood's (1978) summary of studies indicates that efficiencies are acceptable for active invertebrates but lower for eggs and pupae. It is likely that birds would have a sampling bias in a similar direction.

M.6.4 Number of Sample Units.

Preliminary samples using the corer of the said size indicated that any number of cores in excess of about 10 would usually produce no further worthwhile reduction in
sampling error of earthworm numbers and biomass. (*) An N of 42 cores was decided on since a major purpose of the sampling programme was to investigate whether the invertebrates were distributed randomly, regularly, or in aggregations. This number allowed a symmetrical 6x7 grid, with 2m between each core, to be taken and the dispersion pattern to be examined. When such a grid was not laid out, 42 cores were taken over a similar area at random.

The estimation of population mean and variance from samples where cores were taken at exact fixed intervals is of course not strictly statistically valid, since a truly unbiased population estimate can only be assumed if every area within the habitat to be estimated had an equal probability of being sampled. However, since detection of aggregation patterns was one of the aims of samples, a number of the samples could not be taken at random. One method commonly used is that of stratified random sampling (e.g. Southwood 1978) where the habitat to be sampled is divided up into equal areas and then one sample is taken at random within each area. Again, however, the detection of aggregation patterns is not possible with this method unless the habitat is divided into a large number of small

(*) As determined by plotting sample size against population estimate; and also by applying a formula for estimating the N of samples required to give confidence limits to the population estimate of 10% or less (Milner & Hughes 1968, Southwood 1978).
Hughes (1962) describes a method of mapping aggregations by taking paired samples across a habitat, choosing the first sample site by random process, and then taking the paired sample at a fixed distance from the first in a random direction from it. However, the method works best for discrete aggregations and was practically difficult to manage. The 6x7 fixed grid method was the only practicable method of quasi-mapping of areas, which could reveal any coherent aggregation patterns existing over an area meaningful to a foraging bird. Since the method involved pacing an estimated two yards, and an estimation of right-angles by eye, the method in a sense approximated to a stratified random sample. (*)

Strictly speaking, therefore, the calculation of standard errors of estimates derived from such fixed samples are problematical. However, no systematic differences in means or variances were found between samples taken by the fixed method and at random, and there was not enough time available to sample enough fields at random to use only

(*) There were scientifically trivial, but practically important, reasons why this method was the only viable one (lack of time, lack of permissions for anything time-consuming on some fields, lack of an assistant for measuring and keeping inquisitive stock from scattering the contents of previously-bagged cores, etc. etc.).
those samples for estimation of population densities across the study area. It was felt that in this instance the end (detection of whether coherent aggregation patterns existed) justified the means calculated from such samples....

The relationship between sample size and population estimate for three of the subsequent samples (arbitrarily chosen for illustration) is depicted in figure M.2. In each case the variance about the final mean tends to level out well before the final sample size of 42 cores. As a double check, the N of cores required to estimate the population mean with 10% confidence, calculated by applying the formula retrospectively to the estimate and variability of the complete sample of 42 cores, were in each case well below the actual sample size of 42 (the arrows in figure M.2 indicate these calculated sample sizes).

Dung samples were taken with an N of 10 cores. In addition, occasionally the full sample of 42 cores of normal open grass areas could not be taken, and 10-core random samples were substituted. Figure M.2 indicates that in general samples of this size will estimate the true population with acceptable confidence on only some occasions. The important data in part two of the thesis on differences in the Keele study area over a three-week period, and on subsequent shifts, were all taken as full
Figure M.2

Population estimates of earthworms using different sample unit N's

Results for three arbitrarily selected samples. The circles indicate the mean numbers and biomass of earthworms in cores 1-5, then 1-10,...,1-42. The arrows indicate the number of cores required to give 10% confidence to the population estimate given the mean and variability of the actual sample of 42 cores (see text). "All" and "Obs." refer to the different size classes recognised during sorting (see text section M.9.2).
42-core samples. The summary table in appendix one indicates which samples were of size 10 cores.

It was necessary to do this on occasion because taking and sorting the samples was a very time-consuming activity. Sometimes a sample would be taken and no birds would then use the field. Hence a policy was adopted at some times of the year of sampling several fields with only 10 cores taken from each to increase the chances of being able to subsequently relate bird behaviour to prey densities and dispersions.

Thus an unknown amount of error may have been introduced into some of the relationships between prey density and dispersion, and bird behaviour. It may be reasonably assumed that this will have made true relationships between variables more difficult to trace, by increasing error variance, rather than providing a source of any systematic bias.

Finally it should be noted that when in later chapters it is stated that field 'x' contained more or less invertebrates than field 'y', this is a shorthand for "a particular area of c.120 square metres in field 'x'..."; data presented later (section 1.3.8.2) show that there are often significant differences in invertebrate populations between two such areas within the same field.
M.6.5 Samples Taken Close in Time

Samples were taken throughout the year, but one set of 14 samples were taken during a 26-day period between 20th November and 15th December 1979 (see section 21.3.8.1). The location, significance and results of this programme are described later. Since earthworm densities (in the top 7.5cm of the soil) vary seasonally and with short-term changes in temperature and rain (summary and references in Edwards & Lofty 1977 and Waite 1978), the samples were taken within as short a time period as possible. The 26-day period was one of fairly uniform mild and wet weather with no days of frozen soil, and with rainfall and air temperature variations spread quite evenly across the period (figure M.3a & b). There was no significant relationship between air temperature and earthworm numbers, nor was one crop type sampled at systematically differing climatic conditions to other crop types (figure M.3c). Hence differences between samples were not simply the result of systematic bias in sampling different areas on different days. Any variation introduced by climatic variability would therefore seem to be randomly distributed amongst the samples.

M.6.6 Invertebrate Samples and Bird Behaviour

Soil invertebrate data were not available for all
Climatic conditions during a 26-day invertebrate sampling programme in November-December 1979

(a) Frequency distribution of mean 24-hour air temperatures.

(b) Air temperatures and rain days.

(c) Air temperatures and earthworm densities

\( \bar{X} = 9.1^\circ C \)
observations of birds. To ensure an adequate sample N of observations, individual observations of birds were assigned data from a soil sample if they foraged on the relevant field within +/- five days of the invertebrate sample, unless climatic conditions changed dramatically during this period. Again, any error introduced by this procedure is likely to be random rather than systematic.

M.7 Censusing Birds and Habitats

Routine fortnightly censuses of part of the main study area at Keele were carried out throughout the year for three years (naturally some were missed when the author was not at Keele). The area sampled is shown in figure M.1b. An additional 15 fields moving off the south-west corner of the map were added to the census during the final year. Unfortunately at the beginning field numbers were not always recorded, simply the habitat type and the number of each species present.

The census included walks past all of the small copses and through the larger wood at the S.E. corner. Any corvids seen were recorded, but the areas were not systematically searched nor were birds flushed (e.g. see Dunnet & Patterson 1968). Birds in rookeries were not counted. Because of this, the census can only be used to
indicate habitat selection and the relative numbers of four species present in open habitats, and not absolute population densities.

The census took c. 2-3 hours to complete. No attempt could be made to adjust for birds moving from field to field and therefore being counted more than once (unless they were specifically observed to do so) since birds were not marked. Censuses were begun at different points and carried out in different directions on different days to attempt to preclude any systematic error introduced by bird movements. Censuses were conducted between 1000 and 1600 GMT. All birds occupying the censused habitats were counted, whether actively foraging or not (no distinction was made between the activities of birds in the census). The timing of the censuses ensured that neither pre- nor post-roost gatherings were included.
Methods

M.8 List of Recorded Variables

Environmental
1. Date
2. Time
3. Place
4. Habitat (Crop Type)
5. Meteorological
6. Prey Density and Dispersion
7. Length of Observation

Behavioural
Continuous:
1. Paces
2. Feeding Actions:
   Surface Pick
   Surface Probe
   Pounce
   Jump
   Stone-Clod Turn
   Dung Turn
   Dung Crumble
   Deep Probe
   Dig
   Jab
3. Prey Type & Size:
   Grain
   Earthworms:
   Small
   Medium
   Large
   Other Invertebrates:
   Small
   Medium
4. Short Flight
5. Leave Field
6. Displace Conspecific
7. Displaced by Conspecific
8. Leave Field after Attack by Conspecific
9. Displace Other Corvid
10. Displaced by Other Corvid
11. Leave Field after Attack by Other Corvid

Time Sample:
11. Look Up (Vigilance)
12. Look Food
13. Peck
14. Interact
15. Rest-Preen
16. Fly

Social
1. Flock Size
2. Nearest Neighbour Distance
3. Flock Sizes of Other Corvids
M.9 Definition of Environmental Variables

M.9.1 Habitat

Behaviour was not recorded when birds were foraging in woodland, around buildings, or on other 'marginal' land — all of which they rarely did (see sections M.7 and 1.4.1) — but birds' presence was recorded when in these habitats during censuses. Habitats were defined by a combination of 'crop' type and by the current state of the crop, though many of these categories were later merged in the analyses presented in this thesis. Except for the first category the habitats are all agricultural.
When recording behaviour of birds foraging on grassland, an attempt was made to record birds on all crop types. However, the rarity of use of some crops made this impossible. In reality, the number of observations of each species reflected the relative abundance of each crop type fairly closely, except in the case of the magpie which was under-recorded on grazed temporary leys and over-recorded
on non-agricultural grass and ungrazed temporary ley (table M.1). The significance of these patterns is discussed in, for example, sections 1.4.1, 1.4.5.3 and 1.4.5.4.

M.9.2 Prey Density

When sorting soil cores the different invertebrates occurring in each core were recorded and the live wet weight of earthworms (Lumbricidae) in each core measured. On occasion some of the other invertebrates were weighed but this was not done as standard due to the infrequent occurrence of invertebrates other than earthworms in most of the samples. Earthworms were further classed by four size categories - large, medium, small, and those considered too small to be identified by an observer if taken by a foraging bird (the first three size categories are defined in section M.11.3.2 below). Because of lack of time, each earthworm was not classified by species - in any case, earthworm species could not have been determined whilst observing foraging birds. Because of the infrequency of occurrence of invertebrates other than earthworms in winter samples at Keele (where most samples were taken), these items were classed only as occurring above or below the soil surface, and not taxonomically or by size. If there was some doubt as to where the invertebrate occurred, it was classified as 'other'.
Table M.1

Proportion of behavioural observations from each grass crop type compared to proportional use of that crop type by birds determined by census

NAG = non-agricultural grass, TLU = ungrazed temporary ley, TLG = grazed temporary ley, PP = permanent pasture.

<table>
<thead>
<tr>
<th></th>
<th>C. Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>NAG % Observations</strong></td>
<td>7.8</td>
<td>1.4</td>
<td>-</td>
<td>22.9</td>
</tr>
<tr>
<td><strong>% Usage</strong></td>
<td>3.8</td>
<td>1.3</td>
<td>0.7</td>
<td>6.2</td>
</tr>
<tr>
<td><strong>TLU % Observations</strong></td>
<td>13.3</td>
<td>1.4</td>
<td>-</td>
<td>17.1</td>
</tr>
<tr>
<td><strong>% Usage</strong></td>
<td>1.9</td>
<td>-</td>
<td>-</td>
<td>3.7</td>
</tr>
<tr>
<td><strong>TLG % Observations</strong></td>
<td>35.5</td>
<td>15.9</td>
<td>15.0</td>
<td>5.7</td>
</tr>
<tr>
<td><strong>% Usage</strong></td>
<td>38.5</td>
<td>11.8</td>
<td>16.8</td>
<td>39.4</td>
</tr>
<tr>
<td><strong>PP % Observations</strong></td>
<td>43.3</td>
<td>81.2</td>
<td>85.0</td>
<td>54.3</td>
</tr>
<tr>
<td><strong>% Usage</strong></td>
<td>55.8</td>
<td>86.8</td>
<td>82.5</td>
<td>50.6</td>
</tr>
</tbody>
</table>

| N Birds Observed | 90 | 69 | 60 | 70 |
| N Birds Censused | 244| 1219 | 655 | 214 |
As stated in section 2.6.4 the sampling procedure was standardised on earthworms. Hence while earthworm figures are legitimately transformed to population estimates those of other groups are not, although mean numbers per core are given in appendices one and two, and are sometimes used as ranks in statistical analyses, on the presumably not unreasonable assumption that there will be some unspecified positive relationship between the numbers found in a sample and true population densities (*). Hence the following prey density variables are employed in the thesis:

1. Number of very small earthworms per square metre
2. N of small earthworms / square metre
3. N of medium earthworms / square metre
4. N of large earthworms / square metre
5. Mean N of 'above surface' invertebrates (other than earthworms) per core
6. Mean N of 'below surface' invertebrates (other than earthworms) per core

These may be summed and referred to as:

7. N of all earthworms / square metre (sum of 1-4)
8. N of 'field observable' earthworms / square metre (sum of 2-4)
9. Biomass (g) of earthworms / square metre (sum of biomass of 2-4)
10. Mean N of invertebrates other than earthworms / per core (sum of 5-6 plus any unclassified by position in core)

Since the main point of the invertebrate sampling

(*) Phillipson (1971) has discussed the problem of sampling rare and/or very aggregated invertebrates, and detailed the difficulties of devising reasonably cost- and time-effective sampling programmes which provide anything better than confidence limits of 30% to estimates of population means - yet the use of such data is considered justified in the absence of any alternative methods of data collection. This approach is followed here, with the use of numbers or biomass 'per core' to act as a reminder of the degree of error potentially involved in these data.
programme was to relate such prey measures to the behaviour of foraging birds, the second of the two estimates of earthworm numbers (i.e. "field observable") is used throughout the rest of the thesis except where specifically stated otherwise. Qualitatively similar relationships exist between behaviour and \( N \) of all earthworm numbers per metre square in any case, since the two variables were highly correlated both between samples. \( (N_{\text{all EW}} \text{ per metre square with } N \ 'field observable' \text{ EW per metre square for the set of 14 fields sampled in November-December 1979} - r = 0.92; \ N_{\text{all EW}} \text{ per core with } N \ 'field observable' \text{ EW per core for 14 separate samples of 42 cores each} - \text{mean } r = 0.75 \ (\text{range} = 0.59 \text{ to } 0.89); \text{ see further section 1.3.8).}

**M.9.3 Prey Dispersion**

The dispersion of invertebrates within soil samples was tested by two methods - the mean-variance ratio test for statistical heterogeneity, and a test for the spatial pattern revealed in 6x7 grid samples (see section M.12.2.4). Both methods could test whether invertebrates within samples differed significantly or not from a random distribution, either in the direction of greater evenness than expected by chance ('overdispersion') or greater contagion ('aggregation'). However since, as stated above, the sampling procedure was not standardised on inver-
tebrates other than earthworms, a significance test investigating the relationship between the mean and variance of such samples would not be appropriate, and hence this procedure is used only to test the dispersion of earthworms. Testing the 6x7 grid pattern shown by these other invertebrate groups is however considered valid since the test employed is not based on the continuous variability of the samples (see section M.12.2.4). It is hoped that the probability of recording the presence or absence of such invertebrates in any one core is not proportional to the true population densities in the areas from which cores were drawn.

The values resulting from these tests are labelled:

V/M Ratio Method
Grid-Pattern Method

in appendix one.

M.10 Definition of Social Variables

M.10.1 Flock Size

The number of birds present was recorded at the beginning and end of each separate observation of a foraging bird, and the mean used. The 'loose' structure of foraging groups of each species made this a little ambiguous. Usu-
ally the definition of Patterson et al. (1971) was adopted, which states that birds in different fields are taken to be in different flocks. However, on the larger fields birds more than c.200 metres apart were treated as separate groups.

Where more than one species occurred together on a field, the flock size of each species was recorded separately. In some analyses the flock sizes of one or more species were added together - when this has been done it is of course clearly indicated in the text.

M.10.2 Mean Nearest Neighbour Distance

A measure of flock density was calculated as the average distance between flock birds. This was determined for each observation by estimating the distance (with the naked eye) of each bird in the flock from its nearest neighbour at the beginning and end of each separate behavioural observation, and taking the mean. Above c.20 metres MND's were only estimated at large intervals (i.e. 25, 50, 75, 100 and 100+ metres).

This method must be open to error, particularly along the line of sight on flat fields, and as distances between birds increased. Known distances between landmarks on most of the fields used for data collection enabled errors for
larger distances to be lessened. The assumption is made that error was standard between observations. Only one observer recorded these data. NND figures in the thesis should not be taken as accurate measures of absolute distances, and comparisons between the data presented here and data in other studies employing flock density measures should be done with this in mind. Only non-parametric (ranking) statistics were performed to avoid bias introduced by error rate increasing as distance increased, and the use of fixed non-equal intervals at the greater distances.

Because error-rate increased as distance increased, and because the larger distances were estimated at non-equal fixed intervals, the median would have been a more appropriate description of central tendency. However, by the time this was realised much of the original data on which the means were based had been discarded.

Additionally, it was discovered too late that first-neighbour distance was not a good measure of overall flock density for jackdaws in all seasons and for the other three species in spring, summer and autumn, since paired birds or dependent young following an adult kept closer together than the true average flock density. Second-neighbour distance would have been a better measure.
M.11 Definition of Behavioural Variables

M.11.1 Feeding Actions

Ten different foraging behaviours were recognised for birds searching for and taking prey. Most of these followed Lockie (1956a) with some modifications. Dung Crumble and Jab were not listed by Lockie. Holyoak (1974b) described magpies scratching litter aside with one foot but no species was observed to do this during the present study. Pinowski's (1959) description of rooks 'rooting' sounds rather like the Dig action described here (section M.11.1.9).

M.11.1.1 Surface Pick

This was a simple action, the bill being lowered to the ground, the prey item picked up if located and caught, and the bill lifted up again.

M.11.1.2 Surface Probe

The bird either pushed its bill into a tuft of grass and opened it, or used its bill as a lever, first flattening down grass blades to one side and then moving its head over in an arc so that the other side was flattened also (*). It was usually quite straightforward to distinguish
between this action and the similar action of Deep Probing, where the bill was pushed beneath the soil surface and not simply into the grass-mat layer. However the distinction was not always obvious and an unknown proportion of true Surface Probes will have been misclassified as Deep Probes, and vice-versa.

M.11.1.3 Pounce

This action was distinguished from Surface Picking mainly by the speed of its execution. Pouncing was seen in two forms, depending on the nature of the prey. Firstly, a foraging bird could run-hop-fly quickly for a short distance and catch a prey item by moving its bill very quickly to the ground surface. This was most often observed in the summer months and was probably directed at adult dipterans.

The second form of the action, when successful, almost always resulted in the capture of a large earthworm which had been caught partly out of its permanent burrow. A foraging bird would suddenly pounce to one side — sometimes after a period of peering at the ground while standing still, rather like a blackbird (Turdus merula) — and

(*) This was easily distinguished from the often-observed 'bill-wiping' as in that behaviour the head is not moved from one side to the other in an arc, but first one side of the bill is laid against the grass and the head moved so as to wipe its entire length, and then the same is repeated for the other side of the bill.
drive its bill quickly down to the soil surface. Frequently after pouncing the bird then leant back and slowly pulled a length of earthworm out of its burrow. Sometimes the bird would lean back as far as it could without extracting the entire length of the earthworm, at which point it would let go and quickly grasp the earthworm again near the ground surface and continue pulling until it had extracted the rest. Birds probably did not always withdraw the whole earthworm, but broke them in two - large *Lumbricus terrestris*, *Allolobophora longa*, and *A. nocturna* (the three large permanent burrowers present at Keele) all extend their setae into the burrow wall, and expand their posterior segments to grip the wall of the burrow, if caught partly out on the ground surface, and may often be broken in two rather than relinquish their grip (see e.g. Edwards & Lofty 1977).

This latter form of Pounce may at times have been confused with Jab (II.11.1.10), where the bill is driven down quickly but goes beneath the soil surface. The confusion is likely to have been serious only when the action was unsuccessful, since then the bill could be moving with such speed that it might finish somewhat beneath the soil surface. Unsuccessful feeding actions are not analysed in the thesis. Successful actions were probably differentiated correctly most of the time, since when a pounce was successful the prey was grasped with the bill remaining
above the surface, whereas a successful jab left the bill below the surface. Pounce was used mostly by jackdaws taking small invertebrates (the first form of the action) or by carrion crows taking large earthworms (the second form), whereas Jab was mostly used by rooks taking small earthworms (appendix 7.9).

M.11.1.4 Jump (or Snap)

A foraging bird took a flying insect. Although the bird did not always leave the ground to do this, the action is referred to only as jump in the analyses as a shorthand. The key difference between this and Surface Pick or Pounce for an adult winged insect is that in the former action the insect was in the air, whilst in the latter two it was on the ground surface.

M.11.1.5 Stone-Clod Turn

A foraging bird used its bill to turn over a clod of earth, tuft of dry grass, small stone or piece of wood, leaves, etc., and fed on the invertebrates thus exposed. The actions used to catch the prey after moving the object (often by picking or pouncing) were not recorded as Surface Pick or Pounce in addition. If a single movement of an object resulted in more than one capture of a prey item,
then each capture was termed a Stone-Clod Turn, even though only one actual movement of the object may have occurred.

M.11.1.6 Dung Turn

The movement of animal dung by a bird to expose invertebrates. As with Stone-Clod Turn, actions used to take items after the movement of the dung were not classed as separate Surface Picks (etc.) but each prey capture was a separate Dung Turn.

A bird exploiting a large cow pat could make many separate turning or scattering movements in a short space of time. These were treated as but one Dung Turn until the bird moved its feet and therefore began to exploit another part of the pat.

M.11.1.7 Dung Crumble

A rarely used action performed by a few carrion crows, which took pieces of dry dung between the mandibles of the bill, which were then closed to crumble the dung into small pieces. Invertebrates thus exposed could then be eaten. As with the two previous actions, one crumpling movement followed by more than one prey item capture were designated as separate Dung Crumbles.
M.11.1.8 Deep Probe

The bill was inserted into the ground and opened, and often twisted and turned from side to side. If an earthworm or other soil invertebrate was exposed, the bill was closed and the invertebrate extracted. As with the previous three actions and Surface Probe, more than one probing movement at the same spot was counted as one Deep Probe.

M.11.1.9 Dig

The bill was used as a hammer to dig at the ground, pieces of earth being scattered, and an often substantial excavation made. As with some of the other actions, several digging movements at the same spot were treated as one Dig, but more than one prey capture following the digging movements were treated as separate Digs. Deep Probe could sometimes develop into Digging. When this occurred a Dig was recorded.

M.11.1.10 Jab

A swift movement, often (but not always) following a bout of peering, as with Pounce (M.11.1.3), but where the bill was driven beneath the ground surface and a prey item extracted. A small amount of earth was often flicked off
the end of the bill following a Jab.

M.1.2 Microhabitats

In some analyses feeding actions were summed to represent foraging in different microhabitats. The following four microhabitats were defined:

1. Above Soil Surface being the sum of: Surface Pick Surface Probe Pounce Jump
2. Beneath Stone-Clod being the sum of: Stone-Clod Turn
3. Within-Beneath Dung being the sum of: Dung Turn Dung Crumble
4. Beneath Soil Surface being the sum of: Deep Probe Dig Jab

M.1.3 Prey Items

Any of the above feeding actions could result in the capture of a prey item. The following prey items are recognised in the thesis:

Grain
Small Earthworm
Medium Earthworm
Large Earthworm
Small Invertebrate (other than earthworm)
Medium Invertebrate (other than earthworm)
These rather broad categories are all that the recording technique (direct observation of foraging birds) would allow. Earthworms could readily be identified through the telescope, but only some other invertebrate types could be, and those not reliably on every occasion. 'Small' items which could barely be seen were recorded if a bird was seen to make a swallowing motion following a feeding action—a distinct movement in which the bill, head and neck are jerked back, sometimes several times, as the prey is swallowed. Observations by Feare et al. (1974) on captive birds confirmed that such a swallowing action did correspond to one food item ingested.

M.11.3.1 Grain

Birds foraging on sown or stubble fields took cereals one grain at a time. Birds were observed foraging on barley, oats and wheat fields. Grains on fields were identified by reference to the farmer or to Robinson (1951).

M.11.3.2 Earthworms

Earthworms (any Lumbricid species) taken by birds were assigned to one of three size classes:
1. Small = up to one bill length
2. Medium = between one and two bill lengths
3. Large = greater than two bill lengths (*)

Obviously some misclassification will have arisen with such gross categories, especially since earthworms are able to adjust their total length by expanding and contracting segments (see e.g. Edwards & Lofty 1977).

M.11.3.3 Other Invertebrates

Since only some of the other invertebrates taken by foraging birds could be identified through the telescope, these were assigned only by size and taxonomy was ignored. A list of some of the invertebrates positively identified as taken by foraging birds, and of some found within winter soil samples, may be found in section 1.3.7. The size categories employed were:

1. Small = negligible length compared to the bill (and often too small to be seen)
2. Medium = about 1/2 the length of the bill or more

An unknown number of small earthworms will probably have been misidentified as medium, or even small, other invertebrates.

(*) Bill length of carrion crows or rooks, which are roughly similar (table 1.2.1). Since bill-lengths of jackdaws and magpies are about 2/5ths smaller, errors could arise - but in practise the latter two species were not observed to take other than small earthworms.
M.II.4 Foraging and Feeding Rates

The rates per minute, or per 50 paces, of feeding actions and prey types taken could be calculated using the number of paces taken during each separate observation and its duration.

Since the prey items differed in size and chemical composition, foraging rates expressed simply in terms of numbers ingested are limited in value. Hence average weights and chemical composition values were assigned to each of the prey classes recognised, and average energetic and nutrient intake rates could be calculated. The values assigned are listed in Table M.2. The average weight values were obtained by weighing invertebrates from winter soil samples taken at Keele.

For cereals, 50 grains of each type were collected from stubble at the end of December, weighed, and the mean weight of an individual grain calculated. For earthworms, individuals were drawn from samples (from winter core samples) preserved in formalin, dried on blotting paper, and assigned to one of the three size classes. When 25 of each class had been assigned they were weighed and the mean calculated for each size class. For the other invertebrates, individuals were again extracted from preserved (*) samples at random, and assigned as small or medium.

(*) Invertebrates preserved in formalin can lose a varying
Table M.2

Average weights, calorific and gross nutritive values of different prey available to birds foraging on agricultural land in lowland southern Britain in winter

Values for average weights were derived from samples taken during this study (see text); sources for the other columns were Allen et al. 1974, Bolton & Phillipson (1976), Peare et al. (1974), Grant (1955), Lakhani & Satchell (1970), Lawrence & Millar (1945), MAFF (1942), MAFF (1952), Satchell (1967a).

<table>
<thead>
<tr>
<th>Prey Type</th>
<th>Wet Weight (g)</th>
<th>Water Content (%)</th>
<th>Calorific Value (kcal/g)</th>
<th>Protein Content (%N x 6.25)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Dry</td>
<td>Wet</td>
</tr>
<tr>
<td>Invertebrate:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>0.007</td>
<td>75.0</td>
<td>3.83</td>
<td>0.96</td>
</tr>
<tr>
<td>Medium</td>
<td>0.183</td>
<td>(&quot;&quot;&quot;)</td>
<td>4.02</td>
<td>1.00</td>
</tr>
<tr>
<td>Earthworm:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td>0.276</td>
<td>85.0</td>
<td>4.42</td>
<td>0.66</td>
</tr>
<tr>
<td>Medium</td>
<td>0.634</td>
<td>(as above)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>1.470</td>
<td>(as above)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grain:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barley</td>
<td>0.033</td>
<td>14.9</td>
<td>4.10</td>
<td>3.49</td>
</tr>
<tr>
<td>Oat</td>
<td>0.041</td>
<td>13.3</td>
<td>4.25</td>
<td>3.68</td>
</tr>
<tr>
<td>Wheat</td>
<td>0.037</td>
<td>13.4</td>
<td>4.29</td>
<td>3.71</td>
</tr>
<tr>
<td>Acorn</td>
<td>3.310</td>
<td>50.0</td>
<td>4.10</td>
<td>2.05</td>
</tr>
</tbody>
</table>
until 40 items of each size class had been selected. Thus the different invertebrate types were represented in the samples to be weighed in proportion to their abundance in winter soil samples. Invertebrates belonged to the following groups:

- Arachnida
- Coleoptera: imagines and larvae
- Diptera: imagines and larvae
- Lepidoptera: larvae

Rates of ingestion of calorific and protein-containing material were calculated since prey items differed not only in size but in relative value. Cereals were good sources of energy but lower in protein content than invertebrates. Earthworms had higher dry weight calorific values and contained a higher percentage of protein-containing material than other invertebrates. However, because of their greater water content, they had lower wet weight calorific value and about equal protein value.

Further, very little of earthworms' body make-up is in amount of their fresh weight - e.g. Satchell (1971) showed a loss of around 10% after 7 days and 18% after four months. Earthworms may lose more weight than arthropods. The maximum storage period before weighing in the present study was about 7 months; but since the samples from which individual items were drawn had been stored for varying lengths of time, no attempt was made to adjust for this loss of weight during preservation. However, since all invertebrate groups were drawn at random from the same pool of samples, comparisons of weights between invertebrate types will not be systematically biased. Weights given will however probably differ from true fresh weights by a factor of around 10-20%.
the form of chitin (only the setae and gut wall), whereas other invertebrate types can contain between c.5 and nearly 50% chitin (e.g. Turner 1982, Zach & Falls 1978). Chitin is probably indigestible by birds (chitin parts often occur in faeces and pellets). Counterbalancing this, around 20% of the fresh weight of earthworms may consist of soil in the gut (Raw 1966). Because these two factors could not be estimated during the present study, no attempt was made to adjust the values further to account for these differences.

Handling times were not incorporated into the calculations since they proved difficult to record accurately. Interest in the thesis is not on the economics of prey selection, but merely on the comparison within and between species of the reality of what was actually ingested. The longest observed handling times (c.15-20 seconds for large earthworms) were shorter than the average inter-catch time of c.40 seconds for rooks and carrion crows (appendix 7.1).

M.11.5 Short Flight and Leave Field

If a bird took flight, relanded within the same field, and recommenced foraging, this was recorded. Similarly, if an observational bout ended with the bird leaving the field, this was recorded. Average flight rates per minute could then be calculated.
M.11.6 Agonistic Interactions

Agonistic interactions were recorded when they occurred. Prolonged fights were very rarely observed in winter, almost all interactions consisting simply of displacements from an area (e.g. a dung pat) which was followed by the aggressor foraging at the spot vacated in a proportion of the cases observed. The attacked bird moved away, usually only a few metres, and continued foraging.

Some attacks by carrion crows on other birds were followed by the attacked birds leaving the field. This was recorded separately. Hence for each foraging bird the number of times it displaced, or was displaced by, conspecifics or other corvids; and whether or not it left the field if attacked by another bird; was recorded. Rates per minute of agonistic interactions could then be calculated.

M.11.7 Look Up and Look Food

Vigilance data was recorded by measuring the occurrence of looking up in birds actively foraging. All four corvids foraged by walking around a field making occasional pecks at the ground. While walking, birds were either designated as looking for food or looking up. The definition of look up adopted was:
While searching for food a bird would often stop and look up and around. Sometimes the bird would not stop pacing, but the change in direction of its gaze from the ground immediately beneath and to the side of it, to the whole of the field and surrounds was obvious by the change of the bill from below the horizontal to above horizontal, as the bird held its head up. There were usually no grades in between: the bill when walking was either held at varying angles below the horizontal, towards the ground, or it was quickly brought up until above the horizontal as the head was brought up, held, and then quickly returned below horizontal once more as the head was lowered to continue searching for food.

This discrimination was in practice most difficult for the jackdaw, possibly because of a combination of the comparative shortness of the bill and the grey nape; however, the distinction between look up and look food was sometimes not unambiguous for the other species also, and data from such birds were discarded. The low variance found for all species (that for the jackdaw does not differ from the other species) suggest that the distinction the observer was making was a valid one.

The recording method used to collect the data was an instantaneous time sample with a five second interval. On hearing a bleep the observer decided which of several behavioural categories the bird was currently engaged in (see list in M.8); this was spoken into a cassette recorder. The proportion of the total time spent looking up could then be calculated and expressed as a percentage. Any birds which spent in excess of 5% of total time in
activities other than foraging or looking up were not included in the analyses reported here.

Instantaneous time sample was the only practicable recording method available for this behaviour. Criticism of the method and an evaluation of the adequacy of the particular time interval used, given mean bout length duration of the behaviour, is reported in Waite (1978). It was concluded that the behaviour was adequately described by the recording method employed.

M.12 Statistics

M.12.1 Descriptive Statistics

M.12.1.1 Niche Overlap Index

The overlap index of Schoener (1968a) was used:

\[
\text{Alpha}_{ij} = 1 - 0.5 \sum_{x=1}^{n} |P_{i,x} - P_{j,x}|
\]

where \( P \) is the proportion of species \( i \) or \( j \) utilising resource state \( x \), and \( n \) is the total number of states along the resource gradient. Alpha_{ij} is the area common to the utilisation curves of the two species \( i \) and \( j \) along the resource gradient:
This formula is not a competition coefficient since it does not take into account resource availability (e.g. Hurlbert 1978, 1982, Schoener 1974a & b). Since availability could only be accurately measured for habitat in the present study, overlap indices are used in the thesis and not competition coefficients. Given the nature of the measurements, Schoener's index was considered the most suitable available. Linton et al. (1981; see also Abrams 1982) have demonstrated by simulation that Schoener's is the most accurate of the indices available when true overlap is between 7 and 85% (as almost all the values are in the thesis), and as accurate as the others when overlap was less than 7% (as some of the values are in the thesis). Schoener's index is more erratic when true overlap exceeds 85%, but few values in the thesis (and no important ones) exceed this.

