ISSUES IN CORVID BEHAVIOUR AND ECOLOGY

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TEXT CUT OFF IN THE

ORIGINAL

Why...do rooks manouvre 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

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 metereological 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 caryo-
catactes) 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 glan-
darius) foraging on the same field (Williamson 1960 has
recorded this in the Isle of Man). In the mixed agricul-
tural 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-Mersey 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 water-logged 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.

(a)

Built-up area

Land over 500'

0 1
MILE

WATERSHED
BURSLEM
HANLEY
NEWCASTLE UNDER LYME
STOKE
Keele
Keele Hall
Madeley
TRENT
MERSEY
Fowlea Brook
Lyme Brook
River Trent
M.6.
500'
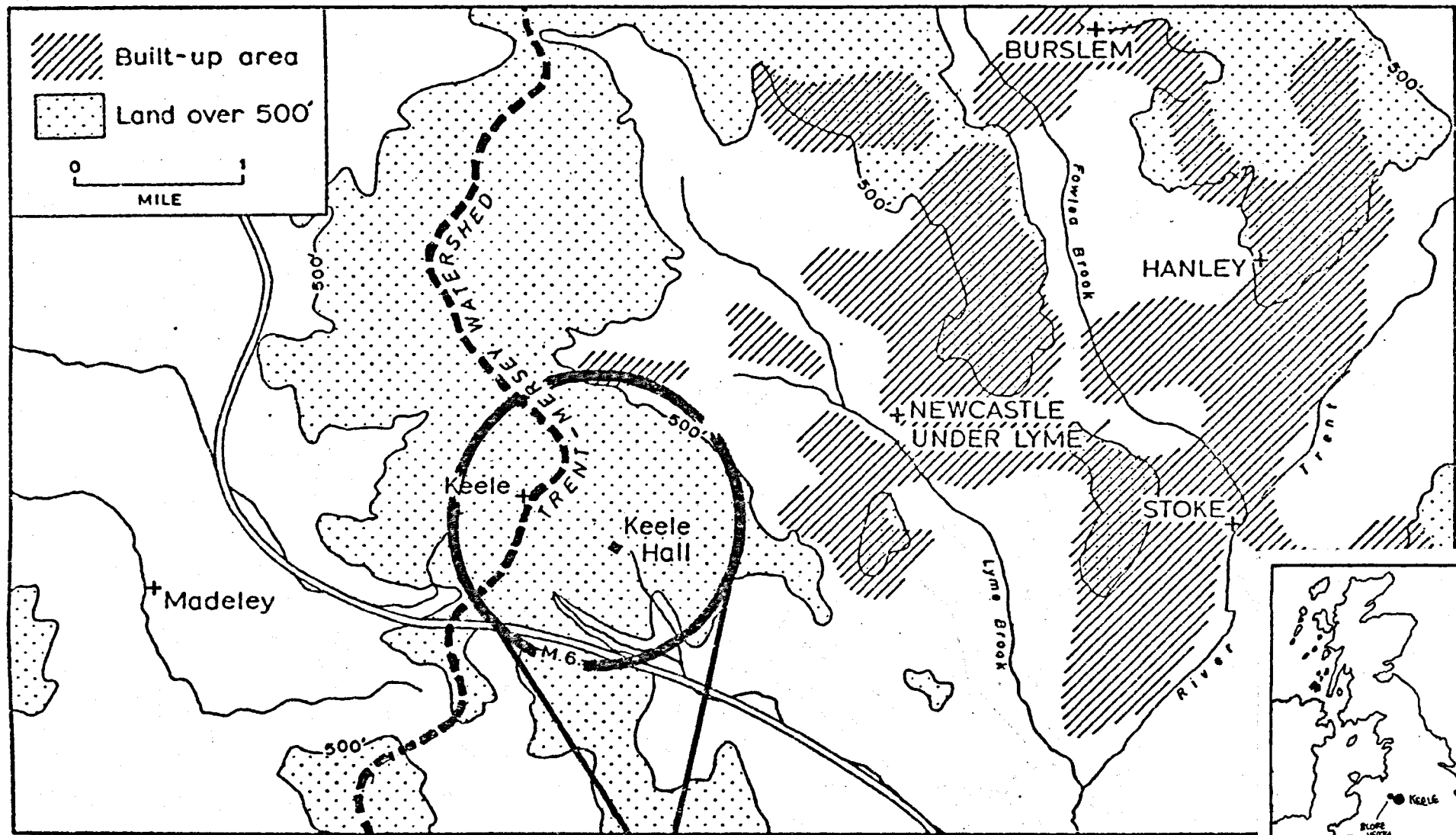
Main Study Area Centred Here

(b)