Matrices of pairwise overlaps for four species are
Presented along with pictorial representation of overlap by dendogram. The true overlap is used for the initial species pair (or pairs), then higher-order relationships are calculated as average overlaps between the remaining species and those already entered onto the dendogram (see e.g. Cody 1974a).

M.12.1.2 Niche Breadth

An index of the variability of each species utilisation of a particular resource gradient was calculated from the formula of Levins (1968):

\[ B_i = \frac{1}{\mathbf{E} \pi_i \mathbf{x}^2} \]

where \( B_i \) is the niche breadth of species \( i \) and \( \pi_i \mathbf{x} \) and \( n \) are as defined for equation (1). Since the maximum of this index will vary depending on the value of \( n \), a standardised value of \( B \) was calculated (see e.g. Hespenheide 1975) as:

\[ B_{\text{norm}} = \frac{(B - 1)}{(n - 1)} \]

This index varies between 0 (extreme specialist) and 1 (extreme generalist).
M. 12. 1. 3 Electivity

As an indicator of selection for the different crop types available, index four of Cock (1978) was used:

\[(4) \quad C_{i,x} = \frac{N_{i,x}}{N_{i,y}} \times \frac{A_x}{A_y}\]

where \(C_{i,x}\) is the index of electivity for crop \(x\) by species \(i\), \(N_{i,x}\) the number of birds of species \(i\) on crop \(x\), \(N_{i,y}\) the number of birds of species \(i\) on all other crops available, \(A_x\) the area of crop \(x\) and \(A_y\) the area of all other crops available. This index was considered to be the most appropriate for the present study of those assessed by Cock (1978) since the value of the index is not affected by the relative abundances of the different crops or birds, so \(C\)'s for different crops may be directly compared both within and between the different bird species.

Since the basic index will vary from 1 to 0 for avoidance, but from 1 to virtual infinity for preference, the index was transformed as follows:
(5) If: \[
\frac{N_{i,x}}{N_{i,y}} / A_x / A_y \]
then: \[
C = -2 \left(0.5 - \left(1 / \left(1 + \left[\frac{N_{i,x}}{N_{i,y}} / A_x / A_y \right]\right)\right)\right)
\]

(6) If: \[
\frac{N_{i,x}}{N_{i,y}} / A_x / A_y \]
equals unity
then: \[
C = 0
\]

(7) If: \[
\frac{N_{i,x}}{N_{i,y}} / A_x / A_y \]
is greater than unity
then: \[
C = 2 \left((1 / \left(1 + \left[\frac{N_{i,x}}{N_{i,y}} / A_x / A_y \right]\right)\right) - 0.5
\]

This gave an easily interpretable scale ranging from -1 to +1, with -1 indicating complete avoidance, 0 no selection, and +1 complete preference.

In addition, figure 1.4.3 plots:

(8) \[
\frac{N_{i,x}}{N_{i,y, total}} / A_x / A_{total}
\]
so that selection may be illustrated in conjunction with relative abundances of bird numbers and crop area. The graph is divided into areas of different strengths of choice — points falling within the same segment indicate similar choice of the crop type, whilst the position of the points relative the x and y axes indicate the actual abundance of crops and birds using them.

The value of such indices as descriptive statistics may be reduced if certain conditions occur. Firstly, a single very large flock recorded on a rare habitat could give a false impression of strong choice for that crop. Secondly, if a crop is proportionally very abundant, it will be difficult for selection to be demonstrated even if it occurs. However, in the present study, the index used found rare crops to be avoided, and the most abundant crop (permanent pasture) represented less than 50% of the total grass types available. Thus neither of these potential situations affected the value of the index as a descriptor of habitat selection in this study.

M.12.1.4 Mean Crowding

Lloyd's (1967) mean crowding index was calculated as:

\[
(9) \quad x = \bar{x} + ((s^2 / \bar{x}) - 1) \ast (1 + (s^2 / N \bar{x}))
\]
where $x$ is the particular earthworm sample mean, $s^2$ the variance, and $N$ the sample size. The index is used when computing Iwao's Patchiness Regression (see e.g. Southwood 1978) to describe the dispersion characteristics of an invertebrate type from a series of samples at different population densities. The index will equal nought when the variance is equal to the mean (i.e. when the distribution does not deviate from a random (Poisson) distribution). Positive values imply aggregation, negative ones over-dispersion.

**M.12.2 Analytical Statistics**

**M.12.2.1 Data Checking and Transformation**

Many of the behavioural variables violated the assumptions of normality, homogeneity of variance, or linearity of relationship, on which parametric statistical tests are constructed. Harris (1975) gives the following limits to the robustness of such tests to violation of these assumptions:

(a) If the test is based on the product-moment correlation coefficient $r$, then any unimodal $X$ and $Y$ population for a sample size greater than 10 is acceptable; if the test is based on $t$ or $F$, even bimodal distributions are acceptable as long as 2-tailed tests of
significance are used.

(b) The ratio between the smallest and largest sample variances should not exceed 20:1.

(c) The relationship between Y and residual Y scores should be linear.

(d) The ratio between the largest and smallest sample size should not exceed 4:1.

(e) Total degrees of freedom for the error term should exceed nine.

Harris states that when violations of assumptions are close to these bounds, then a test at the 5% level might actually come close to a 10% probability of yielding a false rejection of the null hypothesis. This is the case for univariate tests. The only difference between univariate and multivariate tests relevant to this issue is whether the process of linear combination of variables to maximise multiple r (or t or F) could be an additional source of nonrobustness. Harris concludes that this is unlikely.

Checking (d) and (e) for each analysis in the present study was straightforward. Tests of (a) to (c) for each variable were then conducted. In addition, for the variables to be entered into the discriminant function ana-
lyses, both parametric and non-parametric univariate analyses of variance were conducted. Variables failing to meet the criteria demanded by (a) to (c), or which showed badly different p levels on the parametric and non-parametric difference tests, were transformed. Which transformation was suitable was determined by examining the relationship between the sample mean and variance or standard deviation (see e.g. Sokal & Rohlf 1969 or Ferguson 1976).

The transformed variables were checked again. Variables which still failed to meet the criteria set were dropped from analyses involving parametric tests. These mainly involved very infrequent behaviours or those which were not recorded at all for at least one of the species. This meant that several variables which were clearly biologically important in separating the species could not be included in statistical tests of separation - however, these variables were retained when calculating the descriptive statistics of niche overlap and breadth.

M.12.2.2 Discriminant Function Analysis

The program used was that provided by the SPSS package (Nie et al. 1975). A stepwise algorithm was adopted with the selection criteria being to minimise Wilk's lambda. None of the variables entered into analyses were
Methods

intercorrelated beyond 0.50. Discriminant analysis is a technique (rather similar to multiple regression in concept) which combines a set of dependent variables to maximise the difference between a number of groups (rather than maximise the multiple correlation of a group of predictor variables with a dependent variable). It is of particular use in the present thesis where species take several different prey types from several different microhabitats, and may differ from one another on one or several of these dimensions. It is the most appropriate test available of the null hypothesis of equal use of the set of resources by the four species, and is, in its initial stage, simply a multivariate analysis of variance (see e.g. Harris 1975).

Pimentel & Frey (1978) advised against the use of a stepwise procedure for the kind of situation existing in the present study. However, direct-inclusion analyses entering all variables simultaneously made only slight changes to eigenvalues and the percentage of variation explained by each derived discriminant function, and no change to the significance of Wilk's lambda. There were only slight changes to the classification table. However, some of the variables retained had low loadings (< 0.20) on each of the derived functions or they loaded high on the final function in a way which was made biological interpretation of the function difficult. Their exclusion by the stepwise procedure indicates that their partial F ratios
were less than unity - i.e. they were not helpful in successful discrimination between the species in any meaningful way.

One assumption of this multivariate parametric test is that the sample variance-covariance matrices are equal. It was expected that this would be violated (it was) since many similar studies have shown that some species have wide (generalists) and some narrow (specialists) niche breadths (e.g. see Lack 1971, Morse 1971, Schoener 1971). Strictly speaking this renders the test of the null hypothesis of equality of the group centroids invalid. However, the use of discriminant analysis in this situation is justified because of the robustness of the method, especially following appropriate transformation of variables (see M.12.2.1).

In addition Green (1974) gives two more justifications - proceed if each derived function can be interpreted in a biologically meaningful and consistent manner via the pattern of variable loadings; and if each derived function provides significant separation between two or more species consistent with the biological interpretation of the function. Both these proved to be the case in the present study.

M.12.2.3 Path Analysis

Path analysis is introduced in Nie et al. (1975), and
other references are cited in section 2.4.2 below.

Reciprocal pathways in causal path analysis require special treatment compared to simple models which are analysed by ordinary multiple regression analysis. The method of two-stage generalized least squares regression was employed utilising the SPSS routine G3SLS (UMRCC 1979).

M.12.2.3a Other Statistical Tests

Explanation of other tests may be found in standard texts (e.g. Ferguson 1976, Sokal & Rohlf 1969). The use of gamma and partial gamma in the analysis of frequency data is discussed in Nie et al. (1975). Cluster analysis is discussed in, for example, Dixon (1975) and Wishart (1978).

M.12.2.4 Tests of Invertebrate Dispersion

The variance-mean ratio method tests for deviation from a Poisson distribution and may be found described in e.g. Southwood 1978. The formula is:

\[
D = \frac{\text{variance} \ (n - 1)}{\text{mean}}
\]

where \( n \) is the number of sample units and \( D \) is distributed as chi-square with \( n - 1 \) degrees of freedom. The signifi-
cance of deviations from the null hypothesis of a random
distribution can therefore be obtained. Although the use
of tests of biological dispersion based on deviation from a
Poisson or approximation to a negative binomial series have
recently been criticised (e.g. Taylor et al. 1979, Getty
1981) no viable alternative method was available.

The method for testing for coherence of clumping in
the regular 6x7 grids was based on a method described in
Pielou (1977) p.144f. Unfortunately this test is conserva-
tive since it demanded the classification of cores only as
'dense' or 'sparse' such that a fairly equal division of
cores into dense and sparse resulted. The number of dense-
dense joins is then counted and compared to the mean and
variance of the distribution of the number of dense-dense
joins on the null hypothesis of a random mingling of dense
and sparse cores. Thus the test made no distinction
between the following two distributions (taking values of
greater than one as dense) even though (a) clearly has a
more coherent pattern of clumping of higher and lower
actual values than (b):
Actual distribution:

(a) 4 4 3 0 0    (b) 4 2 3 1 0
1 3 0 1 1    1 2 0 1 0
2 2 0 0 2    2 3 0 0 4

Distribution for significance test:

(a) D D D S S    (b) D D D S S
S D S S S    S D S S S
D D S S D    D D S S D

M.12.3 Statistical Routines

Data were analysed by the following computer packages
- ELIB at the University of Keele Computer Centre; BMEDP (Dixon 1975) at the University of Manchester Regional Computer Centre; CLUSTAN 1C (Wishart 1978) at the University of Nottingham Computer Centre; Nottingham Unix Statistical Routines at the Department of Psychology, University of Nottingham; and SPSS (Nie et al. 1975) at UMRC and the University of Nottingham Computer Centre. Additional programs were written by Dr. D.F. Chantrey of the Department of Psychology, University of Keele, and by the author.
PART ONE

BEHAVIOUR of FOUR CORVID SPECIES in SYMPATRY
1.1.1 Four Corvid Species - a Guild?

The first part of the thesis describes the winter behavioural ecology of four Corvid species and the overlap in utilization of the available resource base between them. The four sympatric species occupy an apparently structurally simple environment (open agricultural land) in a similar way (by foraging mainly for agricultural foods or for invertebrates on the ground), and have done for a considerable period of time, more or less stably. This situation means that if the species differ in their use of the available resources, then this must be by some behavioural means other than a simple choice of (for example) gross habitat difference (such as deciduous or coniferous woodland), or vertical height of foraging (ground, trunk, canopy), etc. Alternatively (or in addition), the species might overlap but show direct behavioural means of denying other species access to the resources; or of allowing themselves access to resources despite another species' attempts to exclude them. Thus this part of the thesis seeks to link behavioural interactions between four sympatric Corvid species (carrion crow, rook, jackdaw and magpie) to ecological conditions.
Data are only presented for the four Corvid species commonly foraging on open agricultural land in lowland southern Britain. There are of course other birds and animals which inhabit this environment and which may overlap to varying extents with these species. The winter bird fauna of Keele (excluding exclusively aquatic birds) were classified (with reference to Witherby et al. 1938 and other standard texts) on nine habitat and 11 diet variables:

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grassland</td>
<td>Live Vertebrates</td>
</tr>
<tr>
<td>Plough</td>
<td>Carrion</td>
</tr>
<tr>
<td>Cereal</td>
<td>Human Waste</td>
</tr>
<tr>
<td>Wood Floor</td>
<td>Earthworms</td>
</tr>
<tr>
<td>Trees or Shrubs</td>
<td>Above Soil Surface Invertebrates</td>
</tr>
<tr>
<td>Hedges</td>
<td>Below Soil Surface Invertebrates</td>
</tr>
<tr>
<td>Long Grass or Scrub</td>
<td>Grain</td>
</tr>
<tr>
<td>Damp Meadows</td>
<td>Wild Seeds</td>
</tr>
<tr>
<td>Water Margins</td>
<td>Fruits</td>
</tr>
<tr>
<td></td>
<td>Nuts</td>
</tr>
<tr>
<td></td>
<td>Leaves</td>
</tr>
</tbody>
</table>

Each species was simply coded on each variable depending on whether it utilised that resource frequently (2), occasionally (1), or not at all (0). In addition each species was coded on a variable with the three levels of diurnal, crepuscular or nocturnal.

Figure 1.1.1 illustrates the results of a cluster analysis (using Ward's hierarchical method of linkage with standardised variables) of the species on these gross classifications. Of course similarity between species will
Figure 1.1.1

Dendogram of relationships between the winter bird fauna of Keele, classified on one temporal, nine habitat, and eleven diet variables.
depend on the relative proportion of utilisation of different habitats and prey, and the gross level of classification employed here would be replaced by measures of the exact proportion of time spent on each habitat and the proportion of each food-type in the diet, were precise classification required. However the dendogram serves to indicate that the four Corvid species concerned form a cluster early on which is well separated from any other cluster. (*) The grouping of these coexisting species which used resources in a similar fashion, and where the largest distance between any two members in resource use was much less than the distance between any group member and other clusters of species, agrees with the common definition of a 'guild' (e.g. Cody & Walter 1976, Joern & Lawlor 1981, Root 1967).

1.1.2 Competition and Coexistence (1): Conditions

Whether the four species form a co-evolved community where competition past and present has caused the species to occupy their present niches, or whether separate evolution to different ecological conditions preadapted them to

(*) Overlap is also possible with some of the larger vertebrates, particularly fox (Vulpes fulva) and badger (Meles meles) which are known to take invertebrates, particularly large earthworms, though they are mainly nocturnal in habit and take prey from woodland as well as open land (e.g. Kruuk 1978).
1.1 Introduction

the possibility of coexistence in sympathy, is unknown and is not an argument which will be investigated here (see e.g. Connell 1975, 1980, Diamond 1978, Wiens 1977; a rather similar topic, the investigation of weak and strong function, is considered in some detail in chapter 2.2).

Strictly speaking, the following conditions must be satisfied before one can talk of present competition, rather than coexistence:

(1) "Extensive" overlap in resource use should exist.

(2) At least one species has a major impact on resource abundance.

(3) At least one species is resource-limited (rather than, for example, kept below the carrying capacity of the environment by predation).

(4) The abundance of species A is negatively correlated with the fecundity of species B.

(5) Population density of species A is negatively correlated with that of species B.

MacArthur & Levins (1967) and May & MacArthur (1972) have formulated boundaries to the overlap between species permissible for stable coexistence. However, it has been pointed out that resource-use overlap coefficients based on the amount of similarity between the proportional use of
resources by two species are not necessarily good indicators of competition since overlap could actually be total, and yet coexistence stable, if species A exploited one part of the resource spectrum better, and species B exploited a separate part of the resources better (Abrams 1975, Colwell & Fuentes 1975, Schoener 1974b). Schroder & Rosenweig (1975) have added another potential (though not well documented) criticism of the concept of limiting similarity—that tolerable and optimal overlap may differ, and that one may not, therefore, necessarily expect to find species coexisting at tolerable overlap.

Condition (1) is quantified and examined in the following chapters for the four Corvid species under consideration. Condition (2) has not been quantified but is almost certain to occur. It certainly occurs for stubble grain in winter (Peare et al. 1974) and is likely to occur for invertebrates since almost all are reproductively inactive during winter. Bengtson et al. (1976) have shown by exclusion experiments that golden plovers (*Pluvialis apricaria*) reduced earthworm densities in an Icelandic hayfield by about 50% in only three weeks, and D.B.A. Thompson (pers. comm.) has found comparable results in lowland Britain in winter.

Condition (3) must occur since if resources are super-abundant then there can be no competition even between
species which overlap completely. Resources of many temperate birds are limiting in winter. (*) However, Holyoak (1971) has shown that although mortality is quite high in winter for each of the Corvid species in question, mortality in the breeding season is higher, and also higher in the summer for rooks. Earthworms, a major prey type of rooks and carrion crows (chapter 1.4), are at higher levels in winter than summer, and winter sees an immigration into lowland Britain of grassland foraging Corvidae, Turdidae and Charadridae from Europe, and movements from upland and coastal Britain of Corvidae, Laridae, Charadridae and Scolopacidae. This may be indicative of a relative abundance of prey. However, numbers of birds in the study are changed greatly over the winter in response to climatic conditions (appendix 8) as did earthworm densities in the soil. In addition, densities of all other invertebrate types were lower in winter than at any other season (appendices 1 and 8). Thus the sometimes abundant prey source of earthworms probably fluctuated between levels of scarcity and abundance, and the levels of other invertebrate prey were almost certainly limiting. Jackdaws and magpies did not utilise earthworms much (chapter 1.4) and thus at least

two of the four species were probably resource limited.

Two other additional mechanisms rather than absolute level of prey abundance may have kept bird numbers below the carrying capacity of the environment. The first is high levels of predation on the coexisting species (e.g. Connell 1975, Harriston 1980, Lawton & Strong 1981, Wise 1981). This is highly unlikely to be the case for any of the Corvids in the areas used for data collection in this study (more discussion on this point may be found in chapter 2.2 below), and in fact the references cited above were all invertebrate examples.

A second reason could be that the A-territoriality of carrion crows in particular, and magpies to a lesser extent (see next chapter), which persists in the winter, may mean an excess of food available for territorial members of these species if territory size is governed by the maximum need during the rearing of a brood. The increased amount of food needed then will be offset by increased summer abundance, but it is unknown whether the combined effect is to cause less or more prey than is necessary for survival to exist in the winter territory. The fact that some territories of carrion crows support extra birds in winter (next chapter) may suggest that there is an excess of food - but the fact that some territories do not hold extra birds and others hold more than one, coupled with changes
(usually an extension) of home range size in winter, suggests that range size and the numbers of birds within a territory in winter is dependent on prey abundance. Magpie A-territoriality is more likely to break down in winter and the gregarious behaviour of rooks and jackdaws, with shifting flock size and no overt territoriality (next chapter), suggests that the social system of these three species is unlikely to reduce the effects of resource limitation.

There is no direct evidence from this study on conditions (4) or (5) but evidence from other studies on these Corvid species is described below.

1.1.3 Competition and Coexistence (2): Behaviour

Given a degree of overlap between two species in resource utilisation, various behavioural mechanisms are possible which may modify the overlap or the resulting impact of one species on the other. A species may change its foraging behaviour to alter overlap (many references - example review in Morse 1980, references also listed in chapter 2.2 below). If it is behaviourally dominant it may use agonistic behaviour to reduce another species' contact with, or foraging success on, the resource in question (again, many references; see Morse op. cit. for a review; see e.g. Case & Gilpin 1974, Gill 1974, and Wolf 1978 for theoretical considerations of when to expect such
behaviour; see e.g. Stamps 1977 for a demonstration that the amount of aggression can vary in proportion to the amount of overlap between species). In the extreme case a species may permanently exclude other species by interspecific territoriality (see Norse op. cit. for review of occurrences and Dow 1977b for an extreme example; see e.g. Cody 1973 for a consideration of evidence that interspecific territoriality occurs predictably under certain conditions of overlap and species' territory size; see Gill & Wolf 1979 for the best example of proven adaptive consequences of interspecific territoriality; but see e.g. Murray 1971, 1981 for an alternative consideration of most interspecific territoriality as a non-adaptive trait. Also see e.g. Minot 1981 for a demonstration that, despite high overlap in resource use and a proven deleterious effect of one species on a second's breeding success, yet interspecific territoriality did not occur even though it resulted in individual pairs of one species being in more direct food competition with individual pairs of the other species than with other conspecific pairs, since both species were intraspecifically territorial).

If a species is behaviourally subordinate, it may avoid contact with the other species or use behavioural mechanisms to reduce the effect of overlap - for example, grouping to allow feeding in the presence of the other species through a "strength in numbers" effect, or a
"selfish herd" effect through dilution of attack-rate (see list of references in chapter 2.2), or various forms of cryptic or stealthy avoidance in an attempt to escape detection.

Almost no data have been published on modification of foraging behaviour in the presence or absence of the different species under consideration here, and little quantification of overlap in resource use (though see Nøst 1980a, Loman 1980b; these studies are described below). True interspecific territoriality has never been reported between the four Corvid species under consideration, though varying degrees of aggression within mutually exploited habitats has (e.g. Baeyens 1981, Bossemèt et al. 1976, Nøst 1980a, Roell 1978, Rowley 1973, Vines 1981, Waite 1978).

The aggression reported was almost entirely directed by carrion crows against the three other species. Bossemèt et al. 1976 and Roell 1978 described some evidence that rooks and jackdaws demonstrated a "strength in numbers" method, and magpies behaviour designed to escape detection or the receipt of aggression, in order to forage within carrion crow territories. Waite (1978) however failed to
demonstrate an advantage of flocking by any of these species in terms of a reduction in the effect of carrion crow aggression, nor any behaviour by magpies to attempt to avert carrion crow aggression by avoiding detection.

This part of the thesis quantifies the winter niches of these four species, predicts what short-term behavioural mechanisms might be expected to occur on the basis of this quantification, and what the long-term effects on social organisation might be, and describes the actual behavioural interactions observed and their consequences.
The thesis presents data on four members of the family Corvidae:

- Carrion (or Eurasian) Crow, *Coryus corone*
- Rook, *C. frugilegus*
- Jackdaw, *C. rossdula*
- Magpie, *Pica pica*

General introductions to the natural history of these species are available in Coombs (1978) and Goodwin (1976). This chapter introduces the species and summarises aspects of their morphology, distribution and social organisation that are relevant to later chapters. Some of the material in this chapter will be described only briefly here, but the information is more conveniently presented together than scattered throughout the rest of the text. Reference will be made back to this chapter.

1.2.1 Morphology

The four species are large passerines with a walking gait, though each species hops occasionally, the magpie perhaps more than the three *Coryus* species. Bills are large and heavy. The carrion crow and magpie have tearing edges to the upper mandible. The rook has a comparatively longer and thinner bill, whilst the jackdaw's is shorter
1.2 The Birds

and stubbier. The carrion crow is the largest of the four, with the rook averaging about a fifth lighter. The jackdaw is slightly heavier on average than the magpie, but has a shorter bill.

These characteristics are illustrated in figure 1.2.1 and measurements are summarised in table 1.2.1. Table 1.2.1b indicates that these four species form two groups (carrion crow-rook and jackdaw-magpie) in terms of size when a number of measurements are taken, rather than being equally spaced in size. Figure 1.2.2 illustrates that the three Corvus species have similar ratios of wing-to-tarsus, with Pica pica differing; but that the ratio of bill length-to-depth does not follow a similar generic pattern. These characteristics are likely to be implicated in the foraging behaviour of the birds which is to be discussed later (e.g. see Karr & James 1975).

1.2.2 Distribution

The three Corvus species are old world, north and (mainly) temperate birds. Pica pica has a similar old world distribution but also occurs in western North America at similar latitudes. The extent of north-south ranging of the species varies however, in ways which will be discussed later (figure 1.2.3).
Figure 1.2.1

Portraits of the four Corvid species with which the thesis is mainly concerned

From Goodwin (1976)

<table>
<thead>
<tr>
<th>Carrion Crow</th>
<th><em>Corvus corone</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td><em>C. frugilegus</em></td>
</tr>
<tr>
<td>Jackdaw</td>
<td><em>C. monedula</em></td>
</tr>
<tr>
<td>Magpie</td>
<td><em>Pica pica</em></td>
</tr>
</tbody>
</table>
Table 1.2.1

Morphological characteristics of four corvid species

Data are mean values from sources with the best available sample sizes and/or the most appropriate population samples. (Unfortunately indices of variability were not always given.)

Ratios in (b) were calculated by dividing the value for the larger species by the smaller for each paired comparison, and then averaging the ratios from several different morphological characteristics. The ratios for each individual characteristic are given in appendix six.

(a) Data for Four Species

<table>
<thead>
<tr>
<th></th>
<th>Carrion Crow</th>
<th>Rook</th>
<th>Jack-Caw</th>
<th>Magpie</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Weight</td>
<td>556gm</td>
<td>458</td>
<td>246</td>
<td>227</td>
<td>Seel (1976)</td>
</tr>
<tr>
<td>Length (minus tail)</td>
<td>561mm</td>
<td>303</td>
<td>206</td>
<td>227</td>
<td>Coombs (1978)</td>
</tr>
<tr>
<td>Tail</td>
<td>185mm</td>
<td>166</td>
<td>132</td>
<td>230</td>
<td>Witherby et al. (1938)</td>
</tr>
<tr>
<td>Wing</td>
<td>324mm</td>
<td>308</td>
<td>235</td>
<td>187</td>
<td>(as tail)</td>
</tr>
<tr>
<td>Tarsus</td>
<td>59mm</td>
<td>53</td>
<td>44</td>
<td>49</td>
<td>(as tail)</td>
</tr>
<tr>
<td>Bill Length (*)</td>
<td>52.5mm</td>
<td>56.9</td>
<td>33.1</td>
<td>37.0</td>
<td>(*)</td>
</tr>
<tr>
<td>Bill Depth (**)</td>
<td>19.0mm</td>
<td>17.5</td>
<td>13.5</td>
<td>13.9</td>
<td>(**)</td>
</tr>
</tbody>
</table>

(*) Base of skull to tip; references: Green (1981), Hogstedt (1980b), Olsson & Persson (1979), Picozzi (1975)

(b) Size-ratios between Four Species

Average of: Weight
Length (minus tail)
Tail
Wing
Tarsus
Bill Length
Bill Depth

| Average | Ratio | Ratio Between With 3 Species Pairs Other |
|---------|-------|----------------------------------------|------------------|
| Species | C     | R          | J       | M |

| Carrion Crow | 1.55 | - |
| Rook         | 1.38 | 1.22 |
| Jackdaw      | 1.47 | 1.73 1.45 | - |
| Magpie       | 1.46 | 1.70 1.47 1.21 | - |

Average of: Wing
Tarsus
Bill Length
Bill Depth

| Average | Ratio | Ratio Between With 3 Species Pairs Other |
|---------|-------|----------------------------------------|------------------|
| Species | C     | R          | J       | M |

| Carrion Crow | 1.32 | - |
| Rook         | 1.28 | 1.08 |
| Jackdaw      | 1.33 | 1.43 1.38 | - |
| Magpie       | 1.31 | 1.43 1.38 1.13 | - |
Figure 1.2.2

Relationship between morphological features connected with foraging

The configurations of wing-to-tarsus and bill length-to-depth are often important indicators of differences in foraging techniques (e.g. Karr & James 1975).

Replacing Wing measurements by Body Weight gives a qualitatively similar picture.
Within Britain, the Eurasian crow is represented by its two races, *Corvus corone corone* in the south, and *C. corone cornix* in the north and west. There are few areas where this species was not recorded breeding during the period 1968-72 (figure 1.2.4b). The other three species are restricted to varying degrees in northern and western upland areas, whilst the magpie is absent from parts of East Anglia. These distributions show some relation to the distribution of cattle and sheep (figure 1.2.4a), relationships which will be analyzed later.

In the study areas these four species were sympatric and common. The data in this section, except where specifically stated otherwise, come entirely from the main study area at Keele, an area of mixed farmland with cattle the predominant 'crop' (figure 1.2.4c).

### 1.2.3 Social Organization

Waite (1978) has indicated some links between social organisation and ecological factors within the British Corvidae. The social organisation of the species in the study area in winter is described here.

**Carrion Crow**

Breeders retain exclusive A-type (Hinde 1956)
Figure 1.2.3

World breeding distribution of four corvid species

From Goodwin (1976)
**Corvus corone**
Carrier/house crow

**Corvus frugilegus**
Rock
d

**Corvus monedula**
Jackdaw
Canvas Jackdaw
Corvus c. caurinus

**Pica pica**
Magpie

P. hudsonia occurs in western North America at similar latitudes.
British distribution of four corvid species, the study areas, and some relevant agricultural crops

(a) Distribution of oats and wheat, sheep, and dairy or beef cattle (from Anon. 1976).

(b) Confirmed breeding distribution in 1968-72 (from Sharrock 1976).

(c) Location of study areas with predominant farming types (from Anon. 1976)
territories, though the size and therefore overlap of home ranges may increase, and territorial birds may rarely join flocks at abundant food sources. 'Third' (and infrequently fourth or fifth) birds - often juveniles of the previous breeding season (Charles 1972, Loman 1980a, Tompa 1975, this study appendix 8), but sometimes adult birds of unknown relationship persistently intruding from a nonbreeding flock (Charles 1972), are resident in a proportion of territories in winter. Birds without access to territories appear in flocks which mainly inhabit areas unsuitable for the establishment of breeding territories but which intrude onto the territorial area to varying extents. Both the territorial and non-territorial birds normally fly to communal roosts each evening. In the main study area birds tended to forage mainly on their own on both grassland and arable. Small flocks (6-20 birds) occurred at low frequency on arable, but most of the study area was divided between territorial pairs or family groups (table 1.2.2 and later discussion).


Rook

Overlapping group home ranges, not apparently defended
Table 1.2.2

Proportion of birds found foraging at different flock sizes on grassland and arable during routine censuses of the main study area at Keele in winter.

Percentages within each species and habitat type.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Flock Size</th>
<th>1</th>
<th>2</th>
<th>3-5</th>
<th>6-20</th>
<th>21-40</th>
<th>&gt;40</th>
<th>Total N of Birds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrion Grass</td>
<td></td>
<td>46.4</td>
<td>27.5</td>
<td>23.2</td>
<td>2.9</td>
<td>-</td>
<td>-</td>
<td>156</td>
<td></td>
</tr>
<tr>
<td>Carrion Arable</td>
<td></td>
<td>48.6</td>
<td>35.1</td>
<td>5.4</td>
<td>10.8</td>
<td>-</td>
<td>-</td>
<td>85</td>
<td></td>
</tr>
<tr>
<td>Rook Grass</td>
<td></td>
<td>9.3</td>
<td>11.6</td>
<td>17.4</td>
<td>30.2</td>
<td>19.8</td>
<td>11.6</td>
<td>996</td>
<td></td>
</tr>
<tr>
<td>Rook Arable</td>
<td></td>
<td>-</td>
<td>16.7</td>
<td>16.7</td>
<td>41.7</td>
<td>8.3</td>
<td>16.7</td>
<td>223</td>
<td></td>
</tr>
<tr>
<td>Jackdaw Grass</td>
<td></td>
<td>10.8</td>
<td>16.2</td>
<td>16.2</td>
<td>35.1</td>
<td>16.2</td>
<td>5.4</td>
<td>441</td>
<td></td>
</tr>
<tr>
<td>Jackdaw Arable</td>
<td></td>
<td>18.2</td>
<td>18.2</td>
<td>9.1</td>
<td>27.3</td>
<td>9.1</td>
<td>10.2</td>
<td>214</td>
<td></td>
</tr>
<tr>
<td>Magpie Grass</td>
<td></td>
<td>50.0</td>
<td>29.6</td>
<td>13.0</td>
<td>7.6</td>
<td>-</td>
<td>-</td>
<td>160</td>
<td></td>
</tr>
<tr>
<td>Magpie Arable</td>
<td></td>
<td>43.8</td>
<td>6.3</td>
<td>25.0</td>
<td>25.0</td>
<td>-</td>
<td>-</td>
<td>54</td>
<td></td>
</tr>
</tbody>
</table>
1.2 The Birds

(Coombs 1961, P.T. Green pers. comm., Patterson et al. 1971). Large communal roosts containing birds from more than one group area. There is some evidence that juveniles may at times form separate feeding groups from adult birds (P.T. Green pers. comm., Patterson et al. 1971). In the main study area birds tended to forage most frequently in flocks of 6-20 birds on both grassland and arable, with only c.20% of birds being recorded foraging on their own or in pairs. Solitary birds were not recorded on arable land during routine censuses (table 1.2.2).

(Coombs 1961, Feare et al. 1974, Green 1982, Patterson et al. 1971, this study.)

Jackdaw

Apparently similar to the rook, but studies of individually marked birds in Britain are lacking. In Holland breeding pairs usually foraged together in winter, and birds from the same nesting colony tended to forage together, in overlapping areas with other groups (Roell 1978). Communal roosts formed. In the main study area jackdaws, as rooks, occurred most frequently in small flocks of 6-20 birds on both grass and arable. Somewhat fewer large flocks, and more solitary birds and pairs, were recorded than for rooks (table 1.2.2).

(Coombs 1961, Gyllin & Kallander 1976, Roell
As with the carrion crow, breeders tend to retain exclusive A-type territories, although home range size and overlap tends to increase. Territorial birds leave their territories and join flocks perhaps more frequently than carrion crows (Vines 1981). There is no evidence of 'third birds' resident in territories in winter. Non-breeding flocks partly inhabit areas unsuitable for breeding and partly trespass on territorial areas - these intrusions elicit less frequent agonistic response in winter (Vines 1981) and in general appear to elicit less response from the resident birds than do the corresponding intrusions in the carrion crow. Birds roost communally but these roosts appear to be smaller than those of the other three species; these roosts usually contain only magpies whilst the other three species frequently roost near one another. In the main study area most birds occurred solitarily or in pairs on grassland, whilst on arable birds were either solitary or in flocks. Magpies were more frequently recorded in flocks in the main study area than were crows, but as with the latter species, these flocks were smaller than those of the rook and jackdaw (table 1.2.2).

(Baeyens 1979, 1981, Gyllin & Kallander 1977b,
Hollyoak 1974b, Vines 1981, this study.)
This chapter, like the previous one, collates information which will be referred to in later chapters but which may not be fully analysed here.

1.3.1 Habitats

The areas of lowland Britain used for the study represent a mosaic of open agricultural land intersected with hedges, small copses (both deciduous and coniferous), with the occasional small village or other built-up area. Since all four species only rarely used habitats other than the agricultural land for foraging during the winter (section 1.4.1), only the availability of crop types within this habitat and non-agricultural grassland (sports fields, verges, parks), and the prey within them, will be considered.

There was more grassland available at Keele than arable, both in terms of number of fields and total area of crops. The proportion of arable fields providing cereal prey was higher at the beginning of winter than at the end, by which time most stubble fields had been ploughed and the winter sowings had sprouted far enough to exhaust their seed contents. Ploughed fields provided high invertebrate
intake rates at the time of ploughing, but were hardly used at all by birds after this (section 1.4.1), probably a reflection of their low levels of permanently available invertebrate prey (see below section 1.3.4). Within the grassland available, fields grazed by stock were more abundant than ungrazed fields. Table 1.3.1 summarises average relative crop availability over the study period at Keele, while figure 1.3.1 illustrates the patchwork nature of the crops available at Keele, although most of the arable fields were available in a block at the north-west of the area.

1.3.2 Climate

Certain climatic factors have important effects on prey availability which will be referred to in later chapters. Figure 1.3.2a presents summaries of meteorological data from Keele for the years of the study, and figure 1.3.2b presents a mean annual wind rose for 12 years data. Table 1.3.2 gives the mean number of frozen soil days for the winter months. As might be expected, temperatures and sun hours follow seasonal patterns, but rainfall did not vary consistently with season. However, higher temperatures and transpiration rates in summer led to a seasonal pattern of soil moisture content. Winters during the study differed in their severity - 1980-81 was the mildest,
Table 1.3.1

Crop availability in winter at Keele, Staffordshire.

Percentage of each crop available at the beginning, end and on average during the winter.

Since the area of each crop available was very closely correlated with the number of fields of each crop ($r = 0.97$) only the proportion as number of fields available is given in the table.

<table>
<thead>
<tr>
<th></th>
<th>November</th>
<th>February</th>
<th>Nov-Feb</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ARABLE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barley Sown</td>
<td>0.5</td>
<td>0.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Barley Stubble</td>
<td>21.5</td>
<td>2.2</td>
<td>11.6</td>
</tr>
<tr>
<td>Oat Stubble</td>
<td>1.9</td>
<td>1.3</td>
<td>1.4</td>
</tr>
<tr>
<td>Wheat Sown</td>
<td>6.5</td>
<td>0.0</td>
<td>3.4</td>
</tr>
<tr>
<td>Wheat Stubble</td>
<td>2.8</td>
<td>3.1</td>
<td>2.9</td>
</tr>
<tr>
<td><strong>Total Grain</strong></td>
<td>33.2</td>
<td>6.6</td>
<td>19.7</td>
</tr>
<tr>
<td>Barley Sprouted</td>
<td>1.9</td>
<td>3.5</td>
<td>3.4</td>
</tr>
<tr>
<td>Wheat Sprouted</td>
<td>1.9</td>
<td>4.0</td>
<td>2.0</td>
</tr>
<tr>
<td><strong>Plough/Harrow</strong></td>
<td>5.6</td>
<td>26.5</td>
<td>15.1</td>
</tr>
<tr>
<td><strong>Total Arable</strong></td>
<td>42.6</td>
<td>40.6</td>
<td>40.2</td>
</tr>
<tr>
<td><strong>GRASSLAND</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-Agricultural</td>
<td>9.8</td>
<td>10.6</td>
<td>10.0</td>
</tr>
<tr>
<td>Ungrazed Ley</td>
<td>2.8</td>
<td>9.7</td>
<td>6.6</td>
</tr>
<tr>
<td>Grazed Ley</td>
<td>14.9</td>
<td>11.9</td>
<td>17.0</td>
</tr>
<tr>
<td>Permanent Pasture</td>
<td>29.9</td>
<td>27.0</td>
<td>26.3</td>
</tr>
<tr>
<td><strong>Total Grassland</strong></td>
<td>57.4</td>
<td>59.2</td>
<td>59.9</td>
</tr>
</tbody>
</table>

No. of Censuses 4 4 16

No. of Fields Within Each Census 57 57 57
Figure 1.3.1

Crop availability at the beginning and end of winter at Keele, Staffordshire

(a) Censused on 12-11-60; (b) 28-2-81
Figure 1.3.2

(a) Monthly meteorological data for Keele, 1977 to 1981

(b) Annual wind rose (average of 12 years)

Key for (a):

(1) Top line = mean 24-hr maximum air temperature; bottom line = minimum 24-hr air; middle line = soil temperature at 10 cm.

(2) Solid bar = percentage of days with frozen soil at 1500 hours GMT; open bar = % days with frozen soil at 0900; hatched bar = percentage of days on which ground frost was recorded.

(3) Solid bar = % days with moist soil at both 0900 and 1500; hatched (slope from left bottom to top right) = % days with moist soil at 0900; other hatched = % days with moist soil at 1500.

(4) Total monthly rainfall in millimetres.

(5) Mean daily sun hours.
WIND. Mean Annual Direction and Velocity 1957-1969
(Based on continuous anemograph traces)
Table 1.3.2

Frozen soil at Keele at 10cm depth

Number of days during each month on which the soil was recorded as frozen. Means for the period 1952 - 1969 (data from Deaver & Shaw 1970). Annual mean (excluding 1962-3) = 7.39.

<table>
<thead>
<tr>
<th></th>
<th>November</th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>March</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.11</td>
<td>2.44</td>
<td>4.11</td>
<td>3.94</td>
<td>0.78</td>
</tr>
</tbody>
</table>
with the fewest frozen soil days recorded.

1.3.3 Prey - General

Since the four corvid species under consideration spent little time on habitats other than non-agricultural grassland or agricultural land in the study areas in winter (section 1.4.1), only the availability of different prey types in these habitats is considered here. Similarly, since prey other than cereals and invertebrates were rarely taken, only the availability of these two major prey types will be considered.

1.3.4 Prey on Arable Land

No measurements of the densities or dispersion of prey on arable were made. The analysis in the remaining chapters is mainly based on observations of birds foraging on grassland for important reasons which are given later.

Cereal grains were available in winter at Keele in the form of stubble grain, and to a limited extent as winter sowings. The number of stubble fields declined over the winter months as they were ploughed (compare figures 1.3.1a and b). In addition, Feare et al. (1974) showed that the number of grains within each stubble field left unploughed declined from November to February. It is possible that
average grain quality also declined, though this was not measured. Sowings had sprouted by early winter and the content of the sprouted seeds obviously declined with time. Sowings were not utilised much (section 1.4.1).

Birds were rarely observed to take invertebrates from stubble fields, though when they did they were (in each case where identification was possible) wireworms (Elaterid larvae) or slugs (Pulmonata). Newell's (1967) review of studies indicates that stubble can contain high populations of the slug *Agriolimax reticulatus*, whilst wireworms are probably the second most numerous invertebrate of this kind associated with cereals (e.g. Robinson 1951). Plough was a high source of invertebrate prey often unavailable at other times (e.g. many large earthworms (Lumbricidae) usually too deep in the soil to be accessible), but only for the first few days after ploughing, and was rarely used after that (section 1.4.1).

The generally low use of arable land probably reflects the fact that in general arable land (both under crop and ploughed) holds a much lower invertebrate biomass than grassland (e.g. reviews in Edwards & Lofty 1977, Raw 1967b, Waite 1978, Wallwork 1976); in addition a greater proportion of the fauna of ploughed fields inhabits a lower depth than in grassland, and thus a greater proportion remains unavailable to a foraging bird. (Raw 1967b).
1.3.5 Invertebrate Prey on Grassland - General

The main conclusion to be drawn from the literature on northern temperate grasslands relevant to the thesis is that in winter earthworms (Lumbricidae) form the major part of the total invertebrate biomass, in the rough order of 4/5ths or even more on non-acid soils (e.g. Raw 1966). On ungrazed or recently sown leys the percentage is lower, and in summer the increased biomass of arthropods, especially of adult Coleoptera, may reduce this to somewhere in the region of a half (e.g. Churchfield 1982, Hutchinson & King 1980). Raw (1966) estimated that c.70% of all arthropods on permanent grassland occurred in the top six inches of soil.

Almost all invertebrate types found on grassland are likely to be aggregated in their dispersion (example reviews of all non-micro fauna: Edwards & Lofty 1977, Newell 1967, Raw 1967b, Satchell 1967a, Southwood 1978, Waite 1978). Many factors have been implicated to account for this, including slow dispersion from reproductive centres; climatic effects of rainfall, temperature, etc.; soil type (pH, organic content, compaction, moisture, etc.) and situation (slope, exposure, etc.); and cropping effects, both in the sense of (for example) woodland vs. agricultural use, and within agricultural habitats different cropping regimes will affect densities. Within
grassland most arthropod densities are reduced by grazing (Boyd 1960, Morris 1968, Wallwork 1976), although Morris showed that though in general this was true, the difference was mainly due to adults, whilst larvae of many species were found in higher densities on grazed land. However, Pulmonate slugs tend to occur in higher densities on grazed land (Boyd 1960), dung-inhabiting animals obviously do, and - most importantly - earthworm densities are almost always higher on grazed grassland compared to ungrazed (e.g. reviews in Edwards & Lofty 1977, Satchell 1967a, Waite 1978). Since the present author has summarised the literature on variation in earthworm densities and dispersion, and the causes of variations, in detail (Waite 1978); and since data will be analysed presently from the study areas, no more detail will be given here on general effects on the invertebrate populations of grassland.

Given the fact that most invertebrate types are likely to be aggregated in dispersion, there are two more related questions which will affect a predator of the invertebrate fauna of grassland. The first concerns whether the aggregations form discrete groups with no animals in the space in between, or whether continuous areas of distribution contain areas of higher and lower relative density. Almost all grassland invertebrate types are likely to be distributed in the latter way, though rarer invertebrates may be present in discrete aggregations. One common invertebrate
type with discrete aggregations on grassland are the Pulmonate slugs which gather in roosting aggregations during the day (Cook 1981, Newell 1967).

The second question concerns the extent to which aggregations of the different types overlap, or are independent of, one another. Imagine a generalist predator who takes all of the prey items in figure 1.3.3a. If it is foraging on the first 'field' of the pair, although each separate prey type is aggregated in dispersion, the effect as far as the generalist is concerned (if it takes each type as encountered, an assumption which may of course be only partially correct) is one of a random distribution. If however it forages on the second 'field', its prey will be aggregated in dispersion since the different prey types are aggregated in the same areas. A specialist on prey type 'x' will encounter aggregated prey when foraging on either 'field'.

Few field studies report on this. Salt & Hollick (1946) studied aggregations of wireworms (Elaterid larvae), and correlated the varying densities of these larvae with the abundance of other invertebrate types (also of a size which the four bird species concerned with here could prey on). They found three significantly associated with the wireworms (Chilopoda, Diplopoda and Hymenoptera (ants)), and two significantly inversely related (Staphylinidae lar-
Figure 1.3.3

Theoretical distributions of prey types

(a) two 'fields' with different kinds of patchy distribution of prey.

(b) a series of 'fields' comprising the home range of a group of birds from the single rookery depicted in the inset.
DISPERSION OF 3 PREY TYPES

(a)

separate aggregations

over-lapping aggregations
vae and Nematocera (= mainly Tipulid larvae)), with the variation in the densities of six other types being statistically independent of variation in wireworm numbers, although two of these (Arachnida and parasitic Hymenoptera) showed quite large non-significant positive relationships.

This gives an overall picture which would be a mixture of the two extremes depicted in figure 1.3.3a - i.e. some aggregations overlapping, some independent, and others randomly mingled. Thus the degree of aggregation of overall prey facing a predator would depend on its degree of specialisation of diet and on which particular combination of prey types made up the diet.

A stylistic representation of the general distribution of the prey types potentially available to a predator is given in figure 1.3.3b. Some 'fields' might offer no prey to a predator, perhaps because it is under a habitat (e.g. woodland) which the species does not exploit. Other fields offer few prey, others abundant randomly distributed prey, and others abundant aggregated prey which may be distributed as discrete units (field c) or as denser areas in a continuous distribution (field a).

1.3.6 Invertebrates within Grassland at Keele in Winter

The data on which the following summary and analyses
are based are listed in appendices one and two. This section describes mainly data from Keele in winter, except where specifically stated otherwise. The fields sampled in the other two study areas in winter (all permanent pasture) all held lower earthworm densities than any sampled permanent pasture at Keele, but the densities of other invertebrates were quite similar (appendix one).

Tables 1.3.3 and 1.3.4 summarise the relative densities and dispersions of earthworms and other invertebrates sampled at Keele during winter. Table 1.3.3 indicates that earthworm densities were higher on grazed fields than ungrazed, and on older fields than on more recently ploughed and resown ones; whilst other invertebrates had reduced densities on old grazed fields. Both these trends are similar to those reported elsewhere in the literature (section 1.3.5).

Table 1.3.4 indicates that the populations of earthworms in these fields were often aggregated in dispersion, whilst other invertebrates were rather infrequently so. The latter result is in contradiction to most other studies (section 1.3.5) and may be a result of the gross classification technique - different invertebrate types may have been aggregated in separate areas (cf. Salt & Hollick 1946 and section 1.3.9 below). In addition the insensitivity of the significance test of dispersion dis-
Table 1.3.3

Invertebrate densities in winter samples from Keele

NAG = non-agricultural grassland, TLU = ungrazed temporary ley, TLG = grazed temporary ley, and PP = permanent pasture.

The biomass of earthworms in each separate core was measured, but although the number of other invertebrates in each core was recorded, the biomass in each core was not. A maximum and minimum weight was calculated from weighed samples of different sized invertebrates (see text).

<table>
<thead>
<tr>
<th></th>
<th>Mean per Core</th>
<th>Ratio of Worms:Other (%)</th>
<th>N of Soil Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Worms</td>
<td>Min</td>
<td>Max</td>
</tr>
<tr>
<td>----------</td>
<td>-------</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>NAG</td>
<td>Numbers</td>
<td>0.807</td>
<td>0.401</td>
</tr>
<tr>
<td></td>
<td>Biom(g)</td>
<td>0.419</td>
<td>0.0026</td>
</tr>
<tr>
<td>TLU</td>
<td>Numbers</td>
<td>0.643</td>
<td>0.430</td>
</tr>
<tr>
<td></td>
<td>Biom(g)</td>
<td>0.255</td>
<td>0.0030</td>
</tr>
<tr>
<td>TLG</td>
<td>Numbers</td>
<td>1.040</td>
<td>0.413</td>
</tr>
<tr>
<td></td>
<td>Biom(g)</td>
<td>0.386</td>
<td>0.0029</td>
</tr>
<tr>
<td>PP</td>
<td>Numbers</td>
<td>1.429</td>
<td>0.251</td>
</tr>
<tr>
<td></td>
<td>Biom(g)</td>
<td>0.544</td>
<td>0.0020</td>
</tr>
<tr>
<td>Dung</td>
<td>Numbers</td>
<td>2.700</td>
<td>0.351</td>
</tr>
<tr>
<td></td>
<td>Biom(g)</td>
<td>1.735</td>
<td>0.0049</td>
</tr>
</tbody>
</table>
Table 1.3.4

Invertebrate dispersion in winter samples from Keele

Percentage of samples within each crop and invertebrate type which were aggregated: V/M = variance-to-mean ratio test; Grid = grid-pattern test (see Methods, section 1.2.2.4).

NAG = non-agricultural grassland, TLU = ungrazed temporary ley, TLG = grazed temporary ley, and PP = permanent pasture.

The V/M test was not appropriate for invertebrates other than earthworms (see text); "Either" is the sum of above and beneath surface invertebrates, plus any which could not be classified by position within the core (see text and appendices 1 & 2).

<table>
<thead>
<tr>
<th>Other Invertebrates:</th>
<th>Above Soil</th>
<th>Below Soil</th>
<th>Either</th>
<th>No. of Samples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Earthworms</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NAG V/M Grid</td>
<td>57.1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>0.0</td>
<td>33.3</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>TLU V/M Grid</td>
<td>(100.0)</td>
<td>-</td>
<td>(0.0)</td>
<td>(0.0)</td>
</tr>
<tr>
<td></td>
<td>(100.0)</td>
<td>-</td>
<td>(0.0)</td>
<td>(0.0)</td>
</tr>
<tr>
<td>TLG V/M Grid</td>
<td>33.3</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>50.0</td>
<td>-</td>
<td>50.0</td>
<td>50.0</td>
</tr>
<tr>
<td>PP V/M Grid</td>
<td>71.4</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>66.7</td>
<td>(100.0)</td>
<td>16.7</td>
<td>16.7</td>
</tr>
<tr>
<td>Dung V/M Grid</td>
<td>50.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>All V/M Grid</td>
<td>68.0</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>50.0</td>
<td>50.0</td>
<td>16.6</td>
<td>16.7</td>
</tr>
</tbody>
</table>
cussed in section H.12.2.4 may have caused type II errors - for example some of the figures in appendix two (e.g. A2.2c, A2.3c) show coherent patterns of grouping together of cores with higher numbers of invertebrates, but the significance test, recognising only the presence or absence of invertebrates, fails to show a dispersion significantly different from random.

Table 1.3.4 may also show a tendency for earthworms to be aggregated in dispersion more frequently on permanent pasture than on grazed leys or ungrazed fields, but the data are too few to comment with any certainty on this.

Table 1.3.3 further indicates that earthworms made up the major proportion of the numbers and biomass (*) of invertebrates. The proportion differed between crop types, earthworms forming the highest proportion of the total invertebrate fauna in permanent pasture. These patterns are illustrated for a subset of the samples in figure

(*) The biomass of earthworms was measured directly, but that of other invertebrates in cores was not. In addition, the relative numbers of the different size classes of these invertebrates was not recorded. Hence a maximum and minimum biomass estimate for these invertebrates was calculated by multiplying the number of invertebrates recorded by the mean assigned weight for a small invertebrate (minimum biomass estimate) or a medium invertebrate (maximum biomass estimate) (see table H.2 for assigned weights). The figures for the biomass of these invertebrate types thus contain much potential for error, although the disparity between the contribution of earthworms and other invertebrates is so great that the general conclusion could not be altered given the extent of possible error involved.
1.3 Winter Resources

1.3.9. Since there were far more grazed than ungrazed fields available (table 1.3.1), earthworms were by far the commonest invertebrate prey available. However, it is possible that a greater proportion of the above surface invertebrates were readily available to a bird predator.

1.3.7 Invertebrates Other than Earthworms at Keele in Winter

Since these invertebrates were rarely sampled by the method adopted in winter, no systematic record of relative abundance was taken. The following list mentions the groups more commonly found, of a size which could be taken by birds. The list is similar to those given in the general literature (e.g. Raw 1966, Wallwork 1976).
1.3 Winter Resources

Enchytraeidae - Present commonly. Their dispersion is figured in appendix two. Considered too small to have been a major prey.

Arachnida - Small spiders fairly frequent.
Isopoda - Infrequent.
Chilopoda - Infrequent.
Diplopoda - Infrequent.
Dermaptera - Infrequent.
Hemiptera - Infrequent.
Coleoptera - Frequent, but adults usually only small e.g.: soil or dung dwellers in the winter.
Carabidae - Larvae and fewer adults.
Staphylinidae - Larvae and fewer adults.
Scarabaeidae - Especially *Aphodius rufipes* larvae and adults frequent in dung but often adults also in the open ground; less frequently chafer larvae (unknown spp.).
Elateridae - Frequent as larvae (wireworms), less frequently adults.
Lepidoptera - Noctuidae larvae (cutworms) were occasional.
Diptera - Small adults of many species were frequent, together with Tipulid larvae (leatherjackets) and various other larvae in dung.
Hymenoptera - Ants were fairly frequent.
Pulmonata - Slugs (mostly *Agriolimax reticulatus*) were fairly frequent, but snails were rare.

1.3.8 Earthworms at Keele in Winter

The following species were identified from Keele samples, though the relative numbers in each sample were not recorded due to the excessive time-cost involved:

*Allobophora caliginosa*
*Δ. chlorotica*
*Δ. longa*
*Δ. nocturna*
*Δ. rosea*
*Lumbricus terrestris*
*Octolasion cyanenum*

*L. terrestris*, *Δ. longa*, *Δ. nocturna* and *O. cyanenum* occurred
less frequently in the cores, and were often found occupying a permanent vertical burrow. The other species were mostly found just under the soil surface or amongst the roots of the grass. This agrees with the description in, for example, Gerard 1967 and Satchell 1967a & b.

The relative availabilities of these species to birds will be affected by crypticity and behaviour in addition to abundance. There is little information available in the literature on this, though Bengtson & Rundgren (1978) showed that golden plovers (*Pluvialis apricaria*) demonstrated selection for *A. caliginosa* and undertook *L. terrestris* on an Icelandic hay meadow in summer, and Satchell (1967b) demonstrated a weak selection by captive rooks for the pink form of *A. chlorotica* over the green form. The latter is likely to be the result of crypticity differences, but burrowing behaviour may be implicated in the former study.

The three measures of earthworm density defined in section M.9.2 were strongly intercorrelated. For example, the correlations of the means for the set of 14 fields sampled in November-December 1979 were:

\[ N \text{ of 'all' earthworms per metre square with 'field observable': } r = 0.92; \text{'all' with biomass (g) per square metre: } r = 0.87; \text{ and 'field observable' with biomass: } r = 0.89. \]

The last relationship is illustrated in figure 1.3.4. The
Figure 1.3.4

Relationship between mean numbers and biomass of earthworms in 14 separate winter soil samples
\[ r = 0.893 \]
\[ p < 0.001 \]
\[ y = 0.338x + 13.258 \]

Biomass (g)

Numbers ("field observable")
weight and two measures of earthworm numbers within each core were also strongly intercorrelated within each separate sample of 42 cores:

for 14 samples: 'all' with 'field observable', mean $r = 0.75$ (range 0.59-0.89); 'all' with 'biomass', mean $r = 0.70$ (range 0.48-0.85); and 'field observable' with 'biomass', mean $r = 0.82$ (range 0.70-0.92).

Unless stated otherwise, reference from now onwards is to the number of 'field observable' earthworms and total weight.

1.3.8.1 Dispersion (1): Between Fields

To test whether earthworms were aggregated on a large scale (between fields) 14 separate fields were sampled at Keele over a short time period (see section 1.6.5). The samples were all taken from an area over which a single bird of any of the four Corvid species could (and certainly did, in the case of observed rooks and jackdaws) forage. The fields were chosen so that they roughly reflected the availability of the different grass types (table 1.3.1), and so that they were scattered over the study area, but otherwise selection of fields was arbitrary (figure 1.3.5a).

Data were analysed by analysis of variance. (*) There were highly significant differences between fields for both (*) Summary tables of this and subsequent analyses of
Figure 1.3.5

Earthworm densities within 14 grass fields sampled between 20th November and 15th December 1979 at Keele, Staffordshire

(a) Location of sampled fields within the study area.
(b) Mean numbers of earthworms in each sample.
(c) Mean biomass of earthworms in each sample.
(d) Spatial pattern of variation in numbers of earthworms across the study area.
C = Non-agricultural grass
L = Temporary ley
P = Permanent pasture
Earthworm densities

0/m² 250/m² 500/m²

Rookery

(d)
Earthworm numbers and biomass (numbers $F = 9.766$, df = 13, 574, $p < 0.001$; biomass $F = 7.309$, $p < 0.001$).

Fields differed by up to 10 times in earthworm densities (figure 1.3.5b & c); areas of similar density were not grouped together (figure 1.3.5d), but some of the variation was accounted for by differences in crop type between non-agricultural swards, temporary leys and permanent pastures (numbers $F = 10.078$, df = 2, 585, $p < 0.001$; biomass $F = 7.670$, $p < 0.001$; figure 1.3.5b & c). For earthworm numbers, there was a significant polynomial linear trend of increasing densities from non-agricultural grass through to permanent pasture, as predicted by the results of other studies (see section 1.3.5), but for biomass the means of non-agricultural grass and temporary leys did not differ significantly.

The lowest density measured at any time during winter was 49.3 earthworms per square metre on a sports field on 20-11-79, the highest 541.5 per square metre on a permanent pasture on 11-2-80 (appendix one); these two fields were less than 0.5 km apart (fields 1 and 56 of figure 1.3.1).

Densities under dung were even higher - on average almost twice as high in terms of numbers than in the open grass of grazed fields, with biomass over three times as high (an indication that a greater proportion of the earthworms variance may be found in appendix 3.
under mats were of medium and large size) (table 1.3.3 and appendix one).

1.3.8.2 Dispersion (2): Within Fields

As summarised in table 1.3.4, earthworms were often aggregated on a smaller scale, within the area covered by an individual sample (c.120 square metres). Overall in winter, 68% of fields showed aggregation in the sense of statistical heterogeneity (variance/mean ratio test) and 50% showed a coherent clumping of dense and sparse cores (grid pattern test); 76.5% of fields were aggregated in one of these two senses, while 35.3% were aggregated in both. The grid patterns for all winter samples are given in appendix two, figures A2.1 to A2.17. Visual inspection of these again reveals the insensitivity of the grid-pattern test referred to earlier (e.g. A2.1b, A2.3b, etc.), with samples classified as random on a dense-sparse basis clearly showing coherent grouping when variation in numbers is considered.

For seven large fields simultaneous samples were obtained from two separate areas within the same field. The areas were between 200 and 500m apart. In six out of the seven cases there were significant differences between the two areas in earthworm densities (separate Mann-Whitney U tests). Three of these differences were very large, one
area holding over twice as many earthworms as the other (table 1.3.5). In four of the seven fields there was an obvious difference in slope between the areas, and in each case there were more earthworms at the bottom of the slope (significantly so in three cases), but in the other three fields there was no obvious visible difference between the two areas.

Finally, there were significantly more earthworms beneath dung pats than in the open grass in the two winter examples where dung and open ground were measured simultaneously (table 1.3.5).

The general picture of earthworm dispersion from the complete set of winter samples is given by the use of Iwao's Patchiness Regression (see e.g. Southwood 1978) of the mean population estimate of a sample plotted against Lloyd's (1967) index of aggregation ('mean crowding'), the formula for which is given in section M.12.2.4. Earthworms sampled at different population densities do show a fairly tight regression, (*) indicating that in grass fields in winter they have a characteristic type of dispersion pattern described by the regression equation:

(*) The figure plots only values from samples of 42 cores. There is much more variability about the least squares line if samples of 10 cores are plotted, a further indication (see section M.6.4) that the confidence limits to population estimates based on 10-core samples are uncomfortably wide.
mean crowding = 0.0101 + (1.2237 * mean)

The fact that the line slopes above a line where the variance equals the mean (and thus mean crowding equals the mean) indicates that the characteristic dispersion pattern of grassland earthworms in winter is an aggregated one (figure 1.3.6).

There are too few data to calculate separate regressions for the different crop types, but it was the case that the sample furthest towards the overdispersed side of the random-line was an ungrazed temporary ley, whilst the most patchy fields were all permanent pasture. However, the data are too few to draw any reliable conclusions about any possible crop differences in the dispersion pattern of earthworms.

1.3.8.3 Shifts in the Location of Aggregations (1): Between Fields

A subset of the 14 fields was re-sampled two months after the main sample, and the significant interaction between field and date of sample indicates that earthworm densities shifted in the period between the first and second sample (numbers - \( F = 6.83, \text{df} = 6, 562, p < 0.001 \); biomass - \( F = 3.56, p < 0.001 \)). While some fields were little different in densities on the two
Figure 1.3.6

Iwao's Patchiness Regression describing the characteristic aggregated dispersion pattern of earthworms within grass fields in winter

The figure plots the relationship between different sample means and Lyoyd's (1937) index of mean crowding. The index is equal to 0 when the dispersion is random (Poisson; i.e., when the variance equals the mean), whilst positive values indicate aggregation, and negative values overdispersion (see inset of theoretical dispersion patterns).

The figure plots all winter samples from Keele, Elore Heath and Farmoor where the sample size was 42 cores.

- O = Non-agricultural Grass
- □ = Ungrazed Temporary Ley
- ■ = Gazed Temporary Ley
- ▼ = Permanent Pasture
sampling dates, others were considerably so (figure 1.3.7). The main effect of Date was not significant, probably reflecting the fact that the second period of sampling was a similarly mild and wet one (see figure 1.3.8c). Yet some combination of environmental conditions had caused earthworm densities of some fields to change in a different pattern to others.

1.3.8.4 Shifts in the Location of Aggregations (2):

Within Fields

Two separate areas within each of two different fields were sampled in December 1979 and re-sampled (each core displaced by 1/3 m) two months later. Interaction effects between date and areas of sample were not consistent. In terms of earthworm numbers, in both fields densities had shifted significantly. In one field both areas held similar densities in December, but by February densities had dropped in one area and risen in the other (Area x Date - F = 7.94, df = 1, 164, p < 0.01; figure 1.3.8a). In the second field the pattern was the reverse, densities differing in December, but in February being much more similar, one area rising and the other dropping (F = 15.93, p < 0.001; figure 1.3.8b). However, in terms of earthworm biomass, though the trends were similar, the interactions failed to reach statistical significance in either case (F
Figure 1.3.7

Shifts in earthworm densities within seven grass fields sampled in December 1979 and February 1980
Figure 1.3.8

Shifts in earthworm densities within three grass fields

(a) Changes in densities in two areas within the same field; data for two fields.

(c) Changes in densities across the winter, with changes in the abundance of other invertebrates, soil temperature at 10 cm, and intensity of use of the field by four Corvid species.
Finally, the same area of one field was sampled at monthly intervals throughout the winter of 1979-80 (figure 1.3.8c). In this field the densities of earthworms changed considerably over the winter, and in this instance it was possible to relate a climatic variable fairly closely to this pattern of change (soil temperature at 10 cm); the intensity of use of the field by four Corvid species also followed a similar pattern. The densities of earthworms and other invertebrates were in this case almost perfectly negatively related. This figure indicates that the pattern of shifts depicted in figure 1.3.7 would probably have shown further complicated patterns of variation were data available for all four winter months for all of these fields.

1.3.9 Dispersion of Earthworms and Other Invertebrates Compared

Between winter sample means, there was a significant negative relationship between earthworm densities and that of above soil-surface invertebrates ($r = -0.37$, $df = 30$, $p < 0.05$). This implies that fields holding high earthworm densities held low densities of above soil-surface invertebrates. This will partly be due to the previously mentioned tendency for grazed fields to have higher earthworm
densities but lower arthropod densities than ungrazed fields (sections 1.3.5 and 1.3.8.1). There was no significant relationship between earthworm numbers and the abundance of below soil-surface invertebrates \( (r = -0.02, \text{ ns}) \). Above and below soil-surface invertebrates were positively related \( (r = 0.39, p < 0.05) \). The differing densities of earthworms, above- and below-surface invertebrates for 14 separate fields are illustrated in figure 1.3.9.

There were no more significant relationships between earthworm and other invertebrate numbers within samples than one would expect by chance given the number of relationships investigated, except in the case of permanent pastures, where in 11% of samples there was a significant negative relationship between earthworm numbers and above soil-surface invertebrate numbers per core. Thus not only did fields holding high earthworm numbers in general tend to have low numbers of above soil-surface invertebrates, but within a number of fields areas with more earthworms tended to have fewer above surface invertebrates, and vice-versa.
Figure 1.3.9

Densities of earthworms and other invertebrates within 14 grass fields of different crop types sampled between 20th November and 15th December 1979

[Graph showing densities of earthworms and other invertebrates in different crop types.]
Part One Chapter Four - Resource Utilisation by Four Corvid Species

This chapter analyses the utilisation of the resource base, described in the last chapter, by the four species introduced in chapter 1.2. The data represent the species’ realised niches (sensu Vandermeer 1972), since they were collected as a random sample with respect to each other species’ absence or presence in the short term. Chapter 1.6 will discuss any niche changes associated with interactions between species, whilst chapter 1.5 will describe the overlap of the realised niches between species.

The data used to describe habitat choice were collected over several winters, but the data on foraging behaviour all come from one winter (1980-81). Sufficient habitat data are only available if data from all years are used, whilst systematic recording of the foraging behaviour of all four species could only be carried out in one winter. It may be that the winter 1980-81 was not normal in some respects, and the following chapters should be read with this in mind. It was certainly the case that this winter was milder than others during the study (figure 1.3.2), with fewer frozen soil days. For rooks (the only species with foraging data available from all winters), there were differences between years in various aspects of
behaviour; for example, the proportion of the diet made up of earthworms changed from 55.5% in 1978-79, to 76.1% in 1979-80, and finally to 79.3% in 1980-81.