NEWCASTLE UNDER LYME →

SILVERDALE

UNIVERSITY CAMPUS

KEELE VILLAGE

← MOTORWAY →

0   0.5   1 KM
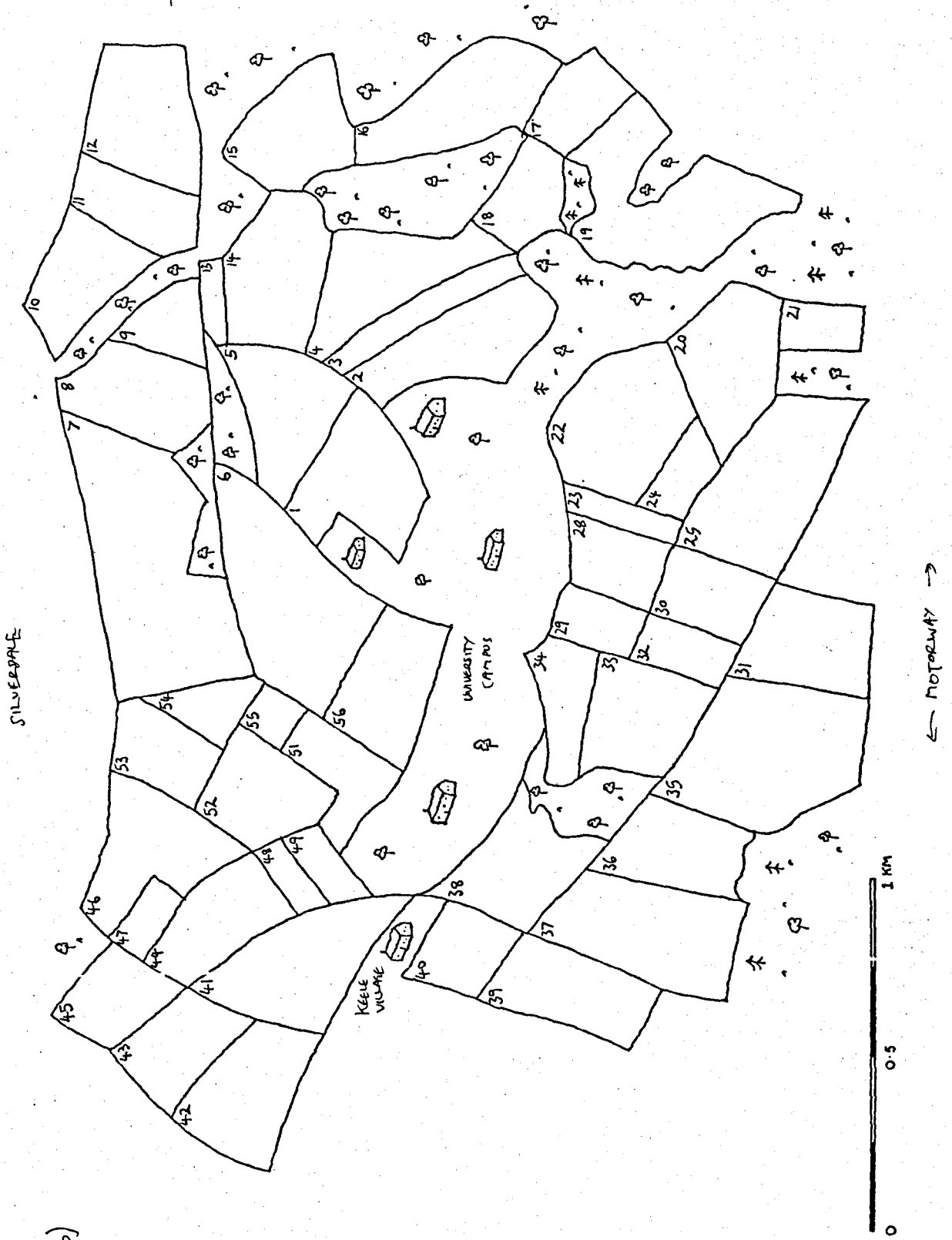
January 1976 (Waite 1976, 1978).

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 Feare 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

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 practise 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 (25-60x60) 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 avail-
able.

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 inver-
tebrate groups, but was not completed within the thesis
period due to the extent of the task (see appendix 8).

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 extrac-
tion (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 combina-
tion of handsorting and flotation in a 25% solution of
magnesium sulphate (Laurence 1954). The absolute effi-
ciency of this method is unknown, though Southwood's (1978)
summary of studies indicates that efficiencies are accept-
able 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 inver-
tebrates were distributed randomly, regularly, or in aggre-
gations. 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 popula-
tion 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).

areas - in fact only as the sample becomes more 'fixed' in its nature.

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

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(*) 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 sam-

ples....

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 occa-

sions. 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 esti-mate 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).

(a)
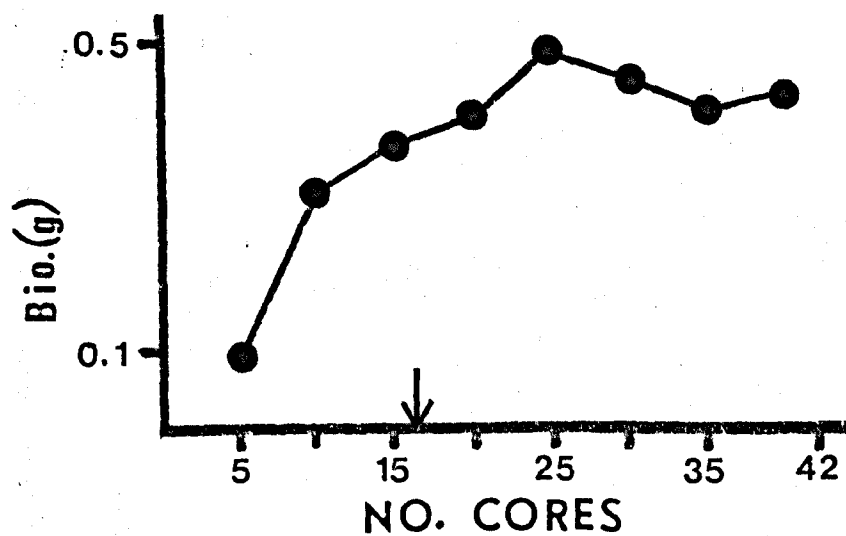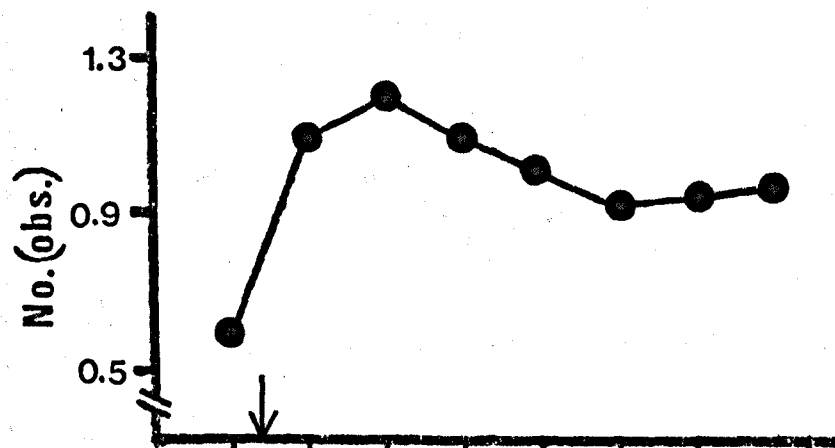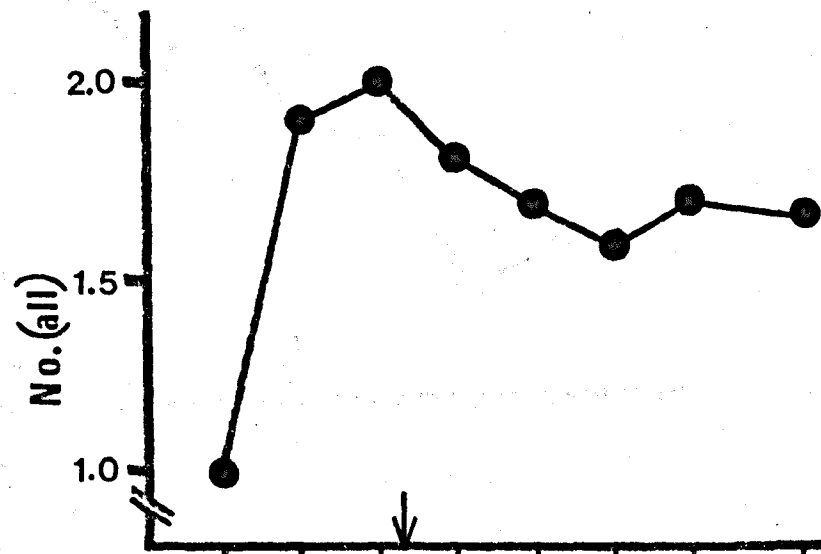
P.P. 18-9-79