In addition, prey types taken were only classified as either earthworms or some other invertebrate type (see Methods for discussion), with only two size-class divisions within the latter group. Thus the data are limited in their detail.

1.4.1 Distribution of Birds Over the Main Study Area

Figure 1.4.1 presents species' distribution maps within the main study area at Keele on six different occasions in winter. (*) These maps will be referred to in later chapters for a number of reasons but may be examined now to provide the following qualitative summary description of the winter distribution of the four Corvid species over the available habitats:

1. Each species was recorded (in these cases, and in most others) only on non-agricultural grassland and agricultural land.

2. Carrion crows and magpies were dispersed over the

(*) Only six full winter maps could be drawn - on other census dates some fields were not covered because of lack of access, human disturbance, or because unique field numbers were not recorded. More censuses were available for analyses where recognition of individual fields was not required.
Figure 1.4.1

Distribution maps for four Corvid species at Keele in winter

(a) 8-11-79
(b) 6-12-79
(c) 12-11-80
(d) 18-1-81
(e) 23-2-81
(f) 28-2-81

**Flock Size**

- ■ = 1
- • = 2
- •• = 3–6
- ••• = 7–20
- •••• = 21–40
- ••••• = > 40
whole area reflecting their (mainly) A-type territoriality (chapter 1.2), while the gregarious rooks and jackdaws tended to be clumped within a few fields at any one time.

(3) Arable land was used less than grassland.

(4) Though the four species were found on the same fields at the same time, often they were spread such that rooks and jackdaws foraged together, but carrion crows and magpies were found less often with rooks and jackdaws or with each other.

(5) Certain fields often held birds while others never did.

(6) Relative flock sizes on fields often shifted between censuses.

Table 1.4.1 indicates that while carrion crows used grassland and arable in total in proportion to their availability, the other three species all selected grassland over arable. All four species were found at higher densities on grassland. This was the case even for carrion crows which, although generally using the two main crop types in proportion to their availability, were found on a few smaller than average fields at very high densities.

1.4.3 Habitat Selection (2): Within Grassland

Four different types of grass crop were available in the study area - non-agricultural cut grass (sports fields, verges, etc.), grazed and ungrazed temporary leys, and grazed permanent pastures (more than 10 years since last known ploughing). The proportion of each species
Table 1.4.1

Proportion and densities of four Corvid species censused on grassland and arable in winter

(a) Percent of birds on each gross crop type (percent within each species) - significant selection of crops over availability is indicated by asterisks; (b) density as numbers of birds per hectare within each species.
### Crop Availability

<table>
<thead>
<tr>
<th>Crop Type</th>
<th>N of Fields</th>
<th>Total Area</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRASS</td>
<td>59.8</td>
<td>61.5</td>
</tr>
<tr>
<td>ARABLE</td>
<td>40.2</td>
<td>38.5</td>
</tr>
</tbody>
</table>

### Proportional Use by Species

<table>
<thead>
<tr>
<th>Crop Type</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Crow</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRASS</td>
<td>81.7</td>
<td>67.3</td>
<td>63.9</td>
<td>74.8</td>
</tr>
<tr>
<td>ARABLE</td>
<td>18.3</td>
<td>32.7</td>
<td>36.1</td>
<td>25.2</td>
</tr>
</tbody>
</table>

### Number of Birds per Hectare

<table>
<thead>
<tr>
<th>Crop Type</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Crow</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>GRASS</td>
<td>137.9</td>
<td>79.7</td>
<td>26.3</td>
<td>26.4</td>
</tr>
<tr>
<td>ARABLE</td>
<td>36.0</td>
<td>36.4</td>
<td>9.5</td>
<td>10.2</td>
</tr>
</tbody>
</table>

---

*Sample N* 411

---

*(b) Sample N* 1219 655 244 214
found on each of these crop types is illustrated in figure 1.4.2a. Most rooks and jackdaws were found on permanent pasture, with small numbers on grazed leys and an insignificant number on ungrazed fields. Most carrion crows and magpies also occurred on permanent pasture, but this time only just over 50% of each species. Most of the rest were on grazed leys, with c.10% of magpies and c.6% of carrion crows on ungrazed fields.

All four species used crops significantly differently from their availability (separate chi-square tests, $p < 0.001$ in each case — on original data with data for non-agricultural grass and ungrazed leys combined). Examination of expected frequencies reveals that for the rook and jackdaw this was due to a strong selection for permanent pasture coupled with strong avoidance of ungrazed fields and a weaker avoidance of ungrazed leys. The distribution of carrion crows and magpies was due to the use of permanent pasture and grazed leys as available (with a weak selection for grazed ley also demonstrated) while avoiding ungrazed leys and more weakly avoiding non-agricultural grass swards. These choices are illustrated in figure 1.4.2b.

Figure 1.4.3 illustrates habitat selection in relation to abundance of the habitats. Most rooks and jackdaws were found on the most abundant crop (permanent pasture) and
Figure 1.4.2

Grass crop use and selection

(a) Proportion of four Corvid species found on different grass crop types in winter (percent within each species).

(b) Habitat selection - the electivity index ranges from -1 (complete avoidance) through 0 (no selection) to +1 (complete selection).
(a) Habitat Use - proportion of each species on each crop type and relative availability

Non-agricultural
Ungrazed Ley
Grazed Ley
Permanent Pasture

Area of Crop

Rook  Jackdaw  Crow  Magpie

(b) Habitat Use - preference/avoidance or use as available?

Non-agricultural
Ungrazed Ley
Grazed Ley
Permanent Pasture

Electivity Index

Rook  Jackdaw  Crow  Magpie
Figure 1.4.3

Habitat selection by four Corvid species in relation to habitat availability

(a) Theoretical values - points falling within the same segment show similar degrees of selection, whilst points high on the X axis represent abundant habitats, and points high on the Y axis represent a large proportion of the species concerned.

(b) Actual winter data for four Corvid species:

C = Carrion Crow
J = Jackdaw
H = Magpie
R = Rook
(a) Theoretical Values

**High Proportion**

- Strong Preference
- Weak Preference
- No Choice
- Avoidance

**Low Proportion**

Low ← Availability → High

**HABITATS**

(n/N)

(b) Recorded Use of Four Grass Crops

Use of Four Grass Crops

- 1.0
- 0.5
- 0.0

- Non-agricultural
- Ungrazed Ley
- Grazed Ley
- Permanent Pasture

HABITATS
this was due to high positive selection. Most carrion crows and magpies occurred on either permanent pasture or grazed ley (the two most abundant crops) and this was due to weaker but also positive selection. Permanent pasture also held the highest densities (numbers of birds per hectare) of the four grass crops of rooks and jackdaws, but the highest densities of carrion crows and magpies were found on grazed leys (table 1.4.2).

In conclusion, rooks and jackdaws preferred the most abundant crop and were found almost exclusively in this habitat and were at their highest densities there; whilst carrion crows and magpies preferred the second most abundant crop and occurred at their highest densities on that crop (grazed temporary leys); but the greater abundance of permanent pasture meant that just over 50% of the individuals of these species were to be found on permanent pasture and only c.40% on grazed leys.

1.4.4 Foraging Behaviour (1): Arable and Grassland Compared

Due to time limitations, very few data on foraging rates are available for birds on arable fields. For what they are worth, these data are presented in table 1.4.3. These preliminary data suggest that stubble grain is an important source of calories for each species, but
Table 1.4.2

Densities of four Corvid species on different grass crops

<table>
<thead>
<tr>
<th></th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Crow</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-agricultural</td>
<td>1.5</td>
<td>0.3</td>
<td>1.6</td>
<td>0.8</td>
</tr>
<tr>
<td>Ungrazed Ley</td>
<td>-</td>
<td>-</td>
<td>0.5</td>
<td>2.4</td>
</tr>
<tr>
<td>Grazed Ley</td>
<td>22.5</td>
<td>17.7</td>
<td>14.2</td>
<td>14.5</td>
</tr>
<tr>
<td>Permanent Pasture</td>
<td>113.9</td>
<td>61.4</td>
<td>9.9</td>
<td>8.6</td>
</tr>
</tbody>
</table>

| Sample N | 996 | 441 | 156 | 160 |
particularly for jackdaws given their low calorific intake rates on grassland. Invertebrates were taken from stubble only at low rates. Plough provided high rates; however, birds only used plough on the day of ploughing and for a few days afterwards while invertebrates turned up by the plough were on the surface. Hence over the whole winter plough was unimportant as a food source and was little utilised (on average over winter 14% of fields were available as plough; during routine censuses 5% of carrion crows were recorded on this habitat, 0.5% of magpies, and no rooks or jackdaws).

Grassland provided a richer source of protein-containing material than arable (table 1.4.3b), and this, coupled with the fact that only c.25% of the area provided grain on average over the winter (table 1.3.1), probably explains the high proportion of each species found on grassland. In addition to gross intake rates of nitrogenous material, a wide range of invertebrates in the diet probably provides particular kinds of nutrients necessary for survival (e.g. Greenstone 1979, Newton 1968; brief review in Morse 1980).

For the remaining chapters in part one, the behaviour of the four species on grassland only is considered. It was decided to concentrate data collection on grassland birds for two reasons — firstly, because each species
Table 1.4.3

Prey intake rates on grassland and arable

The data in brackets are given only as a rough guide to possible population means; sample sizes are given beneath; *inverts* = invertebrates.

(a) Energetic value of intake: kcal ingested per minute.

(b) Gross measure of nutritive value of intake: grams of protein-containing material ingested per minute.

(a) *Mean kcal per minute*

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrion Crow</td>
<td>(0.144)</td>
<td>(0.088)</td>
<td>(0.260)</td>
<td>0.279</td>
</tr>
<tr>
<td>(N = 1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rook</td>
<td>(0.501)</td>
<td>(0.027)</td>
<td>(0.456)</td>
<td>0.240</td>
</tr>
<tr>
<td>(N = 8)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>(0.308)</td>
<td>(0.000)</td>
<td>(0.026)</td>
<td>0.051</td>
</tr>
<tr>
<td>(N = 4)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>No Data</td>
<td>No Data</td>
<td>No Data</td>
<td>0.082</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>(N = 70)</td>
</tr>
</tbody>
</table>

(b) *Protein intake rate (g) per minute*

<table>
<thead>
<tr>
<th></th>
<th>Stubble Grain</th>
<th>Grassland Invertebrates</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>(0.0083)</td>
<td>0.0401</td>
</tr>
<tr>
<td>(N = 8)</td>
<td></td>
<td>(N = 69)</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>(0.0051)</td>
<td>0.0070</td>
</tr>
<tr>
<td>(N = 4)</td>
<td></td>
<td>(N = 60)</td>
</tr>
</tbody>
</table>
spent a majority of their foraging time on grass (section 1.4.2). Secondly, overlap between species when on arable is almost total, given a one-prey (grain) situation (although the different selection patterns for grassland and arable shown in table 1.4.1 will lead to some partitioning in the sense of gross habitat selection). The most important partitioning of resources between species must occur on grassland.

1.4.5 Foraging Behaviour (2): Grassland

1.4.5.1 Feeding Actions and Microhabitat Selection

Table 1.4.4a shows the proportional use of the feeding actions defined in section M.11.1 (proportions were calculated only for actions which resulted in the capture of a prey item, since Waite 1978 has shown peck rate to correlate highly with success rate in most cases). Carrion crows mainly used Surface Pick to capture prey, but also used Dung Turn on 25% of occasions. All other actions were used on less than 10% of occasions, but all actions except Jump were recorded for this species.

Jackdaws used Surface Pick in almost identical proportions to carrion crows (c.40%), but Dung Turned rather more (34.5%). Jackdaws were the only species seen to catch prey by Jumping in the winter, but were not recorded as perform-
Table 1.4.4

Relative frequencies (percent within each species) of successful feeding actions and micro-habitat use by four corvid species

(a) Feeding actions; (b) Micro-habitats. Each species used the four micro-habitats with significantly differing frequencies \((p < 0.01)\) from every other species (separate pairwise comparisons by chi-square on original data).
### (a) Feeding Action

<table>
<thead>
<tr>
<th>Action</th>
<th>Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface Pick</td>
<td>41.6</td>
<td>17.0</td>
<td>41.4</td>
<td>56.0</td>
</tr>
<tr>
<td>Pounce</td>
<td>8.5</td>
<td>0.5</td>
<td>-</td>
<td>8.5</td>
</tr>
<tr>
<td>Jump</td>
<td>-</td>
<td>-</td>
<td>5.2</td>
<td>-</td>
</tr>
<tr>
<td>Surface Probe</td>
<td>8.5</td>
<td>2.8</td>
<td>5.2</td>
<td>9.2</td>
</tr>
<tr>
<td>Clod/Stone Turn</td>
<td>8.3</td>
<td>6.6</td>
<td>12.1</td>
<td>11.3</td>
</tr>
<tr>
<td>Dung Turn</td>
<td>25.1</td>
<td>6.6</td>
<td>34.5</td>
<td>12.1</td>
</tr>
<tr>
<td>Dung Crumble</td>
<td>0.2</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Deep Probe</td>
<td>2.7</td>
<td>36.3</td>
<td>-</td>
<td>0.7</td>
</tr>
<tr>
<td>Dig</td>
<td>1.9</td>
<td>7.1</td>
<td>-</td>
<td>2.1</td>
</tr>
<tr>
<td>Jab</td>
<td>3.2</td>
<td>18.4</td>
<td>1.7</td>
<td>-</td>
</tr>
</tbody>
</table>

| N Actions | 411 | 212 | 174 | 282 |
| N Birds   | 90  | 69  | 60  | 70  |

### (b) Micro Habitat

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Above Soil Surface</td>
<td>56.6</td>
<td>25.0</td>
<td>51.7</td>
<td>73.8</td>
</tr>
<tr>
<td>Beneath Clods/Stones</td>
<td>8.3</td>
<td>6.6</td>
<td>12.1</td>
<td>11.3</td>
</tr>
<tr>
<td>Within/Beneath Dung</td>
<td>25.3</td>
<td>6.6</td>
<td>34.5</td>
<td>12.1</td>
</tr>
<tr>
<td>Beneath Soil Surface</td>
<td>7.8</td>
<td>61.8</td>
<td>1.7</td>
<td>2.8</td>
</tr>
</tbody>
</table>

| N Actions | 411 | 212 | 174 | 282 |
| N Birds   | 90  | 69  | 60  | 70  |
ing four of the 10 actions at all.

Magpies used Surface Pick 56% of the time, the highest proportion for one action by any species. Pounce, Surface Probe, Clod-Stone Turn and Dung Turn were all used in rather similar proportions (c.10%), while three actions were not used and two (Deep Probe and Dig) only rarely.

Rooks Deep Probed most (36.3%) and Jabbed and Surface Picked on 18.4 and 17% of occasions respectively. Other actions were used on less than 10% of occasions, and two actions were not recorded at all. These patterns, including the greater generalisation of carrion crows, are very similar to data from an earlier study (Waite 1976).

If one divides these different feeding actions into those which caught prey from the same microhabitat (table 1.4.4b), then the general picture emerges of the magpie concentrating on above surface prey, the rook on below surface prey, and the carrion crow and jackdaw catching c.50% of their prey above the surface of the soil but both taking a very substantial proportion of the rest from within or beneath animal dung. However, no species was entirely specialised on one microhabitat, but all took at least some prey from each. Each species differed significantly from every other in their proportional use of the different microhabitats (separate chi-squared tests, p < 0.01 or less). Jackdaws and carrion crows, despite
foraging above the soil surface in similar proportions, used the remaining microhabitats differently - jackdaws used dung more than carrion crows and then foraged beneath litter, but rarely beneath the soil surface; while carrion crows used dung less than jackdaws and then foraged equally (c.8% of the time) beneath litter and beneath the soil surface. These data are an indication of the proportion of different items caught in different microhabitats; an analysis taking into account the relative value of different prey items follows in section 1.4.5.4.

1.4.5.2 Prey Selection

As mentioned earlier, only a very crude measure of prey taken was possible. Table 1.4.5 lists the proportions of each invertebrate type and size class, recognised during observations of foraging birds, taken by the four species. All four species took more 'other' invertebrates than earthworms. Carrion crows took somewhat more medium than small 'other' invertebrates, whilst each of the other three species took more small than medium. This difference was most marked in the jackdaw, for whom 88% of the diet comprised small invertebrates.

Jackdaws and magpies took only few earthworms, all small, but these, though unimportant in terms of numbers of items, were sufficient to provide 20 and 16% of calorific
Table 1.4.5

Selection of invertebrate prey types and sizes by four Corvid species

Percentage contribution of each prey type to the diet, within each species, in terms of number of individual items, and of calorific and nutritive value.

Each species differs significantly from every other in the proportions of earthworms to other invertebrates taken (separate chisquares, p < 0.05).

N = Numbers of prey items
C = Calories
P = Protein

<table>
<thead>
<tr>
<th>Earthworms:</th>
<th>Other Invertebrates:</th>
<th>Number of:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small Medium Large</td>
<td>Earthworms</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Items</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Car-</td>
<td>13.9 5.2 6.5</td>
<td>24.2 34.0</td>
</tr>
<tr>
<td>rion</td>
<td>13.7 9.3 33.9</td>
<td>56.9 1.3</td>
</tr>
<tr>
<td>Crow</td>
<td>15.7 10.6 38.7</td>
<td>65.0 1.1</td>
</tr>
<tr>
<td>Rook</td>
<td>38.6 6.1 4.5</td>
<td>49.2 31.1</td>
</tr>
<tr>
<td></td>
<td>38.6 14.4 26.3</td>
<td>79.3 1.2</td>
</tr>
<tr>
<td></td>
<td>41.0 15.3 28.0</td>
<td>84.3 1.0</td>
</tr>
<tr>
<td>Jack-</td>
<td>3.1 - -</td>
<td>3.1 88.6</td>
</tr>
<tr>
<td>Cav</td>
<td>20.6 - -</td>
<td>20.6 22.5</td>
</tr>
<tr>
<td></td>
<td>27.1 - -</td>
<td>27.1 21.4</td>
</tr>
<tr>
<td>Mag-</td>
<td>5.2 - -</td>
<td>5.2 69.4</td>
</tr>
<tr>
<td>pie</td>
<td>16.6 - -</td>
<td>16.6 7.7</td>
</tr>
<tr>
<td></td>
<td>21.8 - -</td>
<td>21.8 7.3</td>
</tr>
</tbody>
</table>
intake respectively, and even more of nitrogenous material. Earthworms provided carrion crows with 57% of their energetic intake, and rooks with almost 80% of theirs. Despite the similarity of the percentage of totalled invertebrates and earthworms in the diets of jackdaws and magpies (96.9 and 94.8% of 'other' invertebrates respectively), there were significant differences between each species and every other in paired comparisons of the frequency of selection of these two gross prey-type divisions (separate chi-square tests on original data, p < 0.05 or less). (*)

For carrion crows and rooks it was in addition possible to test the proportion of different size classes of earthworms in the diet against the relative abundances of these classes in soil samples (data for magpies are also tabulated but no significance test on these data was applied). Table 1.4.6a indicates that the relative frequency of the different size classes of earthworms in the

(*) There are three ways of calculating the mean values in table 1.4.5. The total number of invertebrates taken in the total time summed over all birds may be used; but this will be biased if very long records are abnormal. The proportion of each prey type taken by each individual bird may be calculated, and then these averaged for the species; but this may introduce bias since short records, and very unsuccessful birds, will have equal weighting with more normal birds in calculating the species means. This will tend to underestimate the true importance of the rarer items. Finally, one may express the mean intake rates for a species as percentages. This method gives more equal weighting to birds than the first method, but is a more sensitive reflection of the importance of rarer items. This method was adopted. In practise, the three methods produced only trivial differences for most items and most species.
Table 1.4.6

**Earthworm size-class availability and contribution to diets**

(Percentage of each size class)
(a) Availability and Predation

<table>
<thead>
<tr>
<th>Earthworm Size Category:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>Availability in Soil Core Samples</td>
</tr>
<tr>
<td>Predation by:</td>
</tr>
<tr>
<td>Rook</td>
</tr>
<tr>
<td>Carrion Crow</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>

Test for Selection (on original data):

Soil by Rook predation – chi-square = 1.50, df=2, N.S.
Soil by Crow predation – chi-square = 11.86, df=2, p < 0.01
Soil by Magpie Predation – chi-square assumptions violated

(b) Predation Above and Beneath the Soil Surface

<table>
<thead>
<tr>
<th>Earthworm Size Category:</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
</tr>
<tr>
<td>---------</td>
</tr>
<tr>
<td>Above Soil Surface</td>
</tr>
<tr>
<td>Rook</td>
</tr>
<tr>
<td>Beneath</td>
</tr>
<tr>
<td>Carrion Crow Above</td>
</tr>
<tr>
<td>Beneath</td>
</tr>
</tbody>
</table>

(Assumptions violated for comparisons between microhabitats)
diet of rooks did not differ significantly from that available in the soil, whilst carrion crows selected medium and large earthworms. Since small earthworms were the most frequent size class in the soil (75.4%), the carrion crow's selection meant that they were concentrating on the less abundant size classes. This was probably the result of an inability to catch earthworms beneath the soil surface - table 1.4.6b indicates that rooks took earthworms mainly from beneath the surface of the soil, and that when taking them from above the surface, they were observed to catch only small earthworms. On the other hand the carrion crow, which does not possess the relatively slender probing bill of the rook (section 1.2.1), took most of their earthworms above the surface. When they did forage below the surface their selection of size classes more closely reflected relative abundances of the size classes in the soil; while their selection for medium and large size classes was even more marked above the soil surface.

These data suggest that both species take what they encounter when foraging beneath the soil surface. This probably reflects the fact that until the prey had been located, caught and removed from beneath the surface, its size was not ascertainable. However, the fact that carrion crows showed selection when foraging above the soil surface compared to total availability does not necessarily imply selection compared to what they actually encountered above.
the soil surface while foraging. It is in fact likely that a disproportionate amount of medium and large earthworms are to be found above the soil surface, since it is mainly the larger, permanent burrowers which venture onto the surface to forage which will be available, often partly in and partly out of their burrows (e.g. Edwards & Lofty 1977). These earthworms require speed and stealth to capture, and the failure of rooks to take such prey is commented on further in later chapters.

1.4.5.3 Foraging Rates (1): Grass Crop Types Compared

Each prey type could be taken by a different feeding action and on a different grass crop type. Unfortunately due to time limitations and the rarity of use of some grass habitats by some species (section 1.4.3) few data are available to make comparisons of ingestion rates between grass crop types.

For jackdaws, there were insufficient data from any crop other than permanent pasture to test for significant differences in foraging rates between grass crop types. For rooks there were sufficient data to compare grazed temporary leys and permanent pastures; no significant differences occurred between these two crop types.

There were sufficient data for all crop types for
carrion crows. This species caught medium earthworms by Surface Picking and Surface Probing at higher rates on non-agricultural grass compared to all other crop types (Scheffe tests after separate analyses of variance for each measure); and medium invertebrates by Jabbing and Digging on the other ungrazed crop type, ungrazed ley, faster than on all the other crop types. None of these rates were very high compared to others used by carrion crows, except for medium worms taken by Surface Picking, which was fairly important to this species in terms of calorific intake (figure 1.4.5 in next section), and neither habitat was much used (figure 1.4.2 in section 1.4.3 above). With feeding actions combined into the different microhabitats one further significant difference appeared (not including those already covered by a combination of the feeding actions already discussed) — earthworms (all size classes combined) from beneath the soil surface were also taken at faster rates on ungrazed temporary leys than on any other crop type; but again, earthworms from beneath the soil surface were not a very important prey for this species, and ungrazed leys were little used.

For magpies sufficient data were available to test for differences between non-agricultural grass, ungrazed temporary leys and permanent pastures. Magpies caught small invertebrates by Surface Picking faster on permanent pasture than on either of the ungrazed crops (significant only
for ungrazed leys compared with permanent pasture), but took both small and medium invertebrates by Stone-Clod Turning at a higher rate on ungrazed leys, this time, compared to when foraging on non-agricultural grass and permanent pasture (significant only for the ungrazed ley-permanent pasture comparison). Thus they foraged more successfully for above soil-surface small invertebrates when on permanent pasture, but for invertebrates beneath litter more successfully on ungrazed leys. However, as with carrion crows, these differences may be of limited biological importance. Although magpies utilised permanent pasture a great deal (figure 1.4.2), Surface Picking for small invertebrates was not a very high source of calories for this species (figure 1.4.5); medium invertebrates taken from beneath litter were the third most important source of calories for this species, but the crop on which the fastest rates were recorded — ungrazed leys — was not used much (figure 1.4.2).

1.4.5.4 Foraging Rates (2): Average on Grassland

Since insufficient data were available to take the different grass crop types out as a factor, and since the few significant differences in capture rates between grass crop types seemed, on this preliminary analysis of the few data, to be fairly unimportant biologically, the data for
all crop types were combined for each species for the remaining analyses. Since there was quite close agreement between the proportion of observations during which foraging behaviour was recorded for each species from each crop type, and the proportion of time each species spent on each crop type as measured by routine censuses (except for under-recording of magpies on grazed temporary leys; see section H.9.1); it was felt that such a method of weighting, necessary due to lack of data otherwise, actually represented a kind of species' average for winter foraging on grassland.

The data have been summarised in the form of species' means (with standard deviations and significance tests (*) for differences between species) in appendix seven. These data range from various summations (by prey type, microhabitat, etc.) through to the actual variables recorded in the field in table A7.9. For present purposes, data are selected from tables A7.8 (prey types taken in different

(*) Since there were so many of these analyses (127 in all), full summary tables do not appear in appendix 3. Appendix A7 gives the F ratios and significance levels for each analysis of variance, and also lists the pairwise comparisons between species (using Scheffe's test) which were significant at $p < 0.10$ (the appropriate level for this test - see e.g. Ferguson 1976). The author is aware that approximately 6 or 7 analyses in a set of this number are likely to yield spurious significant F ratios. Far more significant analyses than this were found. Within each separate analysis of variance, the use of Scheffe's test will, of course, have reduced 'experimentwise' error to acceptable bounds.
1.4 Realised Niches

microhabitats) and A7.9 (prey types taken by different feeding actions), and presented graphically and analytically in figures 1.4.4 and 1.4.5.

Figure 1.4.4a compares intake rates per minute of the different prey types from different microhabitats in terms of numbers of items taken per minute. Jackdaws took small prey items quickly from each microhabitat, except beneath the soil surface; magpies took small and medium invertebrates at medium rates; carrion crows took mainly medium items at medium rates; and rooks took small earthworms and beneath-surface invertebrates at medium rates.

However, while describing the speed of capture of items, these data do not reveal much about the value of such differences in foraging rates, since the different prey types differed greatly in size, and also in relative value. Hence the data were transformed to reflect the approximate value of intake of the different prey types. Figure 1.4.4b reveals that jackdaws, despite their fast rate of foraging, actually ingested a lower quantity of calorific value than any other species due to the small size of each individual item taken. In addition it indicates that despite catching a large number of items from dung (table 1.4.4 and figure 1.4.4a), most of these were small, and thus provided a similar proportion of value to the diet as did prey from beneath surface litter. It
Figure 1.4.4

Ingestion rates by four corvid species of prey types taken in different micro-habitats

(a) Mean ingestion rates as number of prey items taken per minute.

C = Carrion Crow
J = Jackdaw
H = Magpie
R = Rook
* = >1 species with same

s = Small Invertebrate
m = Medium Invertebrate
l = Small Earthworm
2 = Medium Earthworm
3 = Large Earthworm

(b) Mean ingestion rates expressed in terms of calorific value of intake (kcal per min.). Key as for (a).

(c) Univariate significant differences between species in ingestion rates (Scheffe tests after analysis of variance). Species not listed together in a cell differ significantly on that variable.
(a) Mean species' ingestion rates as number of prey items taken per minute

Prey Type: | sm123 | sm12 | sm12 | sm123 |
---|---|---|---|---|
Micro-habitat: | Above | Beneath | Stone | Beneath |
| Soil | Within | Clod | Soil |
| Surface | Dung | Turn | Surface |
(b) Mean species' ingestion rates as calorific value of intake

<table>
<thead>
<tr>
<th>Calorific Intake (Kcal per Minute)</th>
<th>0.03</th>
<th>0.02</th>
<th>0.01</th>
<th>0.00</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey Type:</td>
<td>sml23</td>
<td>sml2</td>
<td>sml2</td>
<td>sml23</td>
</tr>
<tr>
<td>Micro-habitat:</td>
<td>Above</td>
<td>Beneath</td>
<td>Stone-</td>
<td>Beneath</td>
</tr>
<tr>
<td></td>
<td>Soil</td>
<td>Within</td>
<td>Clod</td>
<td>Soil</td>
</tr>
<tr>
<td></td>
<td>Surface</td>
<td>Dung</td>
<td>Turn</td>
<td>Surface</td>
</tr>
</tbody>
</table>

- Prey Type: sml23, sml2, sml2, sml23
- Micro-habitat: Above, Beneath, Stone- Beneath, Soil, Surface, Dung, Turn, Surface
(c) Univariate significant differences between species in ingestion rates; species not listed together in a cell differ significantly on that variable.

<table>
<thead>
<tr>
<th>Micro-</th>
<th>Above</th>
<th>Beneath-</th>
<th>Stone-</th>
<th>Beneath</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat:</td>
<td>Soil</td>
<td>Within</td>
<td>Clod</td>
<td>Soil</td>
</tr>
<tr>
<td></td>
<td>Surface</td>
<td>Dung</td>
<td>Turn</td>
<td>Surface</td>
</tr>
<tr>
<td>Prey Type:</td>
<td>snl23</td>
<td>snl2</td>
<td>snl2</td>
<td>snl23</td>
</tr>
<tr>
<td></td>
<td>JC C</td>
<td>JC</td>
<td>J R</td>
<td>RRRRR</td>
</tr>
<tr>
<td></td>
<td>HH</td>
<td>HH</td>
<td>C</td>
<td></td>
</tr>
<tr>
<td>Ingestion Rate per Minute (Ranks only)</td>
<td>M</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>J</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C C</td>
<td>CC</td>
<td>H C</td>
<td>CCCCC</td>
</tr>
<tr>
<td></td>
<td>RJJ</td>
<td>HHRR</td>
<td>HCCJ</td>
<td>HJJJJJ</td>
</tr>
<tr>
<td></td>
<td>CJHHH</td>
<td>CJJJ</td>
<td>CJHH</td>
<td>JHHHH</td>
</tr>
<tr>
<td></td>
<td>RRJRR</td>
<td>RRHH</td>
<td>RRHR</td>
<td>JJHHH</td>
</tr>
</tbody>
</table>
should of course be noted that these comparisons between species will depend crucially on the weights assigned to the different invertebrate types (see methods). If jackdaws selected the larger of the "small" invertebrates available in the soil, then their actual weight of intake rates will be higher than those given here, since every small item ingested was assigned the same average value from soil samples. The transformations should be examined with this in mind. However, although errors are certain, an attempt to assign weight was essential since the range of prey sizes (from a large earthworm to an ant) was so huge. It is not the actual values that are of interest in the following discussions so much as the differences between species within any one foraging action or prey type. The transformations do not, of course, affect tests of significance for differences between species (see methods).

Carrion crows had high rates of calorific gain from medium invertebrates and earthworms above the soil surface and within animal dung; and magpies showed a similar pattern but without the major contribution from earthworms. Rooks gained most of their calories from earthworms taken beneath the soil surface, and from medium soil invertebrates.

Figure 1.4.4c indicates that each species was signifi-
cantly separated from every other species on several variables. Further, each species, with the exception of the magpie, had significantly higher capture rates than any other species on at least one variable - which suggests that each species had at least one prey type/microhabitat combination at which it was more successful than any other species. These patterns of species differences are discussed further in the next chapters.

Figure 1.4.5 breaks the analysis down a little further into each different prey type taken by each feeding action. The general picture is of course similar to that just described, but reveals a few of the finer specialisations shown by particular species, for example the high rates of foraging in three specialised ways (jumping, litter and dung turning) by the jackdaw for small invertebrates. The magpie did this time have significantly higher feeding rates on a variable than the other three species, pouncing for small items significantly faster than the other three. These figures will be referred to in greater detail in the next two chapters which discuss relationships between the four species.
Ingestion rates by four corvid species of prey types taken by different feeding actions

(a) Mean ingestion rates as number of prey items taken per minute.

Pick = Surface Pick  C = Carrion Crow
Pnce = Pounce  J = Jackdaw
Jmp = Jump  H = Magpie
SP = Surface Probe  R = Rook
ST = Stone/Clod Turn  * = >1 species with same ingestion rate
DT = Dung Turn
DC = Dung Crumble
DP = Deep Probe
Dig = Dig
Jab = Jab

s = Small Invertebrate
m = Medium Invertebrate
l = Small Earthworm
2 = Medium Earthworm
3 = Large Earthworm

(b) Mean ingestion rates expressed in terms of calorific value of intake (kcal per min.). Key as for (a).

(c) Univariate significant differences between species in ingestion rates (Scheffe tests after analysis of variance). Species not listed together in a cell differ significantly on that variable.
(a) Mean species' ingestion rates as number of prey items taken per minute

Prey Type: snl23 snl23 s sml2 sml2 sml2 s sml23 sml sml23

Feeding Action: Pick Pnce Jmp SP ST DT DC DP Dig Jab
(b) Mean species' ingestion rates as calorific value of intake

Kcal Ingested per Min.

Prey Type:  sm123 sm123 s sm12 | sm12 | sm12 s | sm123 sm1 | sm123 |
Feeding Action: Pick Pnce Jmp SP | ST | DT DC | DP | Dig Jab
(c) Univariate significant differences between species in ingestion rates; species not listed together in a cell differ significantly on that variable.

<table>
<thead>
<tr>
<th>Feeding Action:</th>
<th>Pick</th>
<th>Pnce</th>
<th>Jmp</th>
<th>SP</th>
<th>ST</th>
<th>DT</th>
<th>DC</th>
<th>DP</th>
<th>Dig</th>
<th>Jab</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prey Type:</td>
<td>sm123</td>
<td>sm123</td>
<td>s</td>
<td>sm12</td>
<td>sm12</td>
<td>s</td>
<td>sm12</td>
<td>sn1</td>
<td>sm1</td>
<td>sm123</td>
</tr>
<tr>
<td>Ingestion Rate per Minute (Ranks Only)</td>
<td>MC C</td>
<td>H</td>
<td>J</td>
<td>C</td>
<td>J R</td>
<td>J C</td>
<td>RRRRR</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td></td>
<td>JH</td>
<td>J</td>
<td>C</td>
<td></td>
<td>III</td>
<td></td>
<td></td>
<td>J</td>
<td>J</td>
<td></td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>C</td>
<td>CRCC</td>
<td>H</td>
<td>CC</td>
<td>H</td>
<td>C</td>
<td>CC</td>
<td>C</td>
<td>RR</td>
</tr>
<tr>
<td></td>
<td>JJJ</td>
<td>CHCJJ</td>
<td>C</td>
<td>JJHJ</td>
<td>HCCJ</td>
<td>HRRR</td>
<td>J</td>
<td>CCCJC</td>
<td>CCJ</td>
<td>CCCCR</td>
</tr>
<tr>
<td></td>
<td>CJRH</td>
<td>JRRHH</td>
<td>H</td>
<td>CHRH</td>
<td>CJJH</td>
<td>CJJJ</td>
<td>H</td>
<td>JJHJ</td>
<td>HHC</td>
<td>JJJJJ</td>
</tr>
<tr>
<td></td>
<td>RRRRR</td>
<td>RJRJR</td>
<td>R</td>
<td>RRJR</td>
<td>RRRR</td>
<td>RRR</td>
<td>RHHH</td>
<td>RRRR</td>
<td>RRRR</td>
<td>RRRR</td>
</tr>
</tbody>
</table>
Part One Chapter Five - Overlap and Partitioning of Resource Utilization

The last chapter described individual resource utilization by four species. This chapter describes the amount of overlap or partitioning of the available resource base between these species. Figure 1.5.1 presents community overlap matrices and individual species' niche breadths for the four corvid species. Four separate resources have been detailed - large scale habitat (between grass crops), use of individual fields at any one time, prey types and sizes, and feeding actions.

1.5.1.1 Nichee Overlap

Overlaps for grass crop type are quite high for all species pairs, with two groups (carrion crow-magpie and jackdaw-rook) sharing overlaps of c.0.95, with overlap between these two groups averaging 0.70 (figure 1.5.1a). When the use of individual fields within the study area is investigated at any one particular time, jackdaws and rooks occurred together on the same field at the same time quite frequently (alpha = 0.65), whilst carrion crows and magpies overlapped much less between themselves and the other two species (figure 1.5.1b). Two groups again appear if one
Individual species' niche breadths, community matrices (where $A = [\alpha(i,j)]$) and community dendograms for four basic resource states

(a) Habitat - $M$ = four categories, non-agricultural grass, grazed and ungrazed leys, and permanent pasture.

(b) Time-space - the use of individual fields at any one time; average alphas for six separate concourses of 36 grass fields.

(c) Prey type - small, medium and large earthworms, and small and medium other invertebrates; proportional use by number of individual prey items ingested.

(d) Foraging technique - proportional use of ten different feeding actions (only actions which led to the capture of a prey item included).
(a) Habitat (Between Grass Crops)

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.10</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.39</td>
<td>.69</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.14</td>
<td>.95</td>
<td>.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.45</td>
<td>.68</td>
<td>.95</td>
<td>.72</td>
<td></td>
</tr>
</tbody>
</table>

(b) Time/Space

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.19</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.34</td>
<td>.28</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.08</td>
<td>.65</td>
<td>.18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.30</td>
<td>.15</td>
<td>.27</td>
<td>.15</td>
<td></td>
</tr>
</tbody>
</table>

(c) Prey Type

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.61</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.54</td>
<td>.73</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.06</td>
<td>.42</td>
<td>.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.20</td>
<td>.56</td>
<td>.65</td>
<td>.81</td>
<td></td>
</tr>
</tbody>
</table>

(d) Foraging Technique

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.41</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.33</td>
<td>.43</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.31</td>
<td>.32</td>
<td>.73</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.24</td>
<td>.35</td>
<td>.84</td>
<td>.78</td>
<td></td>
</tr>
</tbody>
</table>
1.5 Overlap and Partitioning

considers overlap in prey type (different sized earthworms and other invertebrates), but this time it is carrion crow-rook (0.73) and jackdaw-magpie (0.81) who make up the two groups, with average overlap between these two groups of 0.52 (figure 1.5.1c). Finally, yet another different pattern emerges when foraging technique is taken into account. This time carrion crow and magpie overlap highest (0.84) and both overlap highly with the jackdaw (average = 0.75); but the rook is well separated from these three other species (average = 0.37).

Reviews by Cody (1974a) and Schoener (1974a) suggest that habitat selection is the most frequent mechanism in temperate areas acting to reduce overlap between species. Overlap between grass crops was in fact high for these species (as was overlap between all available habitat types - figure 1.5.2), although the choice of habitat in terms of the use of individual fields at the same time did produce low overlaps for most species pairs.

Hespenheide's (1975) review further suggests that most species show lower overlap in foraging behaviour than in prey taxonomy - the implication being that prey taken by different feeding techniques come from different prey populations if the behaviours differ in their relative success rates on different prey. Overlaps in prey (given the crude measure available) in the present study were generally
Figure 1.5.2

Individual species' niche breadths, community matrices (where $A = \{\alpha(i,j)\}$) and community dendograms for habitat use

(a) All crop types, both arable and grassland.

(b) Four grass crops only.
### (a) All Crop Types

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>Niche Overlap Breadth Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rook</td>
<td>0.09</td>
<td>-</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>0.36</td>
<td>0.65 -</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>0.18</td>
<td>0.84 0.73 -</td>
</tr>
<tr>
<td>Magpie</td>
<td>0.29</td>
<td>0.65 0.82 0.68 -</td>
</tr>
</tbody>
</table>

### (b) Grass Crop Types Only

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>Niche Overlap Breadth Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rook</td>
<td>0.10</td>
<td>-</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>0.39</td>
<td>0.69 -</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>0.14</td>
<td>0.96 0.73 -</td>
</tr>
<tr>
<td>Magpie</td>
<td>0.45</td>
<td>0.68 0.95 0.72 -</td>
</tr>
</tbody>
</table>
higher than foraging technique overlap, but this was not
the case in every pair-wise comparison, and in any case the
measure provided only an extremely gross estimate of taxon-
omy.

Neither was it found, as is often the case (e.g. Cody
1974a, Lack 1971, Schoener 1974a), that high overlap on one
resource went consistently with low overlap on another
(though of course only six points are available to test
this with), except for prey type and feeding action in
their respective overlaps with individual field use in
time, where this was (more or less) the case. The signifi-
cance of this is discussed in chapter seven.

1.5.1.2 Niche Breadth

Asymmetry in any species-pair overlap is determined by
the relative niche-breadths of the two species making up
the pair. Niche breadths of the rook and jackdaw for grass
crop choice were lower than those for the carrion crow and
magpie (figure 1.5.1a), reflecting these two species' heavy
use of permanent pasture (section 1.4.3).

At any one time, most jackdaws occupied only a few of
the grass fields available, and rooks also occupied fewer
of those available than did carrion crows and magpies,
which had similar niche breadths (figure 1.5.1b). This
pattern reflects the A-type territoriality of the latter two species, causing an even dispersion over the available area, and the gregariousness of the other two species (see figure 1.4.1 and section 1.2.3). This pattern remains the same when arable crops are included in the analysis, except that magpies show more clumping of use of arable land (figure 1.5.4c) - perhaps an indication that the breakdown of A-territoriality mentioned in section 1.2.3 occurs more frequently on arable crops than grass ones.

Nichee breadths for feeding actions are rather similar for all species, but there are considerable differences on prey type, with jackdaws showing specialisation and carrion crows and rooks generalisation. However, this could be the result of the classification of prey types into only a few categories - it is possible that jackdaws show greater variation within the category of 'small other invertebrate' which made up the bulk of their diet (table 1.4.5). It can be concluded, though, that of the four species jackdaws were most restricted in their choice of gross size class of prey and their avoidance of earthworms.

In summary, there was asymmetry in overlaps between jackdaws and rooks with carrion crows and magpies in habitat and field use in time, caused by the former two species great preference for permanent pasture and their gregarious nature; these two combined resulted in most members of
these two species occurring in only a few of the available grass fields at any one time. However, with regard to feeding techniques asymmetries were less, and apparent asymmetries in prey type may be real or simply the result of the gross taxonomic classification employed.

1.5.2 Space - Time

Since this is of some importance in later discussion, the overlap of birds in space in time will be analysed in a little more detail. Figure 1.5.3 is a stylised representation of the study area maps of figure 1.4.1 which illustrates the use of the different grass fields available. Only four of the 36 grass fields in the area were not used at all at the time of these six censuses - all of them ungrazed grass. Thus most of the available grass fields were utilised by birds at some time, but mostly at different times, and at different times by different species.

The resulting low overlap of most species-pairs on individual fields at any one time is quantified in figure 1.5.4. Rooks and jackdaws tended to occur on the same field at the same time quite frequently (alphas = 0.65 on grass fields, 0.64 on arable), but overlaps for every other pairwise comparison were low (figure 1.5.4a and c). This was not due to species using different fields as such, but to using some of the same fields but at different times -
Figure 1.5.3

Individual grass field use by four Corvid species on six different census dates

NAG = Non-agricultural grass
TLU = Ungrazed temporary ley
TLG = Grazed temporary ley
PP = Permanent pasture

C = Carrion crow(s) present
J = Jackdaw(s) present
H = Magpie(s) present
R = Rook(s) present

Vertically, each rectangle represents a different field; horizontally, the same field at a different time.
Figure 1.5.4

Individual species' niche breadths, community matrices (where $A = [\alpha(i,j)]$) and community dendograms for field use in time

(a) Field use at one time - average alphas for six separate censuses of 36 grass fields

(b) Use of 36 grass fields ignoring time.

(c) Field use at one time - average alphas for six separate censuses of 27 arable fields.

(d) Use of 27 arable fields ignoring time.
(a) Field Use at One Time

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.19</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.34</td>
<td>.28</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.08</td>
<td>.65</td>
<td>.18</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.30</td>
<td>.15</td>
<td>.27</td>
<td>.15</td>
<td>-</td>
</tr>
</tbody>
</table>

(b) Field Use Ignoring Time

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.21</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.47</td>
<td>.43</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.17</td>
<td>.73</td>
<td>.38</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.30</td>
<td>.37</td>
<td>.43</td>
<td>.42</td>
<td>-</td>
</tr>
</tbody>
</table>
### (c) Field Use at One Time

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.11</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.39</td>
<td>.28</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.05</td>
<td>.64</td>
<td>.35</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td>Magpie</td>
<td>.18</td>
<td>.20</td>
<td>.23</td>
<td>.31</td>
<td>-</td>
</tr>
</tbody>
</table>

### (d) Field Use Ignoring Time

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.20</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.27</td>
<td>.41</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.08</td>
<td>.66</td>
<td>.47</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.21</td>
<td>.34</td>
<td>.32</td>
<td>.32</td>
<td>-</td>
</tr>
</tbody>
</table>
this is highlighted by the fact that if one calculates overlaps for fields ignoring when they were occupied by a species, then all overlap values increase considerably except for jackdaw-rook (on both arable and grass) and jackdaw-magpie on arable.

Unfortunately it is not possible to calculate the statistical significance of these species' distributions to see if species were actively avoiding one another, or whether the low overlaps occurred by chance given the large number of fields available in which birds could forage. There are two reasons for this. Firstly, it is impossible to know how many of the fields were actually unavailable to birds due to unacceptably low levels of prey density, human disturbance, or whatever. Thus the 'absent-absent' cell of a 2x2 contingency table of species 'A' presence-absence against species 'B' presence-absence will be inflated by an unknown degree by the inclusion of such fields, tending to produce expected frequencies in the 'present-present' cell underestimated by an unknown degree, and thus increasing the likelihood of producing spurious significant results. Secondly, cell entries are almost certainly not independent of one another in each case - for example, given one rook's choice of a field in respect to carrion crow absence or presence, a second rook's choice may not be influenced solely by carrion crow presence or absence but also by where the first rook went, given the gregarious nature of
this species. Similarly, the choice of a carrion crow made with respect to the presence or absence of other species will also affect the choice of a second crow, irrespective of the distribution of the other species, depending on whether the first carrion crow is an A-territory holder or not, and if it is, whether it is the second bird's mate or not.

However, although we cannot test the possible causes of the behaviour which produces the observed distribution of these species with respect to one another, we can portray the consequences of such behaviour. Table 1.5.1 gives the proportion of times each species occurred on a field at the same time as a small or large number (or in the absence of) each other species. These data suggest that jackdaws and rooks almost always occurred together, but that this was an asymmetrical pattern – jackdaws were almost never without rooks (only on 5.4% of occasions), while rooks were quite frequently to be found without jackdaws (37.5% of occasions). This may suggest that jackdaws were more actively flocking with rooks rather than vice-versa.

Most of the other species' comparisons showed that each species tended to forage apart from any other particular species on between 50 and 60% of occasions. However, carrion crows foraged in the absence of jackdaws on 74.3%
Table 1.5.1

Proportion of foraging time spent in the absence of, or with differing flock sizes of, other Corvid species on grassland

Percent within each subject species and each other Corvid species; results from 249 censused grass fields containing 926 rooks, 441 jackdaws, 156 carrion crows and 160 magpies.
<table>
<thead>
<tr>
<th>Species</th>
<th>Absent or Present</th>
<th>Rook</th>
<th>C.Crow</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook Absent</td>
<td>--</td>
<td>62.9</td>
<td>5.4</td>
<td>63.5</td>
<td></td>
</tr>
<tr>
<td>Flock 1-5</td>
<td>--</td>
<td>18.6</td>
<td>18.9</td>
<td>17.5</td>
<td></td>
</tr>
<tr>
<td>Size 6-20</td>
<td>--</td>
<td>11.4</td>
<td>35.1</td>
<td>9.5</td>
<td></td>
</tr>
<tr>
<td>21-40</td>
<td>--</td>
<td>5.7</td>
<td>29.7</td>
<td>7.9</td>
<td></td>
</tr>
<tr>
<td>&gt; 40</td>
<td>--</td>
<td>1.4</td>
<td>10.8</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Crow Absent</td>
<td>53.6</td>
<td>--</td>
<td>51.3</td>
<td>74.6</td>
<td></td>
</tr>
<tr>
<td>Flock 1-5</td>
<td>44.6</td>
<td>--</td>
<td>45.9</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Size 6-20</td>
<td>1.8</td>
<td>--</td>
<td>2.7</td>
<td>11.1</td>
<td></td>
</tr>
<tr>
<td>21-40</td>
<td>0.0</td>
<td>--</td>
<td>0.0</td>
<td>7.9</td>
<td></td>
</tr>
<tr>
<td>&gt; 40</td>
<td>0.0</td>
<td>--</td>
<td>0.0</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>Jackdaw Absent</td>
<td>37.5</td>
<td>74.3</td>
<td>--</td>
<td>50.8</td>
<td></td>
</tr>
<tr>
<td>Flock 1-5</td>
<td>26.8</td>
<td>8.6</td>
<td>--</td>
<td>47.6</td>
<td></td>
</tr>
<tr>
<td>Size 6-20</td>
<td>25.0</td>
<td>12.9</td>
<td>--</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>21-40</td>
<td>8.9</td>
<td>4.3</td>
<td>--</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>&gt; 40</td>
<td>1.8</td>
<td>0.0</td>
<td>--</td>
<td>0.0</td>
<td></td>
</tr>
<tr>
<td>Magpie Absent</td>
<td>58.9</td>
<td>55.7</td>
<td>56.8</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Flock 1-5</td>
<td>37.5</td>
<td>38.6</td>
<td>35.1</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Size 6-20</td>
<td>3.6</td>
<td>5.7</td>
<td>8.1</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>21-40</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>&gt; 40</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>--</td>
<td></td>
</tr>
<tr>
<td>Any Absent</td>
<td>16.1</td>
<td>41.4</td>
<td>0.0</td>
<td>41.3</td>
<td></td>
</tr>
<tr>
<td>Corvid 1-5</td>
<td>41.1</td>
<td>30.0</td>
<td>18.9</td>
<td>27.0</td>
<td></td>
</tr>
<tr>
<td>Species 6-20</td>
<td>30.4</td>
<td>14.3</td>
<td>32.4</td>
<td>14.3</td>
<td></td>
</tr>
<tr>
<td>Flock 21-40</td>
<td>8.9</td>
<td>7.1</td>
<td>32.4</td>
<td>6.3</td>
<td></td>
</tr>
<tr>
<td>Size &gt; 40</td>
<td>3.6</td>
<td>7.1</td>
<td>16.2</td>
<td>11.1</td>
<td></td>
</tr>
</tbody>
</table>
of occasions, and magpies without carrion crows on 74.6%. In total this meant that jackdaws were never observed without another Corvid species present. Although one does sometimes see jackdaws foraging alone, the census results indicate how rare this was in winter - out of 441 jackdaws censused in 249 different grass fields, none were in a field empty of other Corvids. Rooks foraged alone on 16.1% of occasions, and carrion crows and magpies on 41.4 and 41.3% of occasions respectively.

These patterns of species' distribution will be referred to in later chapters, since they will affect the level of prey availability for each species in any particular field depending on several factors - for example how much the species overlap in diet and microhabitat use, how much they disturb or facilitate one another's foraging effort, and how quickly (or otherwise) prey densities renew themselves.

1.5.3 Foraging Behaviour

Most data in related studies are collected and analysed for each resource dimension separately, as was done in section 1.5.1 above, due to the frequent difficulty of measuring each simultaneously (e.g. Pianka 1981). However, this procedure gives rise to problems when an attempt is made to synthesise the pattern of overlap on the
different dimensions to produce some estimation of the overall degree of overlap or partitioning of the total resource base between species. Traditionally overlap estimates for separate resources are combined by the simple mathematical operation of summation and averaging, or multiplication (e.g. Cody 1974a; or sometimes a combination of the two, e.g. Rusterholz 1981) of the separate alphas. Needless to say such an operation is open to considerable error since to what extent overlap on one dimension determines (summation method) or is orthogonal to (product method) overlap on another can in some cases only be judged by intuition (e.g. May 1975).

Of the four resources in the present study, prey taken from one crop type clearly represents a separate prey resource to prey taken from another, since chapter three has demonstrated reliable differences between crop types in prey densities, and since migration other than dispersal into unfilled habitat is likely to be minimal for these invertebrates in winter (e.g. Edwards & Lofty 1977, Wallwork 1976). In addition it may be (as will be discussed in more detail later) that invertebrate prey taken from a field at one time are effectively separate to that taken at another, since these prey are renewing (to some extent) in their availability, since they were hard to find by a foraging bird, and one item hidden on one visit could move and be available on a second. However, it is difficult to
judge *a priori* whether the two dimensions of prey type and size and feeding action are independent or not. There are two senses in which this should be considered; firstly whether a prey type taken by one feeding action comes from a separate population to the same prey type taken by a different feeding action; and secondly whether some feeding actions are used to capture only certain prey types, and other actions for other prey types.

The relevance of the latter to the choice of sum or product alpha as the appropriate description of true overlap may be illustrated by the following simple case. Consider a species which uses two feeding actions and which takes two prey types. In this simple case suppose it can either take half of each prey type by each feeding action (table a) or all of one prey type by one feeding action and all of the other prey type by the second action (table b):

<table>
<thead>
<tr>
<th>(a)</th>
<th>Feeding Action</th>
<th>(b)</th>
<th>Feeding Action</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>A</td>
</tr>
<tr>
<td>A</td>
<td>.25</td>
<td>.25</td>
<td>.50</td>
</tr>
<tr>
<td>B</td>
<td>.25</td>
<td>.25</td>
<td>.50</td>
</tr>
<tr>
<td></td>
<td>.50</td>
<td>.50</td>
<td></td>
</tr>
</tbody>
</table>

In each case if the proportional use of feeding actions and prey types are considered separately, the species uses each
action in the same proportion and takes each prey type with the same frequency (compare the marginal values to each table). However, inspection of the table entries reveals that a product method of combining the marginal scores would be an appropriate way of describing the true relationship between the proportional use of each feeding action to take each prey type for table a (0.5 x 0.5 = 0.25) whilst a summation method would yield an accurate estimate for table b (0.5 + 0.5 / 2 = 0.5). The same principle will apply when estimating overlap indices between two species.

During the present study prey type and feeding action were in fact measured simultaneously, and thus it is possible to investigate the latter situation empirically by calculating overlap indices for the proportional use of each feeding action for the capture of each prey type. In addition, the data could be transformed to weight the separate prey types by their relative calorific or nutritive value, and then recalculate proportional overlap in these terms rather than in terms of numbers of individual items ingested.

These overlap matrices are presented in figure 1.5.5. This procedure indicates that in terms of numbers of items ingested by each feeding action, carrion crow-magpie and jackdaw-magpie overlap quite highly (alphas = 0.62 and 0.66
respectively), but that the other pairwise overlap coefficients are less than 0.5. In terms of the calorific or nutritive value of intake by different feeding actions, all species except for jackdaw-magpie (where $\alpha = 0.59$) overlap less than 0.5, with overlaps between the rook and the other three species being the lowest.

If one calculates sum and product alphas from the data in figure 1.5.1c and d, summation alphas overestimate, and product alphas underestimate (for every pairwise comparison), the true overlap as revealed in figure 1.5.5a. However, summation alphas in each case overestimated more than product alphas underestimated true overlap. This implies that, for the situation investigated during the current study, independent measurement of these two resource dimensions will lead to error when synthesis is attempted by the combination of independently calculated alphas. When sum and product alphas are calculated for data transformed to represent proportional intake of prey of different calorific value, however, sum alpha grossly overestimates the true alphas given in figure 1.5.5b, whilst product alpha either produces very close agreement or slightly underestimates the true overlap. This suggests that for the most part any of the prey types could be taken by any of the feeding actions, but that at least one of the feeding actions was used to catch a restricted range of prey (e.g. pounce - see description in section
Figure 1.5.5

Individual species' niche breadths, community matrices (where $A = \{\alpha(i,j)\}$) and community dendograms for prey types taken by different feeding actions

(a) Overlap in proportional use as numbers of individual items ingested.

(b) Proportional use as relative calorific value of items (kcal/g).

(c) Proportional use as relative nutritive value of items (grams of protein-containing material).
(a) Numbers

<table>
<thead>
<tr>
<th>Niche Overlap</th>
<th>Breadth</th>
<th>Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>(B st.)</td>
<td>R</td>
</tr>
<tr>
<td>Rook</td>
<td>.37</td>
<td>-</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.27</td>
<td>.43</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.10</td>
<td>.26</td>
</tr>
<tr>
<td>Magpie</td>
<td>.12</td>
<td>.31</td>
</tr>
</tbody>
</table>

(b) Calorific Intake

<table>
<thead>
<tr>
<th>Niche Overlap</th>
<th>Breadth</th>
<th>Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>(B st.)</td>
<td>R</td>
</tr>
<tr>
<td>Rook</td>
<td>.23</td>
<td>-</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.16</td>
<td>.23</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.19</td>
<td>.11</td>
</tr>
<tr>
<td>Magpie</td>
<td>.13</td>
<td>.15</td>
</tr>
</tbody>
</table>

(c) Protein Intake

<table>
<thead>
<tr>
<th>Niche Overlap</th>
<th>Breadth</th>
<th>Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>(B st.)</td>
<td>R</td>
</tr>
<tr>
<td>Rook</td>
<td>.22</td>
<td>-</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.15</td>
<td>.23</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.16</td>
<td>.10</td>
</tr>
<tr>
<td>Magpie</td>
<td>.14</td>
<td>.14</td>
</tr>
</tbody>
</table>
Having shown that the two dimensions are mainly statistically independent, however, does not necessarily imply that the prey taken by different feeding actions come from separate prey populations. However, the feeding actions may be grouped into different microhabitats which are (as data in chapter three has shown) independent of one another - i.e. the microhabitats of above and beneath the soil surface, within or beneath animal dung, and beneath other surface litter. The overlap matrices are given in figure 1.5.6. In general, the differences between these values and those in figure 1.5.5 are trivial, though the alpha for jackdaw-magpie is quite a lot higher when feeding actions are grouped into microhabitats.

In general microhabitat-by-prey will be the most error-free measure, since (for example) a small invertebrate taken by a surface probe may well effectively come from the same prey population as one taken by a surface pick - whereas one taken from beneath the soil surface will be in almost all cases from a separate population to one taken from above (with the possible exception of a few special cases, such as a particular slug species the same individual of which may forage partly above the surface and partly beneath). Medium and large earthworms taken above the surface by carrion crows but below the surface by rooks
Figure 1.5.6

Individual species' niche breadths, community matrices (where A = [alpha(i,j)]) and community dendograms for prey types taken in different microhabitats

(a) Overlap in proportional use as numbers of individual items ingested.

(b) Proportional use as relative calorific value of items (kcal/g).

(c) Proportional use as relative nutritive value of items (grams of protein-containing material).
(a) Numbers

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
<th>Niche Overlap</th>
<th>Breadth Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.36</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.40</td>
<td>.42</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.13</td>
<td>.27</td>
<td>.43</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.16</td>
<td>.29</td>
<td>.62</td>
<td>.79</td>
<td>-</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(b) Calorific Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
<th>Niche Overlap</th>
<th>Breadth Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.25</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.26</td>
<td>.23</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.28</td>
<td>.22</td>
<td>.41</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.17</td>
<td>.15</td>
<td>.48</td>
<td>.72</td>
<td>-</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(c) Protein Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>(B st.)</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>M</th>
<th>Niche Overlap</th>
<th>Breadth Indices</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td>.23</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.24</td>
<td>.23</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.26</td>
<td>.20</td>
<td>.37</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.18</td>
<td>.14</td>
<td>.41</td>
<td>.73</td>
<td>-</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
may not belong to different populations as such, but the predatory behaviour, feeding apparatus and flocking tendencies which differ between the species (discussed elsewhere) make them separate prey populations to some extent. Earthworms below the soil surface may not be available to carrion crows, those above the surface may not be available to rooks. However, there are feeding actions grouped together by this process which do not necessarily sample the same prey population - for example prey taken by jumping will, in a proportion of cases, form an independent source of prey to those taken by a surface pick (e.g. an adult dipteran taken in flight and at rest represent the same prey population, but a flying dipteran and a surface larva do not). Thus true alphas will lie somewhere between those given in figures 1.5.5 and 1.5.6. To be conservative, further analyses in the thesis are either made by microhabitat only, or by both and the results compared.

1.5.4 Discriminant Function Analysis

The results presented so far in this chapter can only indicate pairwise overlap between species. Such a description of the data is limited since it does not reveal whether each species occupies a unique area of niche hyperspace with varying amounts held in common with each other species; or whether the area held in common by species 'A'
with species 'B' is completely separate from the area held in common with species 'C'. This is clearly very important when trying to assess the overall position of any one species in the web of the four species' utilisation of the total resource base.

Secondly, alpha matrices provide only a description of overlap in resource use by the species and not a test of whether the revealed pattern occurs by chance (though see section 1.7.1 below) or whether the species differ significantly from one another in resource use. Finally, the relative importance of the different elements of the particular resource in question is not revealed in an alpha matrix.

All of these can be provided by the use of a stepwise discriminant function analysis. The results of two such analyses are reported here. The first quantified discrimination between species in terms of the rate of ingestion (*) of the different prey types from the different microhabitats, the second employed feeding actions in place of microhabitats. It should be noted that several variables could not be included in these analyses since one or more

(*) Since the transformations to express calorific and nutritive value of intake rates were linear for each variable, the discriminant function analyses (and any other statistical routine based on sums of squares or ranks) of course produce identical output for runs on either original or transformed data.
of the species concerned did not capture a particular prey type in a particular microhabitat, or by a particular feeding action. Thus variables which may be very important biologically in separating species may have been omitted. In addition, it will be remembered that the prey type classifications are gross. Thus the degree of discrimination between species revealed by these analyses will be a conservative estimate of true separation between species.

Table 1.5.2 summarises the results of a stepwise discriminant function analysis for prey types taken by the four Corvid species in the different microhabitats. Table 1.5.2b indicates that the first two functions derived account for 99% of the discriminating information available in the measurement variables, and that these two functions discriminate significantly between the four species.

The loadings of the variables on the different functions allow very clear biological identification of the functions. The first function is characterised by tendencies to take prey, particularly small earthworms, beneath the soil surface, with a weaker tendency to take small earthworms from beneath litter on the soil surface, and an avoidance of small invertebrates above the soil surface. Function two is defined by tendencies to catch medium sized invertebrates above the soil surface and from dung, and to avoid taking small invertebrates from these two microhabi-
Table 1.5.2  

**Discriminant function analysis summary table for invertebrate prey types taken in different micro-habitats**

Only those variables which were included in the discriminant functions by the stepwise algorithm are listed; in addition some variables were not entered into the program because of gross violations of assumptions (see Methods).

Species means and univariate significance tests for all measured variables - both those included in the DF analysis and those omitted - are tabulated in appendix 7.8 and summarized in figure 1.4.4.

Although several variables recorded for only one or some of the four species - and therefore probably biologically important (see text discussion) - were omitted from the analysis because of gross violations of assumptions, significant separation between the four species was revealed.

(a) Classification table listing the proportion of each species predicted as most likely to be of that species, or one of the other three, based on the discriminating information available in the measurement variables.

(b) Standardized, rotated coefficients for each variable on the three derived discriminant functions (only coefficients of 0.20 or greater are included).

<table>
<thead>
<tr>
<th>Actual Species</th>
<th>N</th>
<th>Carrion Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrion Crow</td>
<td>90</td>
<td>51.1%</td>
<td>6.7</td>
<td>4.4</td>
<td>37.8</td>
</tr>
<tr>
<td>Rook</td>
<td>69</td>
<td>4.3</td>
<td>58.0</td>
<td>5.3</td>
<td>31.9</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>60</td>
<td>5.0</td>
<td>0</td>
<td>65.0</td>
<td>30.0</td>
</tr>
<tr>
<td>Magpie</td>
<td>70</td>
<td>22.9</td>
<td>0</td>
<td>25.7</td>
<td>51.4</td>
</tr>
</tbody>
</table>

(a) Overall percentage of cases classified correctly = 55.7%
(b)

<table>
<thead>
<tr>
<th>Micro-habitat</th>
<th>Prey Type</th>
<th>DF1</th>
<th>DF2</th>
<th>DF3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beneath Soil Surface</td>
<td>Small Invertebrate</td>
<td>.47</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td>.62</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium Earthworm</td>
<td>.20</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Large Earthworm</td>
<td>.34</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Above Soil Surface</td>
<td>Small Invertebrate</td>
<td>-.48</td>
<td>-.71</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium Invertebrate</td>
<td></td>
<td>.75</td>
<td></td>
</tr>
<tr>
<td>Within-beneath Dung</td>
<td>Small Invertebrate</td>
<td></td>
<td>-.30</td>
<td>.80</td>
</tr>
<tr>
<td></td>
<td>Medium Invertebrate</td>
<td></td>
<td>.75</td>
<td>-.32</td>
</tr>
<tr>
<td>Within-beneath Stones/Clods</td>
<td>Small Invertebrate</td>
<td>.21</td>
<td></td>
<td>.78</td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<p>| | | | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalue</td>
<td>.830</td>
<td>.477</td>
<td>.009</td>
<td></td>
</tr>
<tr>
<td>Explained Variance (%)</td>
<td>63.1</td>
<td>36.2</td>
<td>.7</td>
<td></td>
</tr>
<tr>
<td>Cumulative Variance (%)</td>
<td>63.1</td>
<td>99.3</td>
<td>100.0</td>
<td></td>
</tr>
<tr>
<td>With 3 Discriminant Functions Included:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wilk's Lambda</td>
<td></td>
<td>.367</td>
<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
<td></td>
<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td></td>
<td>***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>With DF1 removed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wilk's Lambda</td>
<td></td>
<td>.671</td>
<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
<td></td>
<td>18</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td></td>
<td>***</td>
<td></td>
<td></td>
</tr>
<tr>
<td>With DF1 and DF2 removed:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wilk's Lambda</td>
<td></td>
<td>.991</td>
<td></td>
<td></td>
</tr>
<tr>
<td>df</td>
<td></td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>p</td>
<td></td>
<td>p=.96</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
tats. The final, non-significant, function is characterised by tendencies to catch small invertebrates from dung or beneath other surface litter, and to avoid taking medium invertebrates from dung.