(b)
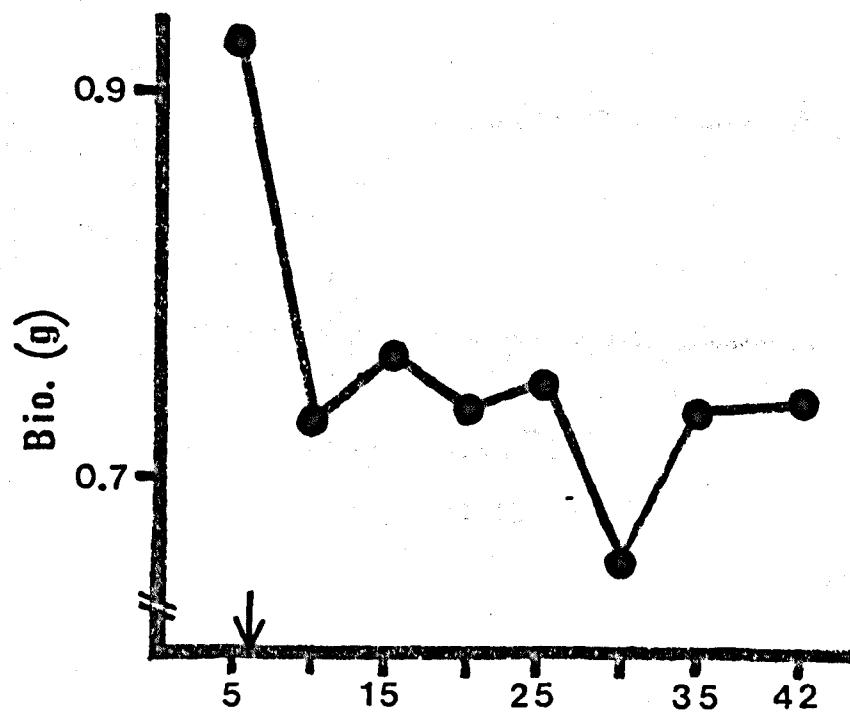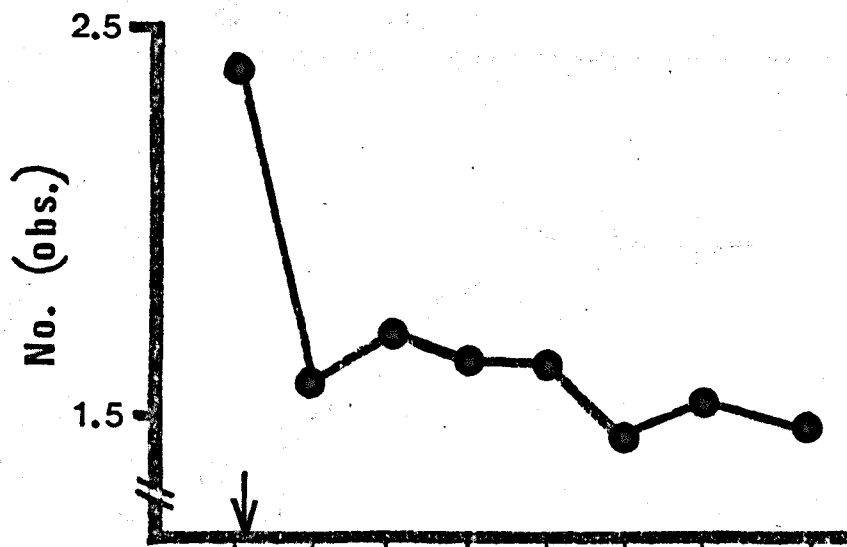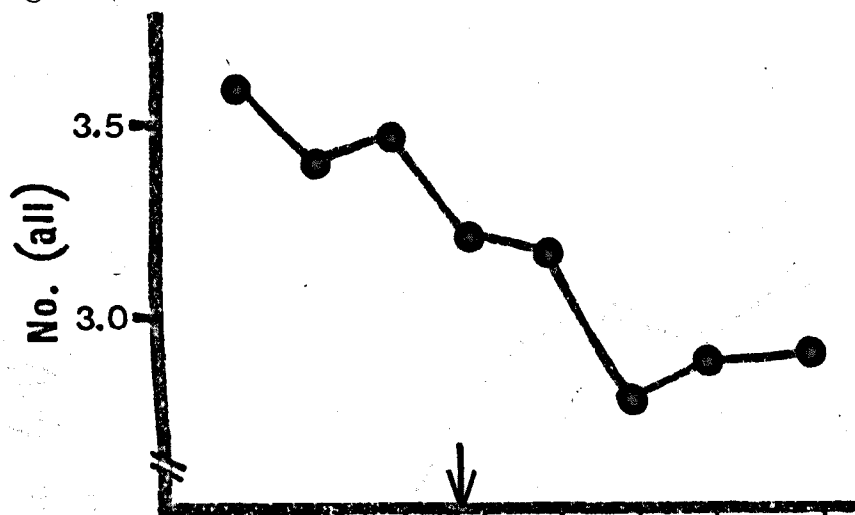
NO. CORES

P.P. 12-11-79

(C)
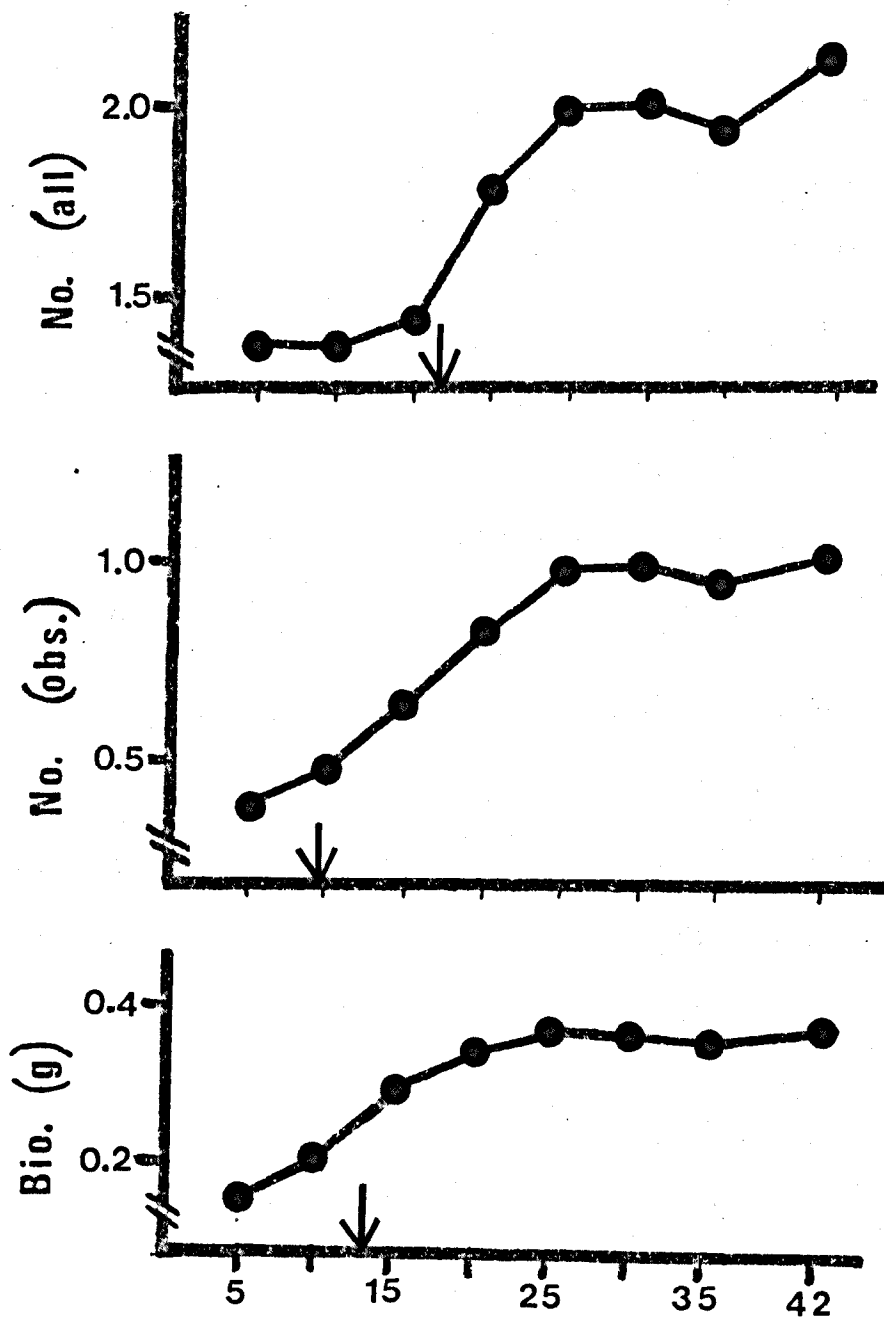
NO. CORES

P. P. 11-12-79

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

Figure M.3

Climatic conditions during a 26-day invertebrate sampling
programme in November-December 1979

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

(b) Air temperatures and rain days.