The positions of the four species in 3-dimensional discriminant space is illustrated in figure 1.5.7a, where summary labels are given to the three functions derived. Each species differed significantly from every other species on at least two of the three functions (separate t-tests on discriminant scores). Since only the first two functions provided significant Wilk's lambdas, the distribution of the species on these two functions is analysed further. Figure 1.5.7b indicates that rooks were mainly associated with function one, which can be seen to consist mainly of prey taken beneath the soil surface, and were more weakly associated with a tendency to take smaller sized invertebrates from elsewhere. Carrion crows were just to the negative side of the below-surface function, but were more strongly positively associated with taking medium invertebrates above the soil surface and from animal dung. Jackdaws tended to avoid foraging beneath the soil surface and showed the same preference for foraging above the surface and from dung as carrion crows, but took mainly small invertebrates rather than show the carrion crow's preference for medium sized ones. Magpies foraged mostly above the soil surface but were more intermediate in their
Summary figures of four Corvid species' positions in discriminant space - measurement variables were prey types taken in different microhabitats

(a) Centroids of four Corvid species in 3-dimensional discriminant space.

(b) Species' centroids on the first two discriminant functions (with 95% confidence estimates about the centroids) superimposed on a plot of the standardized, rotated coefficients of the measurement variables. The non-overlap of the ellipses indicates the significant separation of the four species. Each species pair differed significantly on at least two of the three functions derived (see text).

(c) Niche breadth and overlap of four species expressed as 95% probability ellipses for species' distributions on the first two discriminant functions; c.95% of observations for each species fall within each ellipse, hence their greater size than the confidence ellipses based on the standard errors of the mean figured in (a).
choice of different sized invertebrates from other microhabitatst compared to carrion crows and jackdaws.

Although species were significantly separated from one another in discriminant space, there was still a considerable degree of overlap between them, as is shown by figure 1.5.7c and table 1.5.2a. The figure shows that the three *Corvus* species retained a unique segment of discriminant space to themselves, but that the niche of the magpie is almost completely contained within the niches of the other three species. Carrion crows had the widest niche, with jackdaws and magpies being more restricted, but the variation in niche breadths between species was not very great. These patterns are quantified more precisely in the classification table which shows that overall 55.7% of individual birds could be identified to their correct species on the basis of their rates of foraging for these different prey types in the different microhabitats. The three *Corvus* species tended to be classified as magpies rather than as another *Corvus* species if a mistake was made as to their true species' identity.

The pattern revealed by replacing microhabitats by feeding actions is very similar. Table 1.5.3b indicates that the first two functions are virtually identical, but the third is slightly stronger this time, contributing a (significant) 9% of the discriminating information avail-
Table 1.5.3

Discriminant function analysis summary table for invertebrate prey types taken by different feeding actions

Only those variables which were included in the discriminant functions by the stepwise algorithm are listed; in addition some variables were not entered into the program because of gross violations of assumptions (see Methods).

Species means and univariate significance tests for all measured variables - both those included in the DF analysis and those omitted - are tabulated in appendix 7.9 and summarized in figure 1.5.5.

Although several variables recorded for only one or some of the four species - and therefore probably biologically important (see text discussion) - were omitted from the analysis because of gross violations of assumptions, significant separation between the four species was revealed.

(a) Classification table listing the proportion of each species predicted as most likely to be of that species, or one of the other three, based on the discriminating information available in the measurement variables.

(b) Standardized, rotated coefficients for each variable on the three derived discriminant functions (only coefficients of 0.20 or greater are included).

(a) Overall percentage of cases classified correctly = 55.7%

<table>
<thead>
<tr>
<th>Actual Species</th>
<th>Predicted Species Membership</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Carriage Crow</td>
</tr>
<tr>
<td>Carriage Crow</td>
<td>51.1%</td>
</tr>
<tr>
<td>Rook</td>
<td>2.2</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>5.0</td>
</tr>
<tr>
<td>Magpie</td>
<td>22.9</td>
</tr>
</tbody>
</table>
## Discriminant Function

<table>
<thead>
<tr>
<th>Micro-habitat</th>
<th>Prey Type</th>
<th>DF1</th>
<th>DF2</th>
<th>DF3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deep Probe</td>
<td>Medium Invertebrate</td>
<td>.40</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td>.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jab</td>
<td>Small Invertebrate</td>
<td>.29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td>.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dig</td>
<td>Medium Invertebrate</td>
<td>.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stone/Clod Turn</td>
<td>Small Invertebrate</td>
<td></td>
<td>-.41</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td>-.27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dung Turn</td>
<td>Small Invertebrate</td>
<td></td>
<td>-.74</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium Invertebrate</td>
<td>.93</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surface Pick</td>
<td>Small Invertebrate</td>
<td>-.33</td>
<td>-.57</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Small Earthworm</td>
<td>.54</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pounce</td>
<td>Medium Invertebrate</td>
<td></td>
<td>.92</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Medium Invertebrate</td>
<td>.26</td>
<td>-.31</td>
<td></td>
</tr>
<tr>
<td>Surface Probe</td>
<td>Small Invertebrate</td>
<td></td>
<td>.44</td>
<td>-.42</td>
</tr>
<tr>
<td></td>
<td>Medium Invertebrate</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| Eigenvalue          | .636               | .462    | .106    |
| Explained Variance (%) | 52.7              | 38.3    | 9.0     |
| Cumulative Variance (%) | 52.7              | 91.0    | 100.0   |

With 3 Discriminant Functions Included:

- Wilk's Lambda: .377 (df = 48, P = ***)

With DF1 removed:

- Wilk's Lambda: .617 (df = 30, P = ***)

With DF1 and DF2 removed:

- Wilk's Lambda: .902 (df = 14, P = *)
able. Its interpretation is somewhat different this time, being characterised by tendencies to pounce or surface probe for small invertebrates and to avoid using these actions for catching medium invertebrates. Figure 1.5.8a indicates that magpies were positively associated with this new function and carrion crows negatively associated. Figures 1.5.8b and c, dealing with the first two important functions which account for 91% of explained variance, are very similar to the corresponding figures for microhabitats. The classification tables are also very similar, except that slightly fewer magpies and slightly more rooks are incorrectly classified, and that the incorrectly classified rooks tend to be classed by the algorithm as magpies.
Figure 1.5.8

Summary figures of four Corvid species' positions in discriminant space - measurement variables were prey types taken by different feeding actions

(a) Centroids of four Corvid species in 3-dimensional discriminant space.

(b) Species' centroids on the first two discriminant functions (with 95% confidence estimates about the centroids) superimposed on a plot of the standardized, rotated coefficients of the measurement variables. The non-overlap of the ellipses indicates the significant separation of the four species. Each species pair differed significantly on at least two of the three functions derived (see text).

(c) Niche breadth and overlap of four species expressed as 95% probability ellipses for species' distributions on the first two discriminant functions; c.95% of observations for each species fall within each ellipse, hence their greater size than the confidence ellipses based on the standard errors of the mean figured in (a).
This chapter describes the effects that the absence or presence (in varying numbers) of other Corvid species had on the prey intake rates of each species in turn. Short-term effects like this may occur due to direct competition effects (interference or exploitation), disturbance of foraging behaviour or of prey into anti-predator responses, or to negative or positive relationships between the densities of two species' favoured prey types.

We may distinguish between a species' fundamental niche (the niche occupied without any other species present), its partial niche (the niche occupied when any other particular species is present), and its realised niche (the niche occupied when all guild members are present) (e.g. Vandermeer 1972). This differentiation may be applied to other species' absence or presence both in terms of geographical allopatry or sympatry, or to the short-term effects of the presence or absence of species' while the subject species is foraging in a particular field. The data in this chapter describe the latter situation. The data in chapters 1.4 and 1.5 described the realised niches of these four Corvid species and their resulting overlap with each other species. This chapter
1.6 Partial and Fundamental Niches

considers the data available to describe partial and fundamental niches.

1.6.1 Changes in Prey Intake Rate

Figure 1.6.1 presents mean intake rates in the presence and absence of other Corvid species. Few significant effects were found, but in many cases the number of observations in either presence or absence meant that a test for the significance of effects was likely to reveal only the very strongest of genuine tendencies.

Figure 1.6.1a presents the effect on overall calorific value of intake rate of each separate species. (*) The presence of carrion crows and magpies whilst rooks were foraging was associated with a decrease in the overall intake rates of rooks; the effect of carrion crow presence did not reach statistical significance (analysis of variance: \( p = 0.108 \)), whilst the mean for magpies was based on only six observations. Jackdaws had an opposite, facilitative effect; this was not a significant main effect, but the opposite tendencies of carrion crow and jackdaw pres-

(*) Throughout the rest of the chapter I use the term 'affected by' the absence-presence of other species purely in a statistical sense. The discussion contains some circumstantial evidence and argument on the causality of the observed effects, but it should be remembered that further designed fieldwork would be necessary to assign causality in any rigorous sense.
Figure 1.6.1

Effect of the absence or presence of other Corvid species on prey intake rates

(a) Effects on overall calorific value of intake rate.

Effects on calorific value of intake rate of each prey type taken in each microhabitat: (b) rook intake rates, (c) carrion crow intake rates, (d) jackdaw intake rates, and (e) magpie intake rates.

The bars in figures (b) to (e) should not be misinterpreted: the join between the black and white areas of each bar represents mean intake rate irrespective of the presence or absence of other species, whilst the far end of the black area represents mean intake rate in the presence of the other species, and the far end of the white area mean intake rate in the absence of that species. (No more correct way of representing different means could be found which conveyed the necessary information effectively.) Significant effects (anova: p < 0.05) are flagged by asterisks.
SUBJECT SPECIES:

ROOK

CARRION CROW

JACKDAW

MAPLE

MEAN PREY INTAKE RATE (oral min)

ABSENT PRESENT

ABSENT PRESENT

ABSENT PRESENT

OTHER CORVID SPECIES

(CROW PRESENT: N = only 9)

(CARRION CROW: N = only 5)

(JACKDAW: N = only 16)

(NO SIGNIFICANT EFFECTS)

(NO SIGNIFICANT EFFECTS)

(NO SIGNIFICANT EFFECTS)

(NO SIGNIFICANT EFFECTS)

INTERACTION EFFECT OF CARRION CROW AND JACKDAW ABSENCE - PRESENCE:

p < 0.05
ence did produce a significant interaction ($p < 0.05$).

Data for the carrion crow suffer from a lack of observations in the presence of the other species, but each when present was associated with a similar decrease in carrion crow intake rate. Jackdaws were less affected by other species' presence or absence; rooks appeared to have no effect on jackdaw intake rates, whilst carrion crows were associated with only a weak negative effect. Magpies were associated with a more substantial reduction in jackdaw prey intake rate, but there were only five observations in the presence of magpies. Rooks and carrion crows had weak (non-significant) facilitative effects on magpie intake rate, whilst there were no data when jackdaws were present.

For most species combinations, there were too few data to seriously investigate whether continuous relationships existed between the actual flock size of other species and the prey intake rates of subject species. However, a summary table of the proportion of positive and negative relationships for each particular prey type taken by each feeding action is given in table 1.6.1. This table conveniently summarises the overall effect of other species on the intake rates of each species in turn in a slightly more accurate way than a summary table of the proportion of increases or decreases in the presence-absence of other
Table 1.6.1

Summary table of direction of correlations between flock size of other species and prey intake rates of each species.

Number of positive:negative partial correlations between the different feeding actions for different prey types and the flock size of other species at the time of recording. Asterisks indicate significant (colons non-significant) departures from an even distribution of positive and negative correlations (binomial test p<0.05).

<table>
<thead>
<tr>
<th>Proportion of positive-to-negative correlations; Intake rates correlated with flock size of:</th>
<th>C. Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
<th>All</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>---</td>
<td>3*29</td>
<td>7*25</td>
<td>10*22</td>
<td>2*30</td>
</tr>
<tr>
<td>Rook</td>
<td>14:13</td>
<td>---</td>
<td>15:12</td>
<td>2*25</td>
<td>15:12</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>6:5</td>
<td>3:8</td>
<td>---</td>
<td>3:8</td>
<td>2*9</td>
</tr>
<tr>
<td>Magpie</td>
<td>8:8</td>
<td>7:9</td>
<td>No Data</td>
<td>---</td>
<td>8:8</td>
</tr>
</tbody>
</table>
species, since not only does the inclusion of different levels allow changes in intake rates at different flock sizes to be detected, but also these correlations are partial coefficients for the effect of one species while the simultaneous effect of other species is controlled for statistically.

Carrion crows were in general negatively affected by the presence of each species and their combination. Rooks were negatively affected only by magpie presence. Jackdaws were (significantly) negatively affected by the combination of species' presence, whilst magpies were neutrally affected. It will of course be realised that this summary table treats all prey items with equal weighting — since prey items varied in value, an analysis based on individual prey items is necessary to give a more accurate impression of true effect.

Figure 1.6.1b illustrates which particular prey type intake rates of rooks were affected by the presence of the other Corvid species. Carrion crows had very marked (and significant) negative effects on intake rates of small earthworms above, and large earthworms below, the soil surface. Since the average calorific value of intake rate for large earthworms below the soil surface was the second highest for all rook prey types taken in different microhabitats, this effect has considerable biological importance
for rooks.

Jackdaws, on the contrary, were associated with an increase in rook intake rate for large earthworms below the soil surface, though this was not a significant effect. However, they had an opposite (and significant) effect on another fairly important prey - medium earthworms taken below the soil surface. There were few observations of magpies foraging at the same time as rooks, but for the six observations recorded, the presence of magpies was associated with considerable drops in almost all prey intake rates.

Figure 1.6.1c indicates that rooks were associated with decreases in carrion crow intake rates for the two most important prey - large earthworms and medium invertebrates taken above the soil surface (the latter a significant difference). However, the means were based on only eight observations of rook presence. Partly compensating for these decreases were large increases in intake rates of medium items and small earthworms from dung, the latter a significant effect. The presence of jackdaws and magpies was associated similarly with decreases in intake rates of large earthworms from above the soil surface, the most important prey of all for carrion crows - but again these effects were not significant, possibly, given the consistent trends, because of the small sample sizes for the
The presence of other species tended to have opposite effects for several important items in the jackdaw's diet, producing the rather weak overall effects of figure 1.6.1a. Figure 1.6.1d shows that the intake rates of four prey types - small invertebrates and small earthworms from above the soil surface, and small and medium invertebrates from beneath surface litter - were higher when other species were also present (the latter three significantly so). Intake rates of several other important prey (small and medium items from dung, and medium items from beneath the soil surface) were however much higher when other species were absent, though these were not significant effects.

Rook absence or presence was associated with large changes in intake rates of only two prey types - a decrease in medium invertebrates and an increase in small earthworms from above the soil surface. Neither effect was significant, despite the fairly even division of observations between rook presence and absence.

Carrion crow presence was associated with a fairly large reduction in intake rates of small earthworms above the soil surface - but again this was not significant, despite the even split of sample sizes for carrion crow absence and presence. Other effects were smaller and
tended to be in different directions. One consistent set of differences (though again, small and not significant) was an increase in intake rates of items from beneath litter, and a decrease for items from animal dung, when carrion crows were also present. These were both quite important microhabitats for jackdaws (appendix 7.4).

Magpie presence was associated with decreases in intake rates of most items, and with a significant increase in intake rate of small items above the soil surface, and important prey item. However, there were only five observations when magpies were present.

Figure 1.6.1e indicates that in general magpies were little affected by the combined presence of other species (there were no data for jackdaw presence), except for a fairly large (but not significant) increase in the intake rate of medium items from dung, an important prey item. Taken individually, however, carrion crows had some larger effects - a non-significant decrease in intake rates of medium items from above the soil surface; a significant (though biologically less important) increase in intake rates of small items, and a significant increase in small earthworms, from above the soil surface; and a large (though non-significant) increase in intake rates of medium items from beneath dung. Rooks were associated with only one important effect - a large (but not significant)
increase in the intake rate of medium items from beneath dung.

1.6.2 Niche Breadth and Overlap Changes

It would be instructive to compare niche breadths and overlaps in absence-presence for each pair of species. Such descriptive statistics may be inspected to reveal whether a species expands or contracts its niche in response to another species, and to whether species act to reduce or increase overlap in the presence of one another (e.g. references in section 2.2.10 'Locating small scale prey patches', below). However, only two sets of calculations have been made - carrion crows and magpies in the absence or presence of one another, and jackdaws and rooks in absence-presence. There are two reasons for this - firstly, since both statistics, and especially niche breadths, may be biased by the inclusion of data based on a small number of observations; and secondly since no test may be made of the significance of the changes in these descriptive statistics. These two sets of comparisons were the only two possible with a reasonable split of sample sizes between absence and presence for both sides of the comparison.

Carrion crows reduced their niche breadth when foraging in the presence of magpies compared to the general
carrion crow mean irrespective of which species were absent-present, whilst the niche breadth of magpies was not affected by carrion crow presence. Overlap between the two species was somewhat higher when they were both foraging apart from the other species. Rooks and jackdaws both had reduced niche breadths, and reduced mutual overlap, when foraging apart from one another. (Table 1.6.2)

1.6.3 Discussion (1): How did the Effects Occur?

Facilitative effects of one species' presence on another species' intake rates are unlikely to be due to direct behavioural causes, since no flushing of prey or cooperative hunting occurs. The only direct behavioural mechanisms which could be involved are local enhancement effects facilitating the location of dense prey patches, or a reduction in vigilance leading to more time for foraging. Since I have no data available to test for the occurrence of such mechanisms inter-specifically, no further discussion is possible.

Alternatively, facilitative effects may be due to the fact that high prey densities for one species correlates with high prey densities for the other; when both occur together they are likely to both be on good prey areas and thus have higher intake rates of prey. Thus no direct behavioural interaction between the two species need
Table 1.6.2

Niche breadth and overlap change when foraging in the presence and absence of another Corvid species — proportional calorific intake of prey types in different microhabitats

Data for carrion crow and magpie when together and apart, and for rook and jackdaw.

<table>
<thead>
<tr>
<th></th>
<th>In Absence or Presence</th>
<th>In Absence of One Another</th>
<th>In Presence of One Another</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>C. Crow</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breadth</td>
<td>0.26</td>
<td>0.25</td>
<td>0.18</td>
</tr>
<tr>
<td>Overlap</td>
<td>0.48</td>
<td>0.55</td>
<td>0.46</td>
</tr>
<tr>
<td><strong>Magpie</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breadth</td>
<td>0.17</td>
<td>0.10</td>
<td>0.18</td>
</tr>
<tr>
<td><strong>Rook</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breadth</td>
<td>0.25</td>
<td>0.17</td>
<td>0.21</td>
</tr>
<tr>
<td>Overlap</td>
<td>0.22</td>
<td>0.14</td>
<td>0.28</td>
</tr>
<tr>
<td><strong>Jackdaw</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breadth</td>
<td>0.28</td>
<td>0.18</td>
<td>0.25</td>
</tr>
</tbody>
</table>
necessarily be involved.

Negative effects may be due, as mentioned at the beginning of the chapter, to several mechanisms. Some circumstantial evidence is available to distinguish between the behavioural mechanisms and the indirect one of a negative relationship between prey densities for the two species.

The 30 rooks observed took no small earthworms above, and large earthworms beneath, the soil surface when carrion crows were present. Since earthworms are very important items in the diet of both rooks and carrion crows, it is highly unlikely that this effect can be due to a negative relationship between the favoured prey densities of both species, particularly since intake rates of other earthworm size classes from different microhabitats were not affected by carrion crow presence. Carrion crows also had high intake rates of the affected earthworm classes, but did not exploit others which rooks favoured, for example small earthworms from beneath the soil surface. The fact that the lowering of rook intake rates occurred for earthworm categories which carrion crows also exploited, but not for those which carrion crows did not exploit, strongly suggests that the lowering of rook intake rates observed was the result of superior exploitation of these earthworm categories by the carrion crows. An alternative interpreta-
tion, given the carrion crow aggression described in the next chapter, could be that carrion crow presence was only recorded when these prey were not available on a field.

If this reasoning is correct, then the increase in rook intake rate of large earthworms beneath the soil surface when jackdaws were present (the opposite of the carrion crow effect) can perhaps be explained to some extent by the fact that jackdaw presence and carrion crow presence were negatively related for these observations of rooks (\( \rho = -0.298, N = 69, p < 0.05 \)).

The intake rate of large earthworms by carrion crows from above the soil surface was lower when each of the three other species, and their combination, were present. Since the favoured prey densities of all these species probably do not correlate negatively in each case, the prey density explanation is unlikely to be the cause of this. Since jackdaws and magpies did not exploit this prey type at all, the decrease when they were present could not be the result of exploitation competition, and since they are behaviourally subordinate (see next chapter), nor could it be the result of interference competition.

As described in section M.11.1.3, large earthworms caught above the soil surface require stealth and speed to capture and can easily be disturbed into retreating down their permanent vertical burrows. The most likely
explanation, therefore, of the decrease in carrion crow intake rate on this prey type when other birds were present is that they disturbed a proportion of this prey into unavailability. No fieldwork has been done to test this, but one piece of circumstantial evidence can be offered. If disturbance is the cause, then one might expect the effect to increase at high numbers of other birds' presence. Further, this effect should occur for the larger earthworms but not the smaller ones which do not inhabit permanent vertical burrows and have less effective anti-predator responses; and also the effect should not occur for invertebrates other than earthworms.

As mentioned earlier, insufficient data from the 1980-81 sample were available to test for such a continuous relationship. For this piece of evidence only, data have been utilised from other winters, since there is no reason to believe that the proposed effect would differ in different winters. Figure 1.6.2a indicates that earthworm intake rates did decline with the number of birds in the field. The fact that there was a big difference between carrion crows foraging alone and birds foraging with one other bird present, and a slower decline with further increases in bird numbers, suggests that an explanation based on the disturbance of earthworms down their burrows is likely only to be partially correct. One would not expect the addition of only one extra bird to affect intake
Figure 1.6.2

Prey intake rates of carrion crows when differing numbers of their own and other Corvid species were in the same field.

(a) Intake rates of different size classes of earthworms by numbers and calorific value. Correlations of bird numbers with intake rates of:

<table>
<thead>
<tr>
<th></th>
<th>Rho</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>small earthworms:</td>
<td>-0.474</td>
<td>***</td>
</tr>
<tr>
<td>medium and large earthworms:</td>
<td>-0.253</td>
<td>*</td>
</tr>
<tr>
<td>all earthworms:</td>
<td>-0.385</td>
<td>***</td>
</tr>
<tr>
<td>small ev calorific value:</td>
<td>-0.474</td>
<td>***</td>
</tr>
<tr>
<td>med./lge. ev calorific value:</td>
<td>-0.246</td>
<td>*</td>
</tr>
<tr>
<td>all ev calorific value:</td>
<td>-0.329</td>
<td>**</td>
</tr>
</tbody>
</table>

(b) Intake rates of earthworms and other invertebrates by numbers and calorific value. Correlations of bird numbers with intake rates of:

<table>
<thead>
<tr>
<th></th>
<th>Rho</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>earthworms:</td>
<td>-0.385</td>
<td>***</td>
</tr>
<tr>
<td>other invertebrates:</td>
<td>-0.176</td>
<td>NS</td>
</tr>
<tr>
<td>all invertebrates:</td>
<td>-0.246</td>
<td>*</td>
</tr>
<tr>
<td>ev calorific value:</td>
<td>-0.329</td>
<td>**</td>
</tr>
<tr>
<td>other inv. calorific value:</td>
<td>-0.197</td>
<td>NS</td>
</tr>
<tr>
<td>all invert. calorific value:</td>
<td>-0.354</td>
<td>**</td>
</tr>
</tbody>
</table>

Points for different bird numbers have been grouped together and the mean plotted (+/- s.e.) for ease of interpretation, but correlations were carried out on the original data.
NUMBER OF EARTHWORKS INGESTED PER MINUTE

- --- ALL EARTHWORKS
- --- SMALL EARTHWORKS
- --- MEDIUM AND LARGE EARTHWORKS

CALORIFIC VALUE INGESTED PER MINUTE (KCAL/5)

FLOCK SIZE OF CARRION CROWS AND ANY OTHER CORVID SPECIES:

SAMPLE SIZE: 11 19 27 14 9
Number of invertebrates ingested per minute

Calorific value ingested per minute (kcal/g)

Flock size of carrion crows and any other corvid species

Sample size: 11 19 27 14 9
rates of earthworms to the extent observed if disturbance were the only factor affecting intake rates.

The slopes were different for small and larger earthworms, though not exactly as predicted in the previous paragraph. Carrion crows in fields containing between two and 20 birds had lower intake rates than single carrion crows, but intake rates did not vary much between two and 20 birds. Intake rates when very large flocks were present were nil. Intake rates of small earthworms dropped to nothing when anything above five other birds were present, however - since almost all birds in excess of five others were rooks (see table 1.5.1), and since small earthworms were the most favoured prey type of this species, then this may be the result of superior exploitation competition by the rooks on this prey type in addition to the disturbance effect proposed. This may further be indicated by the fact that carrion crows took earthworms and foraged beneath the soil surface (favoured prey type and microhabitat of rooks) at higher rates on grass crops which rooks did not exploit much (section 1.4.5.3).

Figure 1.6.2b indicates that the slopes for earthworms and other invertebrates did differ; however, intake rates of invertebrates other than earthworms did also decline, in contrast to the prediction of no effect, although the decline was not a significant one. Since the other species
involved also exploited these other invertebrates, the decline could indicate poorer exploitation of these prey types by carrion crows. There was some indication that this might be the case between, for example, carrion crows and magpies foraging for medium invertebrates from dung (section 1.6.1 above and discussion below). Other possible explanations (for example an increase in time spent by carrion crows in agonistic encounters) are discussed in the next chapter.

In summary, carrion crow intake rates of all prey types declined as the number of other birds of any species on the same field increased. Rates of decline differed, and that for invertebrates other than earthworms was not significant; some explanation of these differences is attempted, although the required fieldwork has not been carried out to rigorously differentiate between alternative explanations. As far as the next chapter is concerned, it is the fact of the decline that is important and not the causes.

Carrion crows also showed a large increase in prey taken from dung when rooks were present. Given the decrease in intake rates from dung when magpies were present, an explanation of this could have been a negative relationship between rook and magpie presence for these observations of carrion crows - however, there was no
relationship between the two ($\rho = -0.087$). Alternatively, it could have been the result of high earthworm densities (preferred rook and carrion crow prey) tending to occur on the most heavily grazed (and therefore with most dung) pastures (chapter 1.3).

Since most of the effects for jackdaws were non-significant increases, any true facilitative effects were presumably due to prey density correlations, though the decreases beneath dung and increases beneath litter when carrion crows were present may have been due to superior exploitation of dung by carrion crows causing jackdaws to concentrate more on litter.

Magpies mostly had increased intake rates in other birds' presence, except for medium invertebrates above the soil surface which decreased (non-significantly) when carrion crows were present. They were an important prey. The corresponding increase in intake rates of the same prey type for carrion crows when magpies were present may suggest superior exploitation of that prey by carrion crows. However, in general most effects were facilitative, and this corresponds with a generally negative effect of magpie presence on other species' intake rates. One important example of this may be the decrease in carrion crow intake rates from dung (an important microhabitat for carrion crows - appendix 7.4) when magpies were present, and a
corresponding increase in magpie intake rates in that microhabitat when carrion crows were present. However, some of these comparisons are based on rather few observations and more fieldwork would be required to make more firm decisions.

The niche change of carrion crows when magpies were present mentioned in section 1.6.2 is probably the result of this reduction of intake rates of carrion crows from dung when magpies were present. The decrease in overlap and niche breadths of rooks and jackdaws when apart may have been due to the fact that they so often occurred together (table 1.5.1), that when apart they may well have been on specifically good prey areas for their own particular specialisations of prey types.

1.6.4 Discussion (2): How Important were the Effects?

All of the effects discussed in the last section are biologically important since only those for prey types of important calorific value compared to other prey types were discussed. However, the effects will only be important if a large proportion of time is spent in the absence or presence of the other species. Table 1.5.1 has shown that rooks foraged with carrion crows on 46% of occasions, so the big reduction noted in carrion crow presence of earthworm intake rates were fairly important. The
generally facilitative effect of jackdaw presence (figure 1.6.1a) may also be important since rooks foraged in jackdaw presence on 63% of occasions. Magpie presence was also associated with an important decrease in rook intake rate, but rooks foraged apart from magpies on 59% of occasions.

Carrion crows had reduced intake rates in the presence of each species, but they foraged apart from each species between 56 and 74% of the time, and from any other Corvid on 41% of occasions. In addition, the important reduction of earthworm intake rates at flock sizes above 20 will have been important on 14% of occasions. It was also shown that carrion crows' intake rate was highest when there were no other conspecifics present. Table 1.2.2 indicates that they foraged on their own on 46% of occasions. Magpies, despite the few badly negative effects noted, foraged in the absence of other species in similar proportions to carrion crows.

Jackdaws almost always foraged with rooks, and this species had a neutral effect on jackdaw intake rates. They foraged with carrion crows and magpies on 51 and 57% of occasions. In combination other species had mixed effects on jackdaw intake rates, but the only significant changes were increases in intake rates for three prey types - this may be why jackdaws were able to forage entirely in the presence of other species (table 1.5.1 indicates that
during routine censuses they were never observed on grass fields without at least one other species present).

The significance of these patterns is discussed further in the next chapter.
1.7.1 Long-term Behaviour and Coexistence: Testing the Null Hypothesis

Chapter 1.4 described the use of macro- and microhabitats, and prey types and size selection, by the four species. Since the species were each significantly separated from one another (chapter 1.5), and since the described niches appear to be, as far as one can tell, similar and distinct in other years and other places (see section 1.7.7 below), then one might say that these individual patterns of behaviour represent long-term behavioural mechanisms by which the species can coexist stably in present sympatry.

Since differences will exist between the individuals of the different species, one species will be on average more efficient than another at exploiting certain resources. Morphological adaptations, such as the rook's comparatively long and slender bill, will increase such differences in behavioural efficiency between species. Thus we might term the different patterns of foraging for different prey types in different macro- and microhabitats described in chapter 1.4 as long-term exploitation competi-
tion. Not surprisingly, in this context, chapter 1.5 revealed the magpie *Pica pica* to be more in overlap with the three *Corvus* species than they, congeners, were between themselves.

Although the overlap coefficients given in chapter 1.5 were not truly competition coefficients, since they did not take resource availability into consideration, it is possible to test whether the community matrix of overlaps is a stable structure or whether the same degree of overlap could be the result of chance patterns of resource exploitation by the species concerned. Thus we can test the null hypothesis of a random overlap of species in resource use against the hypothesis that the observed patterns are the result of stable differences in species' exploitation efficiencies and preferences.

The method stems from Sale (1974) and has been used and extended by various authors (e.g. Connor & Simberloff 1979, Grant & Abbot 1980, Hendrickson 1981, Joern & Lawlor 1981, Lawlor 1980, Pianka 1981, Strong et al. 1979, Strong & Simberloff 1981). A stochastic model of community structure is generated by filling a matrix with randomly generated (*) numbers, where the number of columns equals the number of species and the number of rows equals the number of columns.

(*) Actually pseudo-randomly generated by a computer. A listing of the program is given in appendix nine.
of elements to the resource in question. Each column is then converted to proportions and overlap indices between each species pair calculated in the normal way. The program used for the present simulations was written in BASIC and, as with the field data, Schoener's (1968a) index was used to calculate niche overlaps after each randomising run.

The means of 100 such iterations tended to produce alpha values of c.0.65 to 0.70 (cf. Joern & Lawlor 1981) with which to compare actual values. Standard deviations of course varied with the number of elements to the particular resource in question. Differences between observed and randomly generated alphas could be tested for significance by the t-test for the comparison of a single observation against a sample mean.

It is possible to produce null matrices by randomising the order of actual observed proportions within each column of the matrix (cf. Lawlor 1980, Joern & Lawlor 1981, who compared both methods), rather than by generating new numbers. However, alphas produced in this way will of course vary depending on how normal the observed utilisation curves are. If they are skewed due to somewhat higher use by both species of one or a few resource elements which are more common in the environment, then overlap indices calculated from random rearrangements of such skewed dis-
tributions will in fact on average tend to be much lower than is possible in reality, if resource availability is also skewed. Results from such random generations will be biased and not true representations of a null arrangement of the community matrix.

Skewed distributions of both resource availability and utilisation occurred in the present study (chapters 1.3 and 1.4) and hence random generations of overlap matrices based on rearrangement of actual observed proportions were almost always much lower than observed overlaps and did not provide a valid test of the null hypothesis (cf. Joern & Lawlor 1981). In fact, given the skew, a test against the randomly generated sets used here is still likely to produce type II errors; however, without any obvious way of deciding how to assign the limits to any weighting of a random generation to take account of such skew, we are forced to accept this reduction in sensitivity.