(c) Air temperatures and earthworm densities
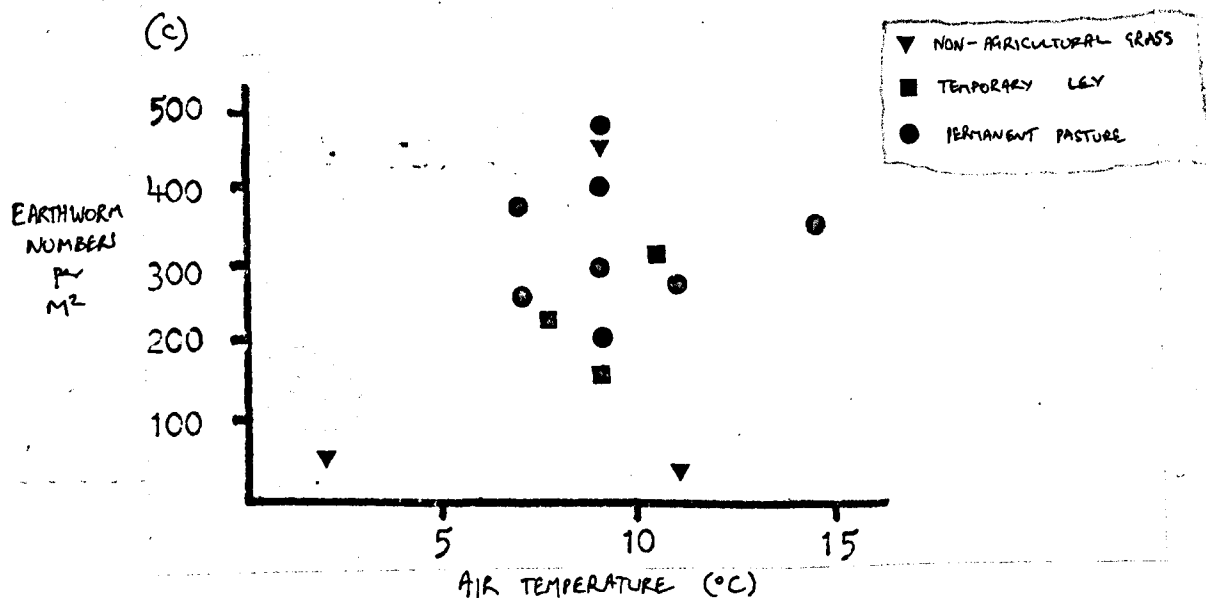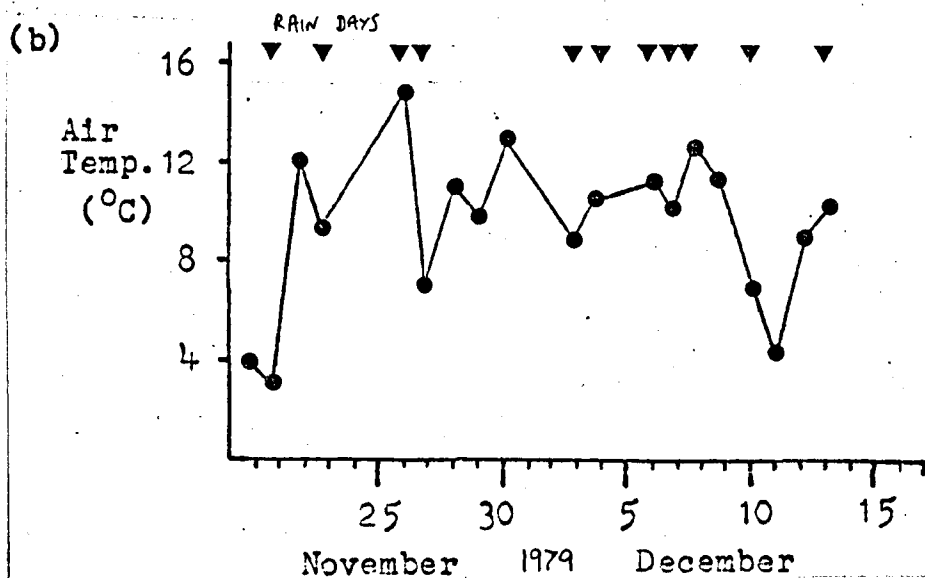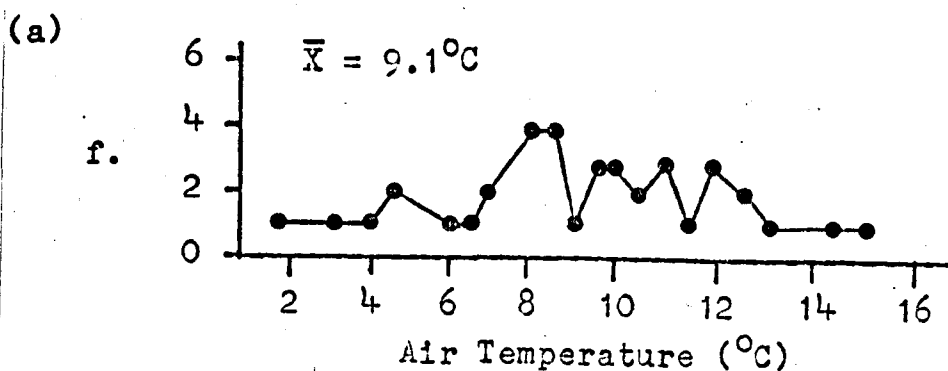
observations of birds. To ensure an adequate sample N of

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 sys-

tematically 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 popula-

tion 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.

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

Social

1. Flock Size
2. Nearest Neighbour Distance
3. Flock Sizes of Other Corvids

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

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.

Crops

1. Non-agricultural grass
     (sports fields, verges, etc.)
2. Ungrazed temporary ley
     (less than 10 years since
     last ploughing)
3. Grazed temporary ley
4. Ungrazed permanent pasture
     (more than 10 years since
     last known ploughing; in
     practise most were much
     older)
5. Grazed permanent pasture
6. Other grass

7. Wheat
8. Barley
9. Oats
10. Rye
11. Maize
12. Other grain

13. Potatoes
14. Sugar beet
15. Swede
16. Other root

17. Kale
18. Other brassica

19. Oilseed rape

20. Marginal
21. Woodland
22. Other

States

1. Sown broadcast
2. Sown drilled
3. Sown drilled through
     stubble
4. Sown drilled through
     grass
5. Sprouted (braird)
6. Standing less than 6"
7. Standing greater than 6"
8. Hay laying cut
9. Hay or silage cleared
     less than two weeks
     previously

10. Stubble
11. Burnt stubble
12. Mucked stubble

13. Plough
14. Harrow-tilth
15. Fallow

When recording behaviour of birds foraging on grass-

land, 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 con-
sidered 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 infre-
quency 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.

		C.Crow	Rook	Jackdaw	Magpie
NAG	% Observations	7.8	1.4	-	22.9
	% Usage	3.8	1.3	0.7	6.2
TLU	% Observations	13.3	1.4	-	17.1
	% Usage	1.9	-	-	3.7
TLG	% Observations	35.5	15.9	15.0	5.7
	% Usage	38.5	11.8	16.8	39.4
PP	% Observations	43.3	81.2	85.0	54.3
	% Usage	55.8	86.8	82.5	50.6
N Birds Observed		90	69	60	70
N Birds Censused		244	1219	655	214

As stated in section M.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 all EW per metre

square with N 'field observable' EW per metre square for

the set of 14 fields sampled in November-December 1979 - r

= 0.92; N all EW per core with N 'field observable' EW per

core for 14 separate samples of 42 cores each - mean r =

0.75 (range = 0.59 to 0.89); 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 con-

tagion ('aggregation'). However since, as stated above,

the sampling procedure was not standardised on inver-

tebrates other than earthworms, a significance test inves-

tigating 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 variabil-

ity 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 begin-

ning 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 NND'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 fol-
lowed 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 flatten-
ing 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 dis-
tance 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 - some-
times after a period of peering at the ground while stand-
ing 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. Fre-
quently 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 (M.11.1.10), where the bill is driven
down quickly but goes beneath the soil surface. The confu-
sion 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 differen-
tiated 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 crumbling 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.11.2 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.11.3 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 swal-

lowed. 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 inver-

tebrates.

(*) 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.11.4 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 inver-

tebrates, 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),
Feare et al. (1974), Grant(1955), Lakhani & Satchell
(1970), Lawrence & Millar (1945), MAFF (1942), MAFF (1952),
Satchell (1967a).

Prey Type	Wet Weight (g)	Water Content (%)	Calorific Value (kcal/g)		Protein Content (%N x 6.25)	
			Dry	Wet	Dry	Wet
Invertebrate:						
Small	0.007	75.0	3.83	0.96	46.87	12.69
Medium	0.183	("")	4.02	1.00	(as above)	
Earthworm:						
Small	0.276	85.0	4.42	0.66	67.10	11.69
Medium	0.634		(as above)			
Large	1.470		(as above)			
Grain:						
Barley	0.033	14.9	4.10	3.49	6.80	5.79
Oat	0.041	13.3	4.25	3.68	8.00	6.94
Wheat	0.037	13.4	4.29	3.71	10.30	8.92
Acorn	3.310	50.0	4.10	2.05	9.10	4.55

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 follow-
ing 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 max-
imum 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, com-
parisons 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 calcula-

tions 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 horizon-
tal, 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 practise most difficult for the

jackdaw, possibly because of a combination of the compara-

tive 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:

$$(1) \qquad \text{Alpha}_{ij} = 1 - 0.5 \sum_{x=1}^{n} |P_{i,x} - P_{j,x}|$$

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:

Species
    i   j

                                                              Niche
                                                              Overlap
    f   Alpha

Resource Gradient
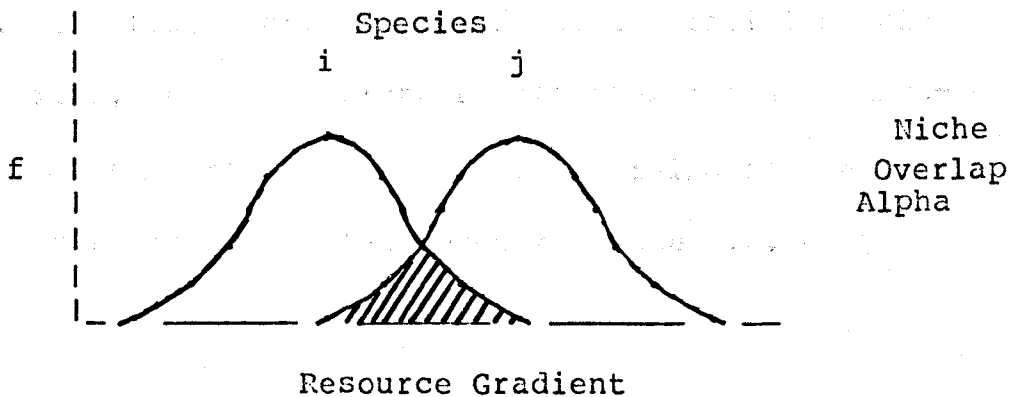
This formula is not a competition coefficient since it does not take into account resource availability (e.g. Hurlbert 1978, 1982, Schoener 1974a & b). Since availability could only be accurately measured for habitat in the present study, overlap indices are used in the thesis and not competition coefficients. 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 intial species

pair (or pairs), then higher-order relationships are calcu-

lated 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 utilisa-

tion of a particular resource gradient was calculated from

the formula of Levins (1968):

(2) B_i = $1/ \sum P_{i,x}^2$

where B_i is the niche breadth of species i and $P_{i,x}$ 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:

(3) B_{STAND} = $(B - 1) / (n - 1)$

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:

$$(4) \qquad C_{i,x} = \frac{N_{i,x} / N_{i,y}}{A_x / A_y}$$

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: $\dfrac{N_{i,x} \ / \ N_{i,y}}{A_x \ / \ A_y}$ is less than unity

Then: $C \ = \ -2 \ (0.5 \ - \ (1 \ / \ (1 \ + \ \left[\dfrac{N_{i,x} \ / \ N_{i,y}}{A_x \ / \ A_y}\right] \ )))$