The results of the test are given in table 1.7.1. Overall, the results suggest that the community's use of the basic resources of grass habitat, prey type and size, and foraging technique did not differ significantly from what one might expect given a random utilisation of resources by each species. However, when prey types and sizes taken from the different microhabitats are tested, the observed overall community alpha was shown to be signi-
Table 1.7.1

Comparison of observed overlap values with randomly generated values

$O = \text{Observed, } N = \text{Null value}; \text{ significant differences are flagged by an asterisk.}$

<table>
<thead>
<tr>
<th>Overall Matrix</th>
<th>Mean Overlap</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass Crop Use</td>
<td>$O &gt; N$</td>
</tr>
<tr>
<td>Prey Type and Size</td>
<td>$O &lt; N$</td>
</tr>
<tr>
<td>Foraging Technique</td>
<td>$O &lt; N$</td>
</tr>
<tr>
<td>Prey from Different Microhabitats</td>
<td>$O &lt; N$ *</td>
</tr>
<tr>
<td>Time/Space</td>
<td>$O &lt; N$ *</td>
</tr>
<tr>
<td>Grass Crop Use</td>
<td></td>
</tr>
<tr>
<td>----------------</td>
<td></td>
</tr>
<tr>
<td><strong>Species</strong></td>
<td>R</td>
</tr>
<tr>
<td>--------------</td>
<td>---</td>
</tr>
<tr>
<td>Rock</td>
<td>-</td>
</tr>
<tr>
<td>C. Crow</td>
<td>O&gt;N</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>O&gt;N*</td>
</tr>
<tr>
<td>Magpie</td>
<td>O&gt;N</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Time/Space</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>Rock</td>
</tr>
<tr>
<td>C. Crow</td>
</tr>
<tr>
<td>Jackdaw</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Prey Type and Size</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>Rock</td>
</tr>
<tr>
<td>C. Crow</td>
</tr>
<tr>
<td>Jackdaw</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Foraging Technique</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>Rock</td>
</tr>
<tr>
<td>C. Crow</td>
</tr>
<tr>
<td>Jackdaw</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Microhabitat/Prey (Numbers of Prey)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>Rock</td>
</tr>
<tr>
<td>C. Crow</td>
</tr>
<tr>
<td>Jackdaw</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Microhabitat/Prey (Calorific Value)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
</tr>
<tr>
<td>--------------</td>
</tr>
<tr>
<td>Rock</td>
</tr>
<tr>
<td>C. Crow</td>
</tr>
<tr>
<td>Jackdaw</td>
</tr>
<tr>
<td>Magpie</td>
</tr>
</tbody>
</table>
1.7 Short-term Behavioural Options

Significantly lower than would be expected by chance. (*) Taking the pairwise comparisons individually, carrion crows and magpies did not overlap significantly less than would be expected by a chance arrangement if numbers of prey items are used as the measure, but did if calorific value is the measure used. Jackdaws and magpies overlapped more, rather than less (but not significantly), than would be expected by a chance utilisation of the available resources.

In terms of the use of fields in time all species, except for the comparison of rook and jackdaw (which often flocked together - chapter 1.5), showed significantly less overlap than would be expected by a chance utilisation of fields - i.e. they tended to avoid one another in time.

In conclusion, the results of the test of this neutral model of community structure suggests that the differing efficiencies and selection for particular prey types, sizes and microhabitats of the four species, were long-term behaviours which resulted in a more stable, structured community than would occur if each species took prey from microhabitats without regard to the others.

(*) Another indication of the importance of recording these two resources together (cf. May 1975 and the discussion in section 1.5.3 above).
1.7.2 Short-term Behaviour: the Options Available

Some overlaps on the basic resources were still fairly high, as revealed in chapter 1.5, and some of the short-term effects on intake rates of prey of foraging on the same field at the same time as certain other species, described in chapter 1.6, suggest that even if a stable community could exist thus, yet there are behavioural options possible which could improve the position of individuals of any one particular species still further, sometimes at the expense of these other species.

Behaviourally dominant species could attempt to exclude species which overlap, or which interfere with their foraging, from resources by direct agonistic behaviour (interference competition). Behaviourally subordinate species could attempt to reduce the effects of a superior exploitation competitor by avoiding foraging in the same place at the same time (if prey are renewing), and attempt to reduce the effects of direct interference competition by behavioural means, e.g. crypticity of behaviour while foraging, or by grouping to penetrate feeding areas through a "strength in numbers" effect or to enjoy a "selfish herd" benefit through dilution of the effects of the aggression.
1.7.3 Predictions about Short-term Behaviour

We can make predictions about which species might be expected to show which of the short-term behavioural options described in the last section, and to what extent they should show them, based on the observed resource utilisation pattern of each species revealed in chapter 1.4, on the overlaps revealed in chapter 1.5, and on the effects of intake rates of prey of the absence or presence of other species described in chapter 1.6. The predictions will be numbered so that simple correspondence may be made between each prediction and the relevant observations given in the next section.

(1) Two species which overlap highly on one resource are likely to have low overlap on another; in particular, two species overlapping highly on basic resource states should have low time-space overlaps.

Given the average overlap between a species and the other three, and the average of the effects described in chapter 1.6, the following predictions may be made about the expected abundances of each species in the study area:

(2) Carrion crow. Mean overlap (calorific value of different prey from different microhabitats) with three other guild members = 0.37 (calculated from figure
1.5.6b), and also occupies a unique area of niche hyperspace (see discriminant function plot, figure 1.5.7c). Predict medium abundance, but A-territoriality may reduce numbers somewhat (see section 1.1.2 above).

(3) Rook. Mean alpha = 0.20, and occupies a unique area of niche space. Predict high numbers, especially since no overt territorial behaviour is apparent.

(4) Jackdaw. Mean alpha = 0.45, and occupies a unique area of niche space. Predict fairly low abundance, though smaller body size than carrion crow and gregarious behaviour may increase the numbers of individuals which may occupy the area.

(5) Magpie. Mean alpha = 0.45, and almost no unique niche space. Predict low abundance, especially since some degree of A-territoriality shown.

These are the expected abundances before taking into account any short-term behaviour on the part of the species which modifies the effect of the overlaps described in chapter 1.5 and the effects of other species on prey intake rates described in chapter 1.6.

The following set of predictions gives the degree to which we should expect each species to show the kinds of
short-term behavioural options described above towards each other species in turn:

(6a) **Carrion crow - rook.** The effects of rooks on carrion crows described in chapters 1.5 and 1.6 were neutral or negative. Although overlap in different prey types taken from different microhabitats was low, the effects of rook presence on prey intake rates of carrion crows (and particularly of earthworm intake rates) were severe. It is predicted that any behaviour on the part of carrion crows directed towards rooks will be negative in intention; and because the main negative effect increased in severity with the flock size of rooks present, behaviour should also increase with rook flock size.

(6b) **Carrion crow - jackdaw.** All effects described were negative or neutral. Overlap between carrion crow and jackdaw on diet/microhabitat was medium (prey numbers, alpha = 0.34; prey calorific value, alpha = 0.41). Jackdaw presence was associated with the same effects as rook presence. A similar negative behavioural response by carrion crows directed at jackdaws is predicted, though higher overlap than with the rook may predict some response irrespective of jackdaw flock size.

(6c) **Carrion crow - magpie.** All effects described were
neutral or negative. Overlap on diet/microhabitat was somewhat higher than for the carrion crow-jackdaw comparison (prey numbers = 0.47, calorific value = 0.48). Carrion crows not classed as their own species during the classification stage of the discriminant function analysis were mostly classed as magpies. Important effects on carrion crow prey intake rate, not due to disturbance of the prey, predicts a negative behavioural response from carrion crows towards magpies, irrespective of magpie flock size.

(7a) Rook - carrion crow. Most effects were neutral, except for some important reductions in intake rates of certain earthworm classes when carrion crows were present. Overlap on diet/microhabitat was low. Some negative behavioural response towards carrion crows is predicted.

(7b) Rook - jackdaw. Effects were neutral or positive. Overlap on diet/microhabitat was low. Jackdaw presence was associated with some increase in rook prey intake rates. A neutral or positive behavioural response on the part of rooks towards jackdaws is predicted.

(7c) Rook - magpie. Effects were neutral or negative. Overlap on diet/microhabitat was low but individual birds not classed as their own species during the
1.7 Short-term Behavioural Options

discriminant analysis classification stage were mostly classified as magpies. Magpie presence was associated with a reduction in rook prey intake rates for most prey types from most microhabitats. A negative behavioural response from rooks towards magpies is predicted.

(8a) Jackdaw - carrion crow. Effects were neutral or weakly negative. Overlap on diet/microhabitat was medium (prey numbers = 0.34, calorific value = 0.41). Some negative behavioural response by jackdaws towards carrion crows is predicted.

(8b) Jackdaw - rook. Effects were neutral or weakly positive. Overlap on diet/microhabitat was low. A neutral or positive behavioural response by jackdaws towards rooks is predicted.

(8c) Jackdaw - magpie. Effects were neutral or negative. Overlap on diet/microhabitat was high (prey numbers = 0.59, calorific value = 0.72). In addition, individual jackdaws misclassified during the classification stage of the discriminant function analysis were mostly classed as magpies. Most effects of magpie presence on jackdaw prey intake rates were negative, though based on few observations. A negative behavioural response by jackdaws towards magpies is predicted.
(9a) Magpie - carrion crow. Effects were mixed. Overlap on diet/microhabitat was quite high (prey numbers = 0.47, calorific value = 0.48). Birds misclassified during the classification stage of the discriminant function analysis were classed as carrion crows or jackdaws. Effects of carrion crow presence on magpie prey intake rates were however mainly neutral or facilitative. Prediction not clear.

(9b) Magpie - rook. Effects were mainly neutral. Overlap on diet/microhabitat was low. Effects of rook presence on magpie prey intake rates were neutral or non-significantly facilitative. A neutral response by magpies towards rooks is predicted.

(9c) Magpie - jackdaw. Effects were neutral or negative. Overlap on diet/microhabitat was high (prey numbers = 0.59, calorific value = 0.72). Birds misclassified during the classification stage of the discriminant function analysis were classed as jackdaws or carrion crows. There were no data on the effects of jackdaw presence on magpie prey intake rates. A negative behavioural response by magpies towards jackdaws is predicted, on the evidence available.

The general position of the magpie *pica pica* is of interest within the guild, of which the other three members
are congeners of a separate genus (*Corvus*). It is usually the case that congeners are closer ecologically than they are to species which are more distant taxonomically (e.g. Cody 1974a, den Boer 1980). However, these four species occupy a man-made environment to which they are fairly new in evolutionary terms. Under these conditions this difference may disappear (see e.g. Lack's 1971 discussion of the Fringillidae from different habitats which now all inhabit farmland). In the present case, rather than the difference disappear, the reverse has in fact become true, with a non-congener overlapping in general more with species from another single genus than they do between themselves. The reason for this may be that the modern farmland habitat which these species now inhabit may quite closely resemble the ancestral habitats of the *Corvus* species; habitats in which they may have come into sympatry before their present sympatry in the farmland habitat. By definition congeners are more recently separated from one another than they are from a species belonging to another genus. The *Corvus* species are likely to be basically similar in their broad habitat but stable differences must exist between them for them to be able to retain their species' identities in sympatry.

It seems likely that the *Corvus* species evolved from some more jay-like form in the course of adaptation to life in more open country (Goodwin 1976). The *Corvus* species
almost certainly evolved to occupy open country habitats earlier than *Pica* species and occupied natural open country (savanna woodland, natural parkland, wood edges, steppe, tundra) before the advent of the modern open agricultural habitats. *Pica* species on the other hand probably evolved as inhabitants of somewhat more wooded country (scrub, forest edge, riparian woodland amongst more open country). With the advent of modern farming around the world several *Pica* species also became associated with this habitat along with the *Corvus* species. Because of modern farmland's relative structural simplicity, the natural habitat differences between the two genera mentioned above were lost and the two came into sympatry. We would expect, therefore, the three *Corvus* species, all evolved to fairly similar natural environments, and probably with some history of sympatry in them, to have stable ecological differences which allowed them to retain species status. *Pica pica*, on the other hand, has probably only come into sympatry with the three *Corvus* species since their move into modern farmland, and may be expected to show no particular uniqueness keeping it stably separated from the other species. Goodwin states that

"The typical magpies show some resemblances to the genus *Corvus*. I think...these represent convergent adaptations to ground feeding in relatively open country and do not indicate...common ancestry." (Goodwin 1976 p.172)
The positions of the four species in niche hyperspace depicted in figure 1.5.7c would seem to confirm this expectation. The three *Corvus* species are significantly separated from one another and each occupies a unique area of niche space. The magpie, however, although it is significantly separated from each other species, and thus may exist in the guild, does not retain a unique area of niche space to itself - its niche is almost completely contained within that of the three *Corvus* species. Similarly, the null test of the basic resource states described in section 1.7.1 indicated that it was the pairings of magpie - carrion crow and magpie - jackdaw which did not have significantly lower overlap on diet/microhabitat than would be expected by a chance use of resources, suggesting again that the magpie in general was not part of the guild which otherwise proved to be structured by long-term behavioural mechanisms. Another indication, therefore, of a potentially unstable position in the community. Thus the following predictions are made:

(9d) The position of magpies within the guild should be relatively unstable. The species should show lower abundance and a tendency to drop out first when conditions become poorer (e.g. where the proportion of rich farmland begins to drop in an area). It should show more tendency to display short-term behavioural options which allow it to retain its place in the
Finally, predictions are made of the type of short-term behaviours each species should show to each other species. Bossema et al. (1976) and Roell (1978), based on observations in Holland, have suggested that carrion crows show agonistic behaviour towards rooks, jackdaws and magpies due to overlap in diet (interference competition). They suggest that a function of rook and jackdaw flocks is to reduce the effects of carrion crow aggression by a "strength in numbers" effect, and that this allows these species to exist within carrion crow territories. Magpies are said to show a tendency to forage near buildings and field edges to reduce the effect of carrion crow aggression. Since the present author has already examined this topic in some detail (Waite 1978), this thesis only discusses immediately relevant points arising, with the presentation of new data.

(10a) Carrion crow - rook. Carrion crows should avoid large flocks of rooks. Since carrion crows are behaviourally dominant over individual rooks (Bossema et al. 1976, Lockie 1956b, Waite 1978), they might also attempt to exclude rooks from their territories. They should attempt to exclude larger flocks of rooks more than smaller ones.
1.7 Short-term Behavioural Options

(10b) **Carrion crow - jackdaw.** Predictions as for (10a), except that the behaviour should perhaps also be shown to some extent at lower flock sizes than for rooks.

(10c) **Carrion crow - magpie.** Predictions as for (10a), but at all flock sizes of magpies.

(11a) **Rook - Carrion crow.** Since rooks are subordinate, they should weakly avoid carrion crows due to the two negative effects on rook prey intake rate in carrion crow presence noted. Given that carrion crows are predicted to attack larger flocks more, we predict that rooks should occur at low flock sizes. Bossema et al.'s (1976) prediction is the opposite, i.e. that rooks should occur at high flock sizes, and also predicts that larger flocks should be able to withstand carrion crow aggression better than smaller ones, and should feed for longer in carrion crow presence.

(11b) **Rook - jackdaw.** Rooks should either ignore or associate with jackdaws.

(11c) **Rook - magpie.** Rooks should avoid magpies. Given that they are behaviourally dominant (Lockie 1956b, Waite 1978), they could also attempt to exclude them from foraging in the same field.

(12a) **Jackdaw - carrion crow.** Predictions as for (11a).
1.7 Short-term Behavioural Options

(12b) **Jackdaw - rook.** Predictions as for (11b).

(12c) **Jackdaw - magpie.** Jackdaws should avoid magpies. Since body sizes are close (table 1.2.1) and no stable dominance relationship has been noted between the two species (Bossema et al. 1976, Lockie 1956b, Waite 1978), it is not clear whether one predicts much agonistic behaviour between the two species or none at all.

(13a) **Magpie - carrion crow.** Predictions not clear (see 9a).

(13b) **Magpie - rook.** It is predicted that magpies should ignore rooks.

(13c) **Magpie - jackdaw.** Prediction as for (12c).

Since the impact of a species on another will depend not only on the average overlap and effect on prey intake rates described above, but on the particular prey-availability conditions at the time and on the numbers of individuals of the other species present, behaviour may vary somewhat from that predicted above. Since aggression or avoidance behaviour must have some cost energetically, it is predicted that species will only show such behaviours when the benefits outweigh the costs. Current prey intake levels may be the proximate mechanism by which a decision
on when behaviour should be shown is made — if conditions become such that prey intake rates of a species drop below a certain level, then the predicted behaviour would begin to operate. This leads to a further prediction:

(14) The level of short-term behaviour displayed by any species should vary depending on the abundance of the other species present and the total calorific value of prey an individual of the other species consumes.

Finally, since the disturbance effect on carrion crows' earthworm prey is not dependent on the disturbing species being food competitors, two more predictions may be made:

(15) Carrion crows should avoid or attack any ground-foraging species which occurs in flocks, and this tendency should be more marked as the flock size of these species increases.

(16) Carrion crows should not attack larger flocks more on arable land since carrion crows do not prey on disturbable earthworms in these habitats, and so the disturbance effect will not exist.
1.7.4 Observations about Short-term Behaviour

(1) In general this prediction did not hold for relationships between the basic resources of grass habitat, prey type and size, feeding action, microhabitat, or the simultaneous measurement of prey from different microhabitats. However, there were indications of negative relationships between the use of space in time and these measures (except grass habitat), although with only six species-pair points to each scattergram, these relationships could not be established statistically. Thus in general the guild members did tend to show the short-term behavioural option of avoidance more towards species with whom they overlapped more on the basic, "long-term" behaviours of diet and microhabitat choice. This is partly illustrated in figure 1.7.3, where it is shown that the linear relationship between body-size ratios between two species and overlap indices is improved by the addition of the time-space alphas.

(2-5) Rooks, as predicted, were the most abundant species in the study area during winter censuses (mean number per census = 152.4). Magpies, also as predicted, were the least abundant (mean = 26.7). The complication of small body size and gregariousness of the jackdaw, and the A-territoriality of the carrion crow made predic-
tion less obvious for these two species. Their mean abundance were 81.9 for the jackdaw and 30.5 for the carrion crow. According to the predictions made before any modifications made possible by short-term behaviour are considered, there were somewhat more jackdaws and fewer carrion crows in the study area than predicted.

The first data relevant to predictions 6 to 13 are presented in figures 1.7.1 and 2. These figures present product alphas for the different prey types taken from different microhabitats (figure 1.7.1) or by different feeding actions (figure 1.7.2) multiplied by grass habitat and the use of different grass fields in time. It has been argued above (section 1.7.1) that the preference and efficiencies of the different species for diet/microhabitat use are likely to be fairly fixed. Individuals of a species may be limited in the extent to which they can alter these behaviours to reduce overlap with other species since their efficiency at foraging for the different prey types in different microhabitats may be determined by, for example, a particular combination of bill shape and size. In addition, it is likely that choice of grass crop type will be reasonably fixed since certain crop types will contain higher prey densities of favoured prey types than others (see information in chapter 1.3 on differences in the
Figure 1.7.1

Community matrices (where $A = \{\alpha(i,j)\}$) and community dendograms for the product of grass habitat, the use of space in time, and prey types from different microhabitats

(a) Numbers of prey items, (b) Calorific value of prey items, (c) Nutritive value of prey items.

The bottom-left triangle to each table is the matrix for the product of the overlap matrix for the different prey types taken from different microhabitats, multiplied by the matrix for the use of different grass crop types; the top-right triangle is the product of this step further multiplied by the matrix for the use of different grass fields in time. The original matrices may be found in chapter 1.5.
(a) Numbers

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td></td>
<td>.06</td>
<td>.16</td>
<td>.03</td>
</tr>
<tr>
<td>Carrion Crowl</td>
<td>.29</td>
<td></td>
<td>.06</td>
<td>.16</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.25</td>
<td>.31</td>
<td></td>
<td>.09</td>
</tr>
<tr>
<td>Magpie</td>
<td>.20</td>
<td>.59</td>
<td>.57</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat

By Time/Space

(b) Calorific Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td></td>
<td>.04</td>
<td>.13</td>
<td>.01</td>
</tr>
<tr>
<td>Carrion Crowl</td>
<td>.16</td>
<td></td>
<td>.05</td>
<td>.12</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.21</td>
<td>.30</td>
<td></td>
<td>.08</td>
</tr>
<tr>
<td>Magpie</td>
<td>.10</td>
<td>.45</td>
<td>.52</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat

By Time/Space

(c) Protein Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rook</td>
<td></td>
<td>.04</td>
<td>.13</td>
<td>.01</td>
</tr>
<tr>
<td>Carrion Crowl</td>
<td>.16</td>
<td></td>
<td>.05</td>
<td>.10</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.19</td>
<td>.27</td>
<td></td>
<td>.08</td>
</tr>
<tr>
<td>Magpie</td>
<td>.09</td>
<td>.39</td>
<td>.52</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat

By Time/Space
Community matrices (where $A = \{alpha(i,j)\}$) and community dendograms for the product of grass habitat, the use of space in time, and prey types taken by different feeding actions

(a) Numbers of prey items, (b) Calorific value of prey items, (c) Nutritive value of prey items.

The bottom-left triangle to each table is the matrix for the product of the overlap matrix for the different prey types taken from different microhabitats, multiplied by the matrix for the use of different grass crop types; the top-right triangle is the product of this step further multiplied by the matrix for the use of different grass fields in time. The original matrices may be found in chapter 1.5.
(a) Numbers

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock</td>
<td>-</td>
<td>.06</td>
<td>.15</td>
<td>.06</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.30</td>
<td></td>
<td>.06</td>
<td>.16</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.25</td>
<td>.30</td>
<td>.07</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.21</td>
<td>.59</td>
<td>.47</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat

(b) Calorific Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock</td>
<td>-</td>
<td>.04</td>
<td>.07</td>
<td>.02</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.16</td>
<td></td>
<td>.01</td>
<td>.12</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.10</td>
<td>.25</td>
<td>.06</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.10</td>
<td>.45</td>
<td>.43</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat

(c) Protein Intake

<table>
<thead>
<tr>
<th>Species</th>
<th>R</th>
<th>C</th>
<th>J</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rock</td>
<td>-</td>
<td>.04</td>
<td>.05</td>
<td>.01</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>.16</td>
<td></td>
<td>.04</td>
<td>.10</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>.07</td>
<td>.22</td>
<td>.06</td>
<td></td>
</tr>
<tr>
<td>Magpie</td>
<td>.10</td>
<td>.38</td>
<td>.42</td>
<td></td>
</tr>
</tbody>
</table>

By Habitat
densities of different types of invertebrate between different grass crop types), and thus choosing a different crop type in an attempt to reduce overlap with another species may not be an economic possibility if individuals of the species then found themselves foraging on much lower levels of prey density.

However, birds did show some tendency to occupy a different habitat type when certain other species were present. The data are summarised in table 1.7.2. For the most part the data show an avoidance of using grassland, and an avoidance of using permanent pasture within grassland, when other species were present. Carrion crows were significantly more likely to be found on grassland if jackdaws were absent and on permanent pasture if rooks were absent. Rooks were less likely to be on grassland or permanent pasture when carrion crows were present. Jackdaws were less likely to be on grassland when carrion crows or magpies were present, and less likely to be on permanent pasture if carrion crows were present. Jackdaws were significantly more likely to be on grassland or permanent pasture if rooks were present. Rook occupancy of grassland or arable was not affected by jackdaw presence or absence, but rooks were significantly more likely to be on permanent pasture if jackdaws were absent (however, even in jackdaw presence, 85% of rooks were on permanent pasture).
Table 1.7.2

Comparison of habitat use by each species in the presence and absence of the other species

Significant differences in pattern of habitat use (chi-square on original data; see table 1.4.2 for sample sizes for each species) are flagged by asterisks.

(a) Habitat choice between grassland and arable in the presence and absence of other species

(b) Habitat choice between different grass crops in the presence and absence of other species (for significance tests non-agricultural swards, ungrazed leys and grazed leys were combined)
(a) Percentage of birds on grassland (Ab = absent, Pr = present)

<table>
<thead>
<tr>
<th>Species</th>
<th>Carrion Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ab Pr</td>
<td>Ab Pr</td>
<td>Ab Pr</td>
<td>Ab Pr</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>---</td>
<td>63 65</td>
<td>71 49</td>
<td>53 80</td>
</tr>
<tr>
<td>Rook</td>
<td>84 77</td>
<td>---</td>
<td>84 81</td>
<td>83 79</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>75 58</td>
<td>30 74</td>
<td>---</td>
<td>72 63</td>
</tr>
<tr>
<td>Magpie</td>
<td>65 79</td>
<td>67 92</td>
<td>73 79</td>
<td>---</td>
</tr>
</tbody>
</table>

(b) Percentage of birds on permanent pasture

<table>
<thead>
<tr>
<th>Species</th>
<th>Carrion Crow</th>
<th>Rook</th>
<th>Jackdaw</th>
<th>Magpie</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ab Pr</td>
<td>Ab Pr</td>
<td>Ab Pr</td>
<td>Ab Pr</td>
</tr>
<tr>
<td>Carrion Crow</td>
<td>---</td>
<td>41 81</td>
<td>55 57</td>
<td>47 64</td>
</tr>
<tr>
<td>Rook</td>
<td>92 76</td>
<td>---</td>
<td>97 85</td>
<td>83 96</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>90 72</td>
<td>0 88</td>
<td>---</td>
<td>79 86</td>
</tr>
<tr>
<td>Magpie</td>
<td>36 56</td>
<td>24 97</td>
<td>39 74</td>
<td>---</td>
</tr>
</tbody>
</table>
All of these tendencies are interpretable in terms of avoidance by overlapping species or by the tendency for rooks and jackdaws to flock together. However, magpies were significantly more likely to be on grassland when carrion crows or rooks were present, and on permanent pasture when each of the other three species were present. These individual patterns are commented upon below. It will be remembered that each species foraged in the presence of other species on something less than 50% of occasions (except for the jackdaw-rook pairing), and thus these effects will not act to change overlap all the time.

In addition to avoidance of gross habitat types, birds were free to use any of a number of different grass fields of any one crop type. Figures 1.4.1a to f give an indication of the number of fields of any one crop type available in the study area, and of the way in which birds occupied them on different occasions. If a species overlaps highly with another, then one way to reduce the effect of this overlap is to forage on a field which does not at that time contain members of the other species. The species may overlap highly in the use of fields as spatial areas (see figure 1.5.4b) but use them at different times. It has been argued in section 1.5.3 above that to some extent invertebrate prey within a field may be renewing, even though few invertebrates reproduced in winter, since the prey were cryptic and hard to find, and any one item
invisible and unavailable on one visit could become visible and available on another due to a change in the spatial position of the prey item (e.g. due to movements connected with foraging, or because climatic conditions caused movement away from or towards a certain area, etc.).

Unfortunately the only data available are four samples taken from the same field at monthly intervals across one winter (figure 1.3.8c). There were some changes in the absolute abundance of different invertebrate types in the top three inches of the soil, and we may expect (though there are no data on this) that small shifts by individual items on any one occasion will cause a bird to locate an item on one visit where it was unable to do so on a former. However, there is no quantification of this nor of whether absolute abundances may shift more quickly than at the monthly intervals sampled.

Although the use of fields at different times, to produce a reduction of the effect of overlap in diet, is dependent on the renewal of prey availability, a reduction of the direct effects of other species on prey intake rates noted in chapter 1.6 is not. The use of any field at a different time to that species will be advantageous.

The use of different fields at different times has been described in detail in section 1.5.2 above. Since prey taken from different grass fields certainly represent
different prey populations (section 1.5.3), and since it may be reasonable to assume that prey taken from the same field on a different occasion (the censuses were a fortnight apart) also do, product alphas are a more appropriate way of combining the separate measurements of these resource states than summation alphas (see section 1.5.3).

The bottom-left triangle of each table, and the first of each pair of dendograms, reveal that the supposition that species may not be able to use grass crop choice as a general method of reducing overlap with other species was correct. Some species still overlap quite highly with others (figures 1.7.1 and 1.7.2).

However, the top-right triangle of each table and the second dendogram of each pair show that the species did use avoidance in time as a method of reducing overlap, and the fact that all species-pair overlaps are now much more similar (the clusters in the dendograms all fuse at a similarly low alpha level) shows that the species which overlapped most on the basic resource states of diet/microhabitat and grass crop showed most avoidance in time.

Since avoidance has reduced the general level of overlap to a low level, the role of direct interference competition is likely to be less connected with reduction of overlap than with the reduction of the effects described
in chapter 1.6. It was generally the case that direct interspecific agonistic behaviour was rarely observed in a way which could be interpreted as interference competition. Most interspecific aggression was directed by carrion crows towards other Corvids. The data are summarised in table 1.7.3, the general conclusion from which is that the data support an interpretation of carrion crow aggression in terms of the disturbance of earthworms described in chapter 1.6.

For each species, and the species combined, carrion crows were more likely to attack a foraging flock the larger it was (row 1 of each table; combined data, chi-square = 16.92, df = 4, p < 0.01). Almost all of the very largest flocks - which had the most marked lowering effect on the earthworm intake rates of carrion crows - were attacked. These effects were predicted on the basis of the prey-disturbance effect, but if the aggression were interference competition, then all flocks should have been attacked.

On average more rook and jackdaw flocks were attacked than magpies, again as predicted on a prey-disturbance hypothesis, since these two species occurred more frequently in larger flocks than magpies, but the opposite to what would be predicted if carrion crows were using aggression as an interference competition mechanism against the
Table 1.7.3

Summary tables of carrion crow aggression and frequency of occurrence at different flock sizes of the other Corvid species

The data for rows 1 to 3 of each table come from all observations of the subject species when a carrion crow was also present on the same field; data for rows 5 to 7 come from routine winter censuses of the main study area. See text for significance tests of the different rows. Data in the rows represent:

(1) The proportion of times foraging flocks were attacked by a carrion crow which was also present in the same field; for these purposes an attack was any agonistic act towards at least one bird in the flock; each flock was therefore either attacked or not. Values in the row are the percentage of flocks within each flock size grouping which were attacked.

(2) The proportion of times an attacked flock left the field; percent within each flock size grouping.

(3) Rate of attacks (II of carrion crow agonistic acts per individual per hour of foraging time when a carrion crow was also present on the field) suffered per individual at different flock size groupings.

(4) Frequency of occurrence of flocks of different sizes when a carrion crow was also present on the field as a percentage of the total flocks seen.

(5) Frequency of occurrence of flocks of different sizes when a carrion crow was not present on the field as a percentage of the total flocks seen.

(6) Proportion of times each flock size grouping was recorded with a carrion crow also present (percentage within each flock size grouping).
### Rook Flock Size:

<table>
<thead>
<tr>
<th></th>
<th>1-2</th>
<th>3-5</th>
<th>6-20</th>
<th>21-40</th>
<th>&gt;40</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Flocks Attacked</td>
<td>32.0</td>
<td>52.6</td>
<td>55.5</td>
<td>92.9</td>
<td>100.0</td>
<td>59.4</td>
</tr>
<tr>
<td>2. Flocks Leaving</td>
<td>75.0</td>
<td>60.0</td>
<td>61.0</td>
<td>46.1</td>
<td>75.0</td>
<td>61.9</td>
</tr>
<tr>
<td>3. Attack Rate</td>
<td>166.1</td>
<td>59.9</td>
<td>26.0</td>
<td>95.5</td>
<td>69.7</td>
<td>79.1</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>1-2</th>
<th>3-5</th>
<th>6-20</th>
<th>21-40</th>
<th>&gt;40</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>5. Crow Present</td>
<td>23.1</td>
<td>26.9</td>
<td>30.8</td>
<td>15.4</td>
<td>3.8</td>
<td>--</td>
</tr>
<tr>
<td>6. Crow Absent</td>
<td>16.7</td>
<td>13.3</td>
<td>30.0</td>
<td>23.3</td>
<td>16.7</td>
<td>--</td>
</tr>
<tr>
<td>7. With Crow</td>
<td>54.5</td>
<td>63.6</td>
<td>47.0</td>
<td>36.4</td>
<td>16.7</td>
<td>46.4</td>
</tr>
<tr>
<td>8. N Observations</td>
<td>11</td>
<td>11</td>
<td>17</td>
<td>11</td>
<td>6</td>
<td>56</td>
</tr>
</tbody>
</table>

### Jackdaw Flock Size:

<table>
<thead>
<tr>
<th></th>
<th>1-2</th>
<th>3-5</th>
<th>6-20</th>
<th>21-40</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Flocks Attacked</td>
<td>13.8</td>
<td>66.7</td>
<td>76.5</td>
<td>85.7</td>
<td>47.7</td>
</tr>
<tr>
<td>2. Flocks Leaving</td>
<td>25.0</td>
<td>75.0</td>
<td>33.5</td>
<td>50.0</td>
<td>48.4</td>
</tr>
<tr>
<td>3. Attack Rate</td>
<td>2.6</td>
<td>55.0</td>
<td>102.4</td>
<td>145.2</td>
<td>53.9</td>
</tr>
<tr>
<td>4. N Observations</td>
<td>29</td>
<td>12</td>
<td>17</td>
<td>7</td>
<td>65</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>1-2</th>
<th>3-5</th>
<th>6-20</th>
<th>21-40</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>5. Crow Present</td>
<td>27.0</td>
<td>5.5</td>
<td>50.0</td>
<td>16.7</td>
<td>--</td>
</tr>
<tr>
<td>6. Crow Absent</td>
<td>26.3</td>
<td>26.3</td>
<td>26.3</td>
<td>21.0</td>
<td>--</td>
</tr>
<tr>
<td>7. With Crow</td>
<td>50.0</td>
<td>16.7</td>
<td>64.3</td>
<td>42.8</td>
<td>48.6</td>
</tr>
<tr>
<td>8. N Observations</td>
<td>10</td>
<td>6</td>
<td>14</td>
<td>7</td>
<td>37</td>
</tr>
</tbody>
</table>
## Magpie Flock Size:

<table>
<thead>
<tr>
<th>Category</th>
<th>1-2</th>
<th>3-5</th>
<th>6-20</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Flocks Attacked</td>
<td>30.4</td>
<td>40.0</td>
<td>50.0</td>
<td>32.1</td>
</tr>
<tr>
<td>2. Flocks Leaving</td>
<td>42.9</td>
<td>50.0</td>
<td>100.0</td>
<td>47.1</td>
</tr>
<tr>
<td>3. Attack Rate</td>
<td>24.6</td>
<td>8.2</td>
<td>69.2</td>
<td>24.8</td>
</tr>
<tr>
<td>4. N Observations</td>
<td>46</td>
<td>5</td>
<td>2</td>
<td>53</td>
</tr>
<tr>
<td>5. Crow Present</td>
<td>61.3</td>
<td>25.8</td>
<td>12.9</td>
<td>--</td>
</tr>
<tr>
<td>6. Crow Absent</td>
<td>96.9</td>
<td>3.1</td>
<td>0.0</td>
<td>--</td>
</tr>
<tr>
<td>7. With Crow</td>
<td>38.0</td>
<td>88.9</td>
<td>100.0</td>
<td>49.2</td>
</tr>
<tr>
<td>8. N Observations</td>
<td>50</td>
<td>9</td>
<td>4</td>
<td>63</td>
</tr>
</tbody>
</table>
species with which it most overlapped (compare the last entry to row 1 of each table; the values are ranked exactly as the prey-disturbance hypothesis would predict, but exactly opposite to what an interference-competition hypothesis would predict, since carrion crows overlapped least with rooks and most with magpies in the important resource states). Similarly, individual rooks and jackdaws were attacked more frequently than magpies, and these species were more likely to leave the field after attack by a carrion crow than magpies were (compare the last entry to rows 2 and 3 of each table), again as would be predicted by the prey-disturbance hypothesis since more rooks and jackdaws occurred in larger flocks, but the opposite to what an interference-competition hypothesis would predict.