(6)   If: $\dfrac{N_{i,x} \ / \ N_{i,y}}{A_x \ / \ A_y}$ equals unity

Then: $C \ = \ 0$

(7)   If: $\dfrac{N_{i,x} \ / \ N_{i,y}}{A_x \ / \ A_y}$ is greater than unity

Then: $C \ = \ 2 \ ((1 \ / \ (1 \ + \ \left[\dfrac{N_{i,x} \ / \ N_{i,y}}{A_x \ / \ A_y}\right] \ )) \ - \ 0.5)$

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) $\dfrac{N_{i,x} \ / \ N_{i,total}}{A_x \ / \ A_{total}}$

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:

$$(9) \qquad \overset{*}{x} = \bar{x} + ((s^2 / \bar{x}) - 1) * (1 + (s^2 / N\bar{x}))$$

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 assump-

tions 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 assump-

tions:

(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 distribu-

     tions 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 univari-
ate 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 vari-
ables to be entered into the discriminant function ana-

lyses, both parametric and non-parametric univariate ana-
lyses 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 stan-
dard deviation (see e.g. Sokal & Rohlf 1969 or Ferguson
1976).

The transformed variables were checked again. Vari-
ables 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 bio-
logically important in separating the species could not be
included in statistical tests of separation - however,
these variables were retained when calculating the descrip-
tive 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

intercorrelated beyond 0.50. Discriminant analysis is a
technique (rather similar to multiple regression in con-
cept) which combines a set of dependent variables to maxim-
ise 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 dif-
ferent 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 interpre-
tation 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 mean-
ingful 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 follow-
ing 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 pat-
tern of variable loadings; and if each derived function
provides significant separation between two or more species
consistent with the biological interpretation of the func-
tion. 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:

$$(10) \qquad D = \frac{variance\ (n-1)}{mean}$$

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 conservative 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
— BLIB at the University of Keele Computer Centre; BMDP
(Dixon 1975) at the University of Manchester Regional
Computer Centre; CLUSTAN 1C (Wishart 1978) at the Univer-
sity of Nottingham Computer Centre; Nottingham Unix Sta-
tistical Routines at the Department of Psychology, Univer-
sity of Nottingham; and SPSS (Nie et al. 1975) at UMRCC
and the University of Nottingham Computer Centre. Addi-
tional 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

Part One Chapter One - Introduction

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 structur-
ally 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 exam-
ple) gross habitat difference (such as deciduous or coni-
ferous 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 allow-
ing themselves access to resources despite another species'
attempts to exclude them. Thus this part of the thesis
seeks to link behavioural interactions between four sympa-
tric Corvid species (carrion crow, rook, jackdaw and mag-
pie) 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 over-
lap 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 vari-
ables:

Habitat	Diet
Grassland	Live Vertebrates
Plough	Carrion
Cereal	Human Waste
Wood Floor	Earthworms
Trees or Shrubs	Above Soil Surface Invertebrates
Hedges	Below Soil Surface Invertebrates
Long Grass or Scrub	Grain
Damp Meadows	Wild Seeds
Water Margins	Fruits
	Nuts
	Leaves

Each species was simply coded on each variable depending on
whether it utilised that resource frequently (2), occasion-
ally (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

KEELE WINTER BIRD FAUNA — CLASSIFIED ON 9 HABITAT AND 11 PREY VARIABLES

SIMILARITY COEFFICIENT

24.86290
22.25832
19.65374
17.04916
14.44458
11.84000
9.23542
6.63084
4.02626
1.42168

BRAMBLING
CHAFFINCH
REDPOLL
SISKIN
BULLFINCH
TREE SPARROW
GREENFINCH
ROBIN
DUNNOCK
WREN
JAY
GREAT TIT
NUTHATCH
WILLOW TIT
COAL TIT
MARSH TIT
BLUE TIT
LONG-TAILED TIT
BLACKCAP
GOLDCREST
TREECREEPER
LESSER SPOTTED WOODPECKER
GREAT SPOTTED WOODPECKER
GREEN WOODPECKER
REDWING
FIELDFARE
MISTLE THRUSH
SONG THRUSH
BLACKBIRD
WOODCOCK
WOODPIGEON
COLLARED DOVE
STOCK DOVE
FERAL DOVE
REED BUNTING
CORN BUNTING
YELLOWHAMMER
LINNET
HOUSE SPARROW
MEADOW PIPIT
SKYLARK
PHEASANT
GREY PARTRIDGE
RED-LEGGED PARTRIDGE
TAWNY OWL
BARN OWL
LITTLE OWL
KESTREL
SPARROWHAWK
ROOK
CARRION CROW
JACKDAW
MAGPIE
STARLING
BLACK-HEADED GULL
LESSER BLACK-BACKED GULL
SNIPE
LAPWING
GOLDEN PLOVER
MOORHEN
PIED WAGTAIL
GREY WAGTAIL
HERON

OPEN — HABITAT

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

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(*) 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).

the possibility of coexistence in sympatry, 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 func-

tion, 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 corre-

lated 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 indica-
tors 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 docu-
mented) 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 fol-
lowing chapters for the four Corvid species under con-
sideration. Condition (2) has not been quantified but is
almost certain to occur. It certainly occurs for stubble
grain in winter (Feare et al. 1974) and is likely to occur
for invertebrates since almost all are reproductively inac-
tive during winter. Bengtson et al. (1976) have shown by
exclusion experiments that golden plovers (_Pluvialis apri-_
caria) 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

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(*) For example: small insectivorous woodland passerines – Betts 1955, Gibb 1954, Haftorn 1956; nuthatches, Sittidae, and woodpeckers, Picidae – Stallcup 1968; finches, Fringillidae – Newton 1967; hawks, Accipitridae – Opdam 1975; waders, mainly Charadridae and Scolopacidae – Baker & Baker 1973).

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, sug-
gests 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 shift-
ing 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 condi-
tions (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 inter-
specific territoriality (see Morse op. cit. for review of
occurrences and Dow 1977b for an extreme example; see e.g.
Cody 1973 for a consideration of evidence that inter-
specific 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 inter-
specific 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.