A qualitative description of the nature of carrion crow interspecific aggression also tends to support the prey-interference hypothesis. The attack-rates in row 3 of the table are over-estimates of the true rate of attacks when carrion crows were present on a field with other species. True attack rates were probably much less. Attacks were so infrequently observed during general observations that the only way to collect sufficient data was to do so opportunistically — i.e. whenever the author happened to notice species foraging in the same field as carrion crows, the birds were watched for a maximum of five minutes and the number of interactions recorded.
Observations in this way revealed very low interaction rates, but even so the 5-minute maximum imposed meant that true rates were greatly overestimated. It was felt that some arbitrary limit had to be imposed otherwise one might watch for an hour or more without observing any interactions at all and make quantification impossible.

However, there was another type of interaction which was rather different in character. Often an attack would be made by a carrion crow flying from the far side of the field, from a perch, or from a neighbouring field. The attack would be brief and either the attacked birds left or relanded to resume foraging. Often a proportion of the flock left and the remainder resumed foraging. The carrion crow would either fly back out of the field, or land and perhaps display for a while before either attacking again or beginning to forage. These attacks were often so brief and unheralded that the observer was often only aware of an attack when all the birds in a field suddenly became alert or took flight, and a carrion crow would then be observed flying fast across the field towards a flock, often calling stridently. The carrion crow would fly through a flock "putting the birds up" like an attacking raptor, though a carrion crow was never observed to make actual contact with another Corvid, and the banking and swerving of the carrion crow at the last moment seemed designed to avoid this (the only contact ever observed was in fact when rooks or
1.7 Short-term Behavioural Options

jackdaws which had taken flight then "mobbed" the attacking carrion crow).

This type of attack was clearly very different in kind to the type of quick displacement of one individual of another species from, for example, a cow pat, which was the type of infrequent interaction seen in the situation described at the beginning of last paragraph. However, the author could not form any clear decision rules on how to differentiate unclear examples, and thus the different kinds of interactions are not differentiated in the data presented in table 1.7.3. The actual duration of the latter kind of attack was often as low as 10 or 20 seconds. This was the time recorded, though often it is likely that the carrion crow had been present on perch or in the next field for some time beforehand. Thus the rates given in row 3 are probably overestimates of the true rates of attacks per hour of foraging together. The observed rates of aggression probably did not have any significant effect on the attacked species' ingestion rates (cf. the effects of similarly low intraspecific agonistic behaviour between foraging rooks which Patterson (1975) has demonstrated has a negligible effect on intake rates), unless the attack was one which resulted in the birds leaving the field to forage elsewhere. The opportunistic method of collecting data did not allow quantification of this rate - one would need to record the proportion of all foraging flocks which were the
victims of carrion crow aggression, and the proportion of birds which left the field as a result of this. The author's impression is that the effect of carrion crow aggression varied from nil to serious disruption, probably depending on different environmental conditions prevailing at the time.

The data in table 1.7.3 also generally do not support the hypothesis of Bossema et al. (1976) and Roell (1978) that rooks and jackdaws flocked to reduce the effect of carrion crow aggression. Rooks and jackdaws were not less likely to leave a field when attacked if they were in a larger flock - thus there were no "strength in numbers" effects (row 2 of each table; combined data, chi-square = 4.50, df = 4, n.s.). Similarly, the rate of attacks suffered by an individual bird did not decline for any species with increasing flock size (and in fact increased for jackdaws), and thus neither was there any "selfish herd" dilution effect of carrion crow aggression achieved by flocking (row 3 of each table).

The results to predictions (15) and (16) also support the prey disturbance hypothesis. Carrion crows were occasionally observed to attack flocks of black headed gulls (Larus ridibundus), starlings (Sturnus vulgaris), mixed flocks of Turdidae, feral doves (Columba livia var. domestica) and woodpigeons (Columba palumbus) on grassland. The
latter two species are certainly not in any sense food competitors, but could disturb earthworms equally as much as the other species. Unfortunately no quantification is available of the frequency of attacks compared to the frequency of foraging without being attacked, nor of the relative frequency of attacks on different flock sizes of other species. However, an early field note, written before any evidence had appeared to suggest that large earthworms were an important prey of carrion crows and might be disturbed by the actions of other species foraging in the field, noted that carrion crows were quite often observed to fly past solitary corvids to attack corvid flocks, and flew past solitary corvids to attack flocks of other species.

No data are available to test prediction (16), that larger flocks on arable should not be attacked more frequently. One final piece of evidence is a quite strong correlation between the overall rate of carrion crow attacks against any other Corvid, and the density of earthworms in the field \( (r = 0.550, N = 16, p < 0.05) \). An interpretation of this interesting relationship could be that the more earthworms present, the higher proportion of the carrion crow diet they form, and the more benefit a carrion crow could gain by removing other birds from a field. One last point which also supports the prey disturbance hypothesis, but not an interference competition
hypothesis, is that when an attack was obviously intended to remove birds from a field, the carrion crow almost never continued the attack beyond the field limits, although the removed birds were often still within the boundaries of the carrion crow's territory; this is quite unlike the description of attacks by resident carrion crows on flocks of non-breeding conspecifics by, e.g., Charles (1972), Spray (1978) and Yom-Tov (1974), which were attacked until they had left the territory. Were the attacks on other species interference competition, one would have expected the carrion crows to attempt to exclude the flocks from their entire territories, and not just from a particular grass field. Data from the Scottish studies just mentioned suggested that a territorial pair of carrion crows could keep their territories free of large flocks of conspecifics.

The individual predictions will now be examined in turn.

(6a, 7a, 10a, 11a) Carrion Crow - Rook

It was predicted that carrion crows should avoid or show aggression towards larger flocks of rooks. Some weaker avoidance of carrion crows by rooks was predicted.
The two species did show low overlap in the use of fields at the same time (time-space alpha = 0.28; figure 1.5.4) and product alpha was reduced to a very low level (using prey numbers for the diet component of product alpha, alpha = 0.08; using calorific value, alpha = 0.04; figure 1.7.1) by this avoidance. The data cannot distinguish which species tended to show most avoidance. Carrion crows also showed the predicted agonistic behaviour towards rooks, and did attack bigger flocks more, again as predicted (although, unlike the combined species' data, this trend did not reach statistical significance, probably due to the limited sample size; row 1 of table 1.7.3a, chi-square = 5.58, df = 4, n.s.). Larger flocks did not withstand carrion crow attacks better, unlike Dossema et al. (1976) and Roell (1978) predicted (row 2, chi-square = 0.16, df = 4, n.s.).

Rooks tended to forage in large flocks more frequently when carrion crows were absent, and in smaller flocks when carrion crows were present (though again this trend failed to reach statistical significance; rows 5 and 6, chi-square = 3.40, df = 2, p = 0.18). Thus the prediction that, because of the carrion crow's tendency to attack larger flocks more, rooks should occur at lower flock sizes, was supported when carrion crows were present. However, they did still occur at large flock sizes quite frequently, although carrion crows were present at fewer
of the observed larger flocks (row 7), suggesting that there was some other, unidentified, reason for flocking by rooks (see part two of the thesis). There was no tendency for individual birds in larger flocks to receive fewer attacks from carrion crows (row 3; correlation on ungrouped flock size measures, $r = -0.018$, n.s.), and hence no "selfish herd" benefit to flocking for rooks of a reduction of individual attack rate suffered.

(6b, 8a, 10b, 12a) Carrion Crow - Jackdaw

It was predicted that carrion crows should show some negative behavioural response to jackdaws, especially at higher flock sizes because of the prey disturbance effect, but also at lower flock sizes because of diet/microhabitat overlap. Jackdaws were predicted to show some weak avoidance and similar flock size effects to those predicted for rooks in carrion crow presence.

The two species did show lower overlap in the use of fields at the same time than did carrion crow - rook (alpha = 0.15), which was necessary to reduce product alpha to a similarly low level (prey numbers = 0.06, calorific value = 0.05). Thus avoidance reduced overlap to near zero, and little interference competition aggression is expected.

The data in table 1.7.3 for jackdaws are similar in trend to those described for rooks, and again pointed to carrion
crow aggression as the result of earthworm interference and not interference competition. Row 1 indicates that carrion crows attacked larger flocks more frequently (chi-square = 9.51, df = 3, \( p < 0.05 \)). Larger flocks did not leave after carrion crow attacks less frequently than smaller ones (row 2: no test due to chi-square assumptions violated) and individual attack-rate suffered by jackdaws actually increased with flock size (\( r = 0.426, p < 0.001 \)), thus there was no benefit derived in reducing the effect of carrion crow attacks by flocking.

Jackdaws did not however show any clear trend to occur in smaller flocks when carrion crows were present and larger ones when they were absent (rows 5 and 6), and carrion crows were present at a substantial proportion of occurrences of the larger flocks (row 7). Since aggression rate was higher on larger flocks, this suggests there was some other, unidentified reason for jackdaw flocking. The tendency for jackdaws to associate with rooks (section 1.5.2) also remains an enigma since rooks were more likely to be attacked by carrion crows and, since carrion crows were not observed to single out one species for attack when attacking a mixed flock, associating with rooks will mean increasing the frequency with which individual jackdaws will suffer carrion crow attacks (however, there were some weak facilitations of prey intake rates when in rook presence - see chapter 1.6).
(6c, 9a, 10c, 13a) Carrion Crow – Magpie

It was predicted that carrion crows should show a negative behavioural response towards magpies at all flock sizes because of the prey disturbance effect and quite high diet/microhabitat and grass crop overlaps. Magpies, however, though expected to avoid carrion crows because of this overlap, had increased prey intake rates for some key prey items when carrion crows were present. Thus no clear prediction about their behaviour could be made. Avoidance was quite marked in these two species (alpha = 0.27), though not as low as one might have expected; whether this was the result of the two species' A-territoriality reducing the number of alternative fields available, or because magpies did not avoid carrion crows, cannot be determined by the data. The avoidance shown did reduce product alpha to a low level (prey numbers = 0.16, calorific value = 0.12).

Carrion crows attacked larger magpie flocks more frequently (row 1, though no test of the significance of this trend may be made due to violation of assumptions), contrary to an interference competition hypothesis but consistent with the prey disturbance hypothesis, although magpies rarely occurred in flocks (rows 5 and 6). Rather strangely magpies were more likely to be in a flock if a carrion crow was also present (rows 5 and 6, chi-square
assumption violations), even though there was no indication that larger flocks withstood carrion crow aggression better (row 2, chi-square violations), and larger flocks did not suffer less aggression per individual than smaller ones (row 3, $r = 0.077$, n.s.). As noted in chapter 1.6, magpies tended to have higher intake rates for some important prey types when carrion crows were present, possibly due to superior exploitation competition but also quite likely due to a positive relationship between the likelihood of carrion crow presence and high prey densities. Thus, since magpie A-territoriality was less fixed in winter than that of the carrion crow (chapter 1.2), it may be that larger magpie flocks occurred when carrion crows were present because prey were attracted to forage on a field containing high prey densities.

(7b, 8b, 11b, 12b) Jackdaw - Rook

Neutral or associative behavioural responses were predicted on the part of both species, and indeed overlap in the use of fields at the same time was far higher than for any other species-pair combination ($\alpha = 0.65$). However the strength of the tendency to flock together, described elsewhere, is in excess of the predictions based on chapters 1.5 and 1.6.

Rooks were sometimes observed to displace jackdaws
during foraging, perhaps especially from cow pats, though this was so infrequently observed that it could not be quantified by the methods used.

(7c, 9b, 11c, 13b) Magpie - Rook

It was predicted that rooks should show a negative behavioural response to magpies but that magpies should behave neutrally towards rooks. The two species showed the predicted low overlap of field use in time (alpha = 0.15), though the data cannot show whether the avoidance was mainly due to rook behaviour or not. Product alpha was reduced to a very low level indeed (prey numbers = 0.03, calorific value = 0.01).

Field notes kept for the last five years contain only two descriptions of a rook displacing a foraging magpie.

(8c, 9c, 12c, 13c) Jackdaw - Magpie

The high overlap on diet/microhabitat and some negative effects of magpie presence on jackdaw prey intake rates (there were no data to test for the reverse effect) led to a prediction of marked negative behavioural response on the part of both species. Since the two species were close in weight it was not clear whether one would predict much interspecific aggression as interference competition,
or little aggression because its outcome was less predictable. Overlap of field use at the same time was very low (alpha = 0.15) producing a low product alpha (prey numbers = 0.09, calorific value = 0.08). Thus avoidance produced the predicted effect. Agonistic interactions were observed but again so infrequently that their rate could not be quantified by the methods used.

(9d) The General Status of the Magpie

Several predictions were made based on the fact that one guild member (the magpie) belonged to a separate genus (Pica) to the other three (Corvus), and retained little unique niche space to itself. The first was that it should show low abundance. Data described above have shown that there were fewer magpies in the study area than any other species.

It was also predicted that they would need to show generally more tendency to display short-term behavioural options than the other three species to retain a place in the guild. Since they were smaller than two of the other members, and almost the same size as the other, avoidance was the most obvious mechanism available. It was the case that magpies in general showed the lowest mean overlap in the use of fields at the same time as the three other
species (table 1.7.4). Thus magpies in general showed more avoidance behaviour than the other species, reducing their general product overlap to the same low level as that of the other three species (table 1.7.4). This is also well illustrated by the relationship between body-size ratios between species and resource overlap indices before and after the addition of the overlap measure of avoidance behaviour (figure 1.7.3). Since three species are congeneres we might expect, if they are part of a stably structured community, to show a positive linear relationship between overlap in body size and overlap in prey type/microhabitat/grass habitat use. This is because predator size generally correlates with the size of prey items taken (see e.g. Ashmole 1968, J.H. Brown 1975, Hespenheide 1973, 1975, Karr & James 1975, D.S. Wilson 1975); and thus two species close in size will be expected to show less overlap on prey type or habitat choice, whilst two species differing greatly in size can overlap more in prey type and habitat since differences in prey size choice will mean they are exploiting effectively separate prey populations.

Figure 1.7.3a shows that the three *Corvus* species do show the predicted linear relationship, but that their relationships with *Pica pica* are scattered widely around the *Corvus* regression line. Thus in terms of morphological adaptation and long-term behaviour, magpies were not part
Figure 1.7.3

Relationship between body size ratios and overlap indices for four Corvid species of two genera

(a) Product alpha: grass habitat choice x calorific value of prey type (not size)/microhabitat; (b) grass x prey type/microhabitat x use of space in time.

Body-size ratios are the mean of weight, length (minus tail), tail, wing, tarsus, bill length, and bill depth (see table 1.2.1).

Full lines are the regression lines calculated for the three pairings of *Corvus* species (carrion crow - jackdaw, carrion crow - rook, and jackdaw - rook). The dashed lines merely enclose the outermost points of the *Corvus* pairings - they have no statistical validity as confidence limits, of course.
(a)

\[ \alpha \]

GRASS HABITAT

\times

PREY TYPE - MICROHABITAT

(b)

\[ \alpha \]

GRASS HABITAT

\times

PREY TYPE - MICROHABITAT

\times

TIME - SPACE

SIZE - RATIOS BETWEEN SPECIES
of a stable community. However, when the use of the short-term behavioural option of avoidance in time is added (figure 1.7.3b) the magpie points fall much closer to the Corvus regression line, except for the relationship between magpies and rooks, where the overlap is much less than predicted by the body-size difference between the two species. Thus we have another indication of the magpie's use of short-term behaviour to stabilise its position in the guild.

A further indication of the magpie's position is its use of grass habitat types. Figure 1.4.2 indicates that it showed more tendency to use crops in proportion to their availability than the three Corvus species - again perhaps an indication either that it entered these habitats later than the other three species, or that the ancestral habitats of the Corvus species were more similar to modern farmland than that of Pica pica was. However, table 1.7.2 gives another indication of the kinds of mechanisms which allow magpies to exist in farmland despite this. Unlike most of the other species, which tended to avoid or show no effect of other species' presence on their gross habitat choice, magpies were in each case more likely to occur on grassland (significantly so in two cases) and on permanent pasture (significantly so in all three cases) when the other species were present. Since grassland was more abundant than arable, and since permanent pasture was the
most abundant grass crop, these are beneficial tendencies for magpies. This may be another indication of magpie's exploitation efficiency compared to the other species which allows it to exist despite not occupying any unique portion of the niche hyperspace available. (It will be recalled that data in chapter 1.6, including niche overlap shift in carrion crow presence-absence in the favour of the magpie, suggested that magpies were superior exploitation competitors compared to the other species for certain prey items).

Yet another short-term behaviour which may help magpies to exist is its rarity of occurrence in flocks (table 1.7.3 - 79% of magpies were on their own or in pairs, and only 6% in flocks of 6-20 birds). Flocks greater than this very rarely occurred, and were not recorded during routine censuses; since carrion crows attacked larger flocks of each species more frequently, this was probably the reason for magpies suffering the lowest average carrion crow attack rate per individual of the three species (24.8 per hour of foraging together with carrion crows, compared to 79.1 for rooks and 53.9 for jackdaws), and thus it will have been disrupted in its foraging less frequently.

--------//--------

In conclusion, short-term behaviour reduced overlap
between each species pair in their use of resources to very low levels, and table 1.7.4 indicates that behaviour reduced the average overlap between each species and the other three guild members to almost identical low levels, suggesting a stable, structured community was formed. It might be expected that initial high levels of overlap on basic resources would be modified by behaviour to enable coexistence, though surprisingly this is not frequently reported in the literature, apart from the large number of references which cite interference competition aggression (see references in section 1.1.3 above) but which mostly do not calculate its effect on species coexistence (see Gill & Wolf 1979 for a notable exception); and for studies demonstrating niche shifts to reduce overlap (again see references in section 1.1.3; a good example is Alatalo's 1981 study of Parus species in winter).

However, Schroder & Rosenweig (1975) showed that initial high overlap between two Dipodymus species (c.0.7 to 0.9 in different areas) was reduced by avoidance behaviour (to c.0.2 to 0.4). They further showed by an exclusion experiment that in fact the true competition coefficient was zero because removal of one species had no effect on the abundance or fecundity of the other despite the fact that resources probably were limiting. As they point out, one would expect to find optimal not tolerable alphas in nature since selection will be expected to select for
Table 1.7.4

Mean overlap between each Corvid species and the other three guild members

<table>
<thead>
<tr>
<th></th>
<th>Overlap in Time-Space</th>
<th>Grass Habitat x Diet/Microhabitat x Time-Space</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carrion Crow</td>
<td>0.24</td>
<td>0.10</td>
</tr>
<tr>
<td>Rock</td>
<td>0.36</td>
<td>0.09</td>
</tr>
<tr>
<td>Jackdaw</td>
<td>0.33</td>
<td>0.10</td>
</tr>
<tr>
<td>Magpie</td>
<td>0.19</td>
<td>0.09</td>
</tr>
</tbody>
</table>
behaviours which will reduce competition as far as possible, either mutually or at the expense of one of the species.

1.7.5 Ecological Impact

Prediction (14) stated that the level of short-term behaviour displayed should vary depending on the abundance of other species and the total calorific value of prey which they consumed. This is reasonable since a very abundant species with which species A overlaps a little will actually have more overall effect on species A than a rare, small, species with which it overlaps highly. Pianka (1974) defined a simple index of ecological impact as:

\[ L = \alpha \sum_{j} \cdot x_j \]

where \( x_j \) is the abundance of species \( j \).

Figure 1.7.4 plots the ecological impact of each species on each other, and the total impact (L) suffered by each species. Interestingly, despite this weighting by species' abundances, the general conclusion is not dissimilar to that of the last section - initial impacts are high but the introduction of short-term behaviour reduces total impact suffered by each species to similarly low levels (black bars of the histogram). Figure 1.7.4b
behaviours which will reduce competition as far as possible, either mutually or at the expense of one of the species.

1.7.5 Ecological Impact

Prediction (14) stated that the level of short-term behaviour displayed should vary depending on the abundance of other species and the total calorific value of prey which they consumed. This is reasonable since a very abundant species with which species A overlaps a little will actually have more overall effect on species A than a rare, small, species with which it overlaps highly. Pianka (1974) defined a simple index of ecological impact as:

$$ L = \alpha \cdot x_j $$

where $x_j$ is the abundance of species $j$.

Figure 1.7.4 plots the ecological impact of each species on each other, and the total impact ($L$) suffered by each species. Interestingly, despite this weighting by species' abundances, the general conclusion is not dissimilar to that of the last section - initial impacts are high but the introduction of short-term behaviour reduces total impact suffered by each species to similarly low levels (black bars of the histogram). Figure 1.7.4b
Figure 1.7.4

Ecological impact of each Corvid species on the other guild members

(a) Ecological impact = species abundance x alpha; (b) impact = abundance x mean calorific intake rate x alpha.

 Hatch bars: impact where alpha = calorific value of diet/microhabitat; cross-hatch bars: product alpha = diet/microhabitat x grass habitat choice; solid bars: product alpha = diet/microhabitat x habitat x use of space in time.
IMPACT OF EACH OF 3 OTHER SPECIES, AND THEIR TOTAL IMPACT (SMALL LETTERS), ON EACH OF 4 CORVID SPECIES (LARGE LETTERS)
"Eco logical Impa ct" (L = μ × Abundance × Mean Ne w Intake Rate)

Impact of each of 3 other species, and their total impact (small letters) on each of 4 corvid species (large letters)
1.7 Short-term Behavioural Options

further adjusts $L$ by the average calorific intake rate of each species (see appendix 7.1). (*) Again, total impacts after avoidance behaviour has been taken into account are similarly low, except for the jackdaw's, which is greatly inflated by its tendency to flock with rooks - despite low diet/microhabitat overlap the sheer numbers of rooks and its relatively high prey intake rate make its impact on jackdaws heavier than any other species-pair combination. Since jackdaws seem to actively associate with rooks and are themselves quite abundant in the study area (see e.g. section 1.5.2 above) this would seem to suggest that this level of impact is "acceptable", and that the impacts of the other species on one another after short-term behaviour is taken into account become minimal and suggest a stable community will exist, comprised of a certain number of individuals of each species.

1.7.6 General Consequences of Overlap and Short-term Behaviour

Since earthworms formed the major part of the biomass of invertebrate prey available in winter (chapter 1.3), it is not surprising that rooks, the major exploiters of them,

(*) Without further adjustment by the proportion of the active day spent feeding, which may well increase with smaller body size (e.g. Gibb 1954), this adjustment for consumption is inadequate.
were the most abundant species of the four in winter in the study area. Jackdaws were the second most abundant species despite high overlaps with carrion crows and magpies and some negative effects of these two species' presence on jackdaw prey intake rates. They used short-term avoidance behaviour to offset this, but their persistent tendency to flock in general, and especially to flock with rooks, may be connected with their abundance — although this study could only find negative consequences of flocking (an increase in carrion crow aggression) and only weak advantages, and a similar disadvantage to conspecific flocking, to their association with rooks. This aspect certainly deserves further study.

The results presented in chapters 1.5, 1.6 and the present chapter have suggested that the carrion crow is the unhappiest member of the guild — it overlaps quite highly with jackdaws and magpies, and other species' presence had a severe effect on intake rates of one of its major prey types, large earthworms caught above the soil surface. Other data in chapter 1.6 suggested that in addition carrion crows were poorer exploitation competitors than magpies for some shared key prey types. Tables 1.4.4 and 1.4.5, the niche breadth measures on most resources, and the probability ellipse in figure 1.5.7c, show that in terms of prey selection and feeding action/microhabitat use, carrion crows were more generalist than any other
species. A generalist amongst specialists is likely to be a poorer competitor on those resources on which overlap occurs (e.g. Norse 1980). Usually a behaviourally dominant species' niche breadth is smaller than a subordinate's when in sympatry, often the result of expansion of niche by the subordinate to reduce the effect of overlap (Norse 1974). This was not the case in the present guild - carrion crows, the dominant species, had generally wider niche breadths on most resources than the other three species. This is a further indication, along with the evidence just considered in section 1.7.4, that direct interference competition is of limited importance in this guild.

Various evidence has been presented to show how magpies, despite occupying no unique portion of the available niche hyperspace, manages to survive in the guild, mainly through a variety of short-term behavioural options and apparently superior exploitation efficiency of certain key prey. Its behavioural plasticity is perhaps reflected by its recent spread into many cities. It occurs, unlike the *Corvus* species, in the new world (figure 1.2.3). However, it must remain vulnerable despite these mechanisms and is predicted to drop out of the guild first as conditions get worse. Its distribution within Britain would seem to support this prediction (figure 1.2.4b). It has a more restricted breeding range than the other three species and is the rarest of the four in Britain (estimated number of
breeding pairs in Britain and Ireland: carrion crow = c.1 million, rook = c.1.5 million, jackdaw = c.500,000, magpie = c.250,000 - Sharrock 1976). The restricted British range of magpies, mainly in the north, is not a latitude effect - figure 1.2.3 indicates that it exists further north than either the jackdaw or rook on the continental mainland. However, figures 1.2.4a and c suggest that it is more sensitive to a loss of good quality grazing land.

1.7.7 Other Studies, Other Areas

A brief comparison of relevant material from other published studies on these species may give an indication as to how specific the situation that has been described is to one winter on the western side of lowland southern Britain.

Holyoak (1974b) described the gross habitat choice of magpies at Tring, Hertfordshire (rather similar lowland farmland to that of the current study, but with more arable). In winter, the situation was generally similar to that described in this thesis. Most birds were on grassland, and somewhat more on permanent pasture than on grazed leys. The proportion of birds on stubble declined from November through to February, while the use of other arable crops (potatoes, fallow, sowings and marginal land) increased.
Peare (1978) showed that most rooks were found on grassland in Hampshire in winter (59.4%), a lower figure than the present study (81.7%), but there were somewhat fewer grass fields available (c.50% compared to c.60% at Keele). Only 35.8% of rooks were on grass in Aberdeenshire, an area of very high rook density, even though c.50% of fields available were grass (Peare et al. 1974).

Rooks foraging on grass in Aberdeenshire ingested invertebrate prey at a rate of 0.26 kcal per minute. The average at Keele was a very similar 0.24 kcal per minute.

Holyoak (1970) quantified the usage of different feeding actions by carrion crows. There were some sex differences, but comparison with table 1.4.4 of the present study reveals some interesting similarities and differences. In both studies carrion crows surface picked the same (c.40%) but while Holyoak's Tring birds surface probed a great deal (37.5 – 50%), Keele birds did not (8.5%) but dung-turned more (25.1%). Rates of the other actions were rather similar. Olsson & Persson's (1979) data from Sweden were more similar to Holyoak's than to those of the present study, with more actions above the soil surface and less use of dung than at Keele.

Lockie's (1956a) data from mixed farmland in winter at Oxford for rooks was almost identical to the data given in table 1.4.4, if one assumes that Jabs in the present study
1.7 Short-term Behavioural Options were coded by Lockie as surface probes (Lockie did not define Jab as an action). The jackdaw data, though not quite so perfectly similar as that just described for the rook, were still very similar. Olsson & Persson's data from Sweden showed jackdaws making much less use of dung than the jackdaws in Lockie's or the present studies. Their data for rooks were, though not as perfectly so as Lockie's, still very similar, though instead of deep-probing 36.3% of the time and digging 7.1%, the Swedish birds deep-probed 3.6% and dug 34.3% — probably suggesting a difference in definition by the authors of the different studies rather than differences in the behaviour of the birds.

The close similarity of these data on habitat and feeding action/microhabitat choice from various other locations perhaps confirms the suggestion in (for example) section 1.7.1 above that these are rather fixed and unchanging long-term behavioural characteristics of the different species. Though the data are, as stated earlier, rather crude, comparisons of the choice of prey types and sizes in the present study show more differences to those of other studies. Indeed, diet composition showed signs of differences for rooks in the different winters of the present study, as was stated at the beginning of chapter 1.4.
1.7 Short-term Behavioural Options

The data in Peare et al's (1974) study in Aberdeenshire indicate that rooks took fewer earthworms than in the 1980-81 winter at Keele both in terms of percentage of the diet (Keele = 47.1% by numbers, 79.3% by calories; Aberdeenshire = 19.7% by numbers, 51.9% by calories), and in terms of rate of capture per minute (0.65 per minute at Keele, 0.34 per minute at Aberdeenshire), but more similar proportions to the earlier Keele winters.

Nogstedt (1980b) showed that in the breeding season magpies and jockdaws overlapped by only 0.54 in the taxonomic make-up of prey taken, suggesting discrimination between the species in the present study may have been improved had taxonomic distinction been possible within the category employed of "invertebrates other than earthworms." Earthworms were more important to magpies than jockdaws in this study, forming 25% of the biomass of prey fed to nestlings; earthworms represented 16.6% of the calorific value of adult magpies' diets at Keele in winter.

Data in Holyoak (1970), and Lockie (1955, 1956a) show that it was the case that larger species, and even the larger sex within carrion crows, took significantly larger invertebrate prey items.

The data from these studies suggest that the proportion of prey types in the diet will vary with availability in the environment, but that the different species tended
to take particular major prey types irrespective of the place of study.

There are few data on behavioural mechanisms. Hogstedt (1980a) reported that magpies directed more aggression towards jackdaws at that point in the breeding season when they were most in food competition, though he did not detail whether this behaviour was adaptive interference competition which resulted in a reduction of the effect of jackdaw presence. The fact that magpie breeding success was significantly depressed in jackdaw presence suggests it was not an effective behavioural mechanism. Lockie (1956b) reported low rates of interspecific aggression between carrion crows, rooks and jackdaws in the same flock although, as stated earlier, Bossema et al. (1976) and Roell (1978) witnessed more frequent carrion crow aggression. Roell and Vines (1981) both showed that larger flocks of jackdaws and magpies respectively were able to feed on artificially provided dense clumps of non-invertebrate food.

Higuchi (1979) reported that jungle crows (*Coryus macrorhynchos*) were behaviourally dominant to carrion crows at Japanese rubbish dumps, and drove them away; yet in areas where carrion crows did not occur jungle crows occupied habitats which only carrion crows occupied in areas of sympatry. This suggests once more in a very different
situation that exploitation competition is important in determining community structure in these species, and that the role of true interference competition is limited. Loman (1980), studying habitat use of the same four species as considered in this thesis, presented some data which may suggest that magpies were the most likely species to show avoidance behaviour, as they were in the current study.

1.7.8 Consequences on Long-term Social Organization

It is to be expected that the interaction described will have some effect on the long-term social organisation of the species. Almost no work has been done on this, although Dossema et al. (1976) made some speculations about the role of carrion crow aggression in the evolution of flocking by rooks and jackdaws (which could not be supported by the present study), and about the evolution of colonial nesting by rooks, hole nesting by jackdaws, and the addition of domes to magpie nests. Daeyens (1981) and Vines (1981) have reported predation by carrion crows on magpie nests with some indication that choice of nesting area and use of a dome could reduce the level of this predation.

One particularly interesting study is that of Hogstedt (1980a) which showed that magpie breeding success was adversely affected by jackdaw presence, and that this was
almost certainly the result of direct food competition. Jackdaws were not affected by magpie presence because their gregarious behaviour enabled them to forage further from the nest as prey were depleted. Magpies, however, were forced by their own A-territoriality, and the threat of carrion crow predation on an unprotected nest, to forage in the over-used area around the nest.

Hogstedt suggests that magpies might be better off (other things considered) breeding colonially like the jackdaw. This is rather interesting in the light of the present study's findings which suggest that in winter the magpie is not a stable member of the community, that it may have come into the habitat more recently than the Corvus species, and that it may not have adapted yet to the guild in a long-term sense. It is also of interest that the closely related yellow-billed magpie *Pica nuttalli* has evolved to semi-coloniality (Verbeek 1973) where birds hold A-territories which may vary greatly in size, and the adults may forage widely from the nest and may join other pairs to do so (a rather similar social organisation to that shown, as far as is known, by jackdaws and also choughs, *Pyrrhocorax pyrrhocorax*, in Europe).

One area which has not been investigated by the present thesis is the remarkably different social organisation found amongst the four species when on arable land.
Flocks of rooks and jackdaws on stubble are very dense, compact and large compared to when on grassland. Carrion crows, though sufficient data are not yet available to quantify this, appear to show less aggression towards birds of the other species on stubble, and often forage amongst flocks. Yet overlap on this resource is total. It may be that the prey is superabundant temporarily and hence not limiting, or "new" in evolutionary terms, or indefensible against the increased number and density of birds which can forage on it. The situation deserves further study.

Rooks did not gain an advantage in terms of reduced carrion crow aggression by flocking on grassland. In fact, their flocking attracted increased interference by carrion crows. Since rooks were so clearly specialists on subsurface earthworms, an aggregated prey, it is suggested that rooks flocked to enhance exploitation of these prey. This is investigated in part two of the thesis.