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Almost no data have been published on modification of
foraging behaviour in the presence or absence of the dif-
ferent species under consideration here, and little quan-
tification of overlap in resource use (though see Hogstedt
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, Bossema et al. 1976,
Hogsted 1980a, Roell 1978, Rowley 1973, Vines 1981, Waite
1978).

The aggression reported was almost entirely directed
by carrion crows against the three other species. Bossema
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.

Part One Chapter Two - The Birds

The thesis presents data on four members of the family

Corvidae:

      Carrion (or Eurasian) Crow   Corvus corone
      Rook   C. frugilegus
      Jackdaw   C. monedula
      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 Corvus 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

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)

Carrion Crow   Corvus corone
Rook   C. frugilegus
Jackdaw   C. monedula
Magpie   Pica pica

PLUMAGE: BLACK

Corvus corone
CARRION CROW
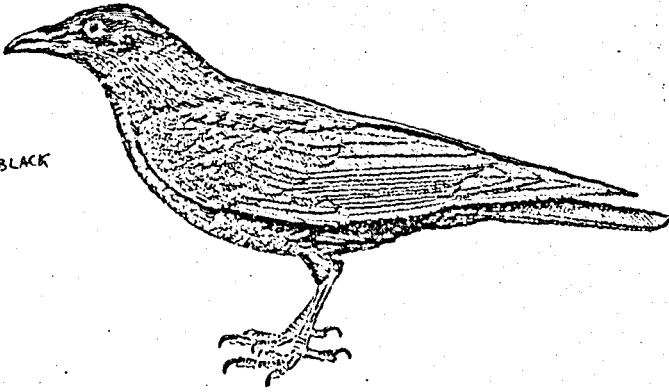
ADULT

FIRST-YEAR

GREYISH-WHITE

BLACK

PLUMAGE: BLACK

Corvus frugilegus
ROOK
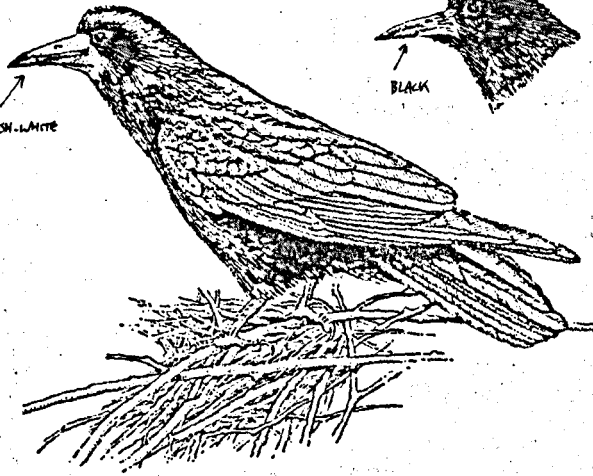
Corvus monedula
JACKDAW
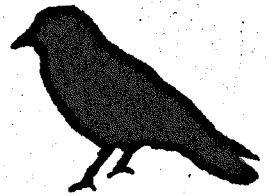
PLUMAGE: BLACK
WITH
GREY NAPE
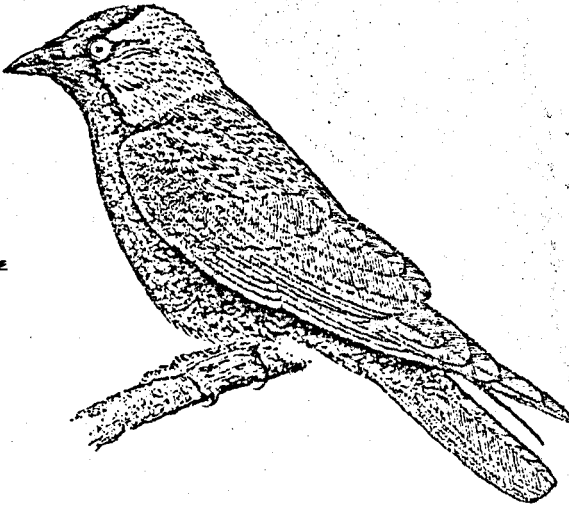
Pica pica
MAGPIE
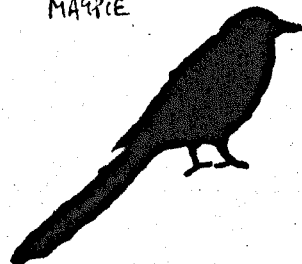
PLUMAGE: BLACK
AND
WHITE
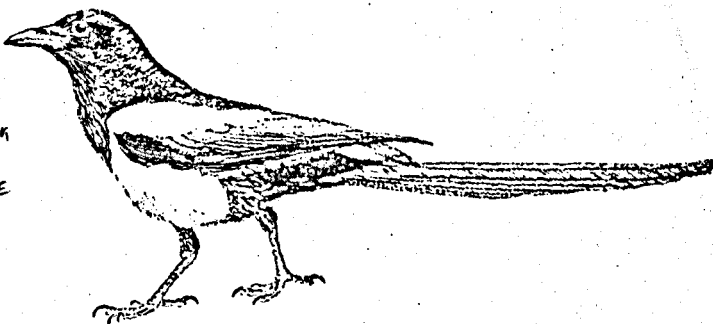
Table 1.2.1

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 characteris-
tic are given in appendix six.

(a) Data for Four Species

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

(*) Base of skull to tip; references: Green (1981), Hogstedt
    (1980b), Olsson & Persson (1979), Picozzi (1975)
(**) At nostril; references: Hogstedt (1980b), Holyoak (1970),
    Olsson & Persson (1979)

(b) Size-ratios between Four Species

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

	Average Ratio With 3 Other Species	Ratio Between Species Pairs			
		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 With 3 Other Species	Ratio Between Species Pairs			
		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.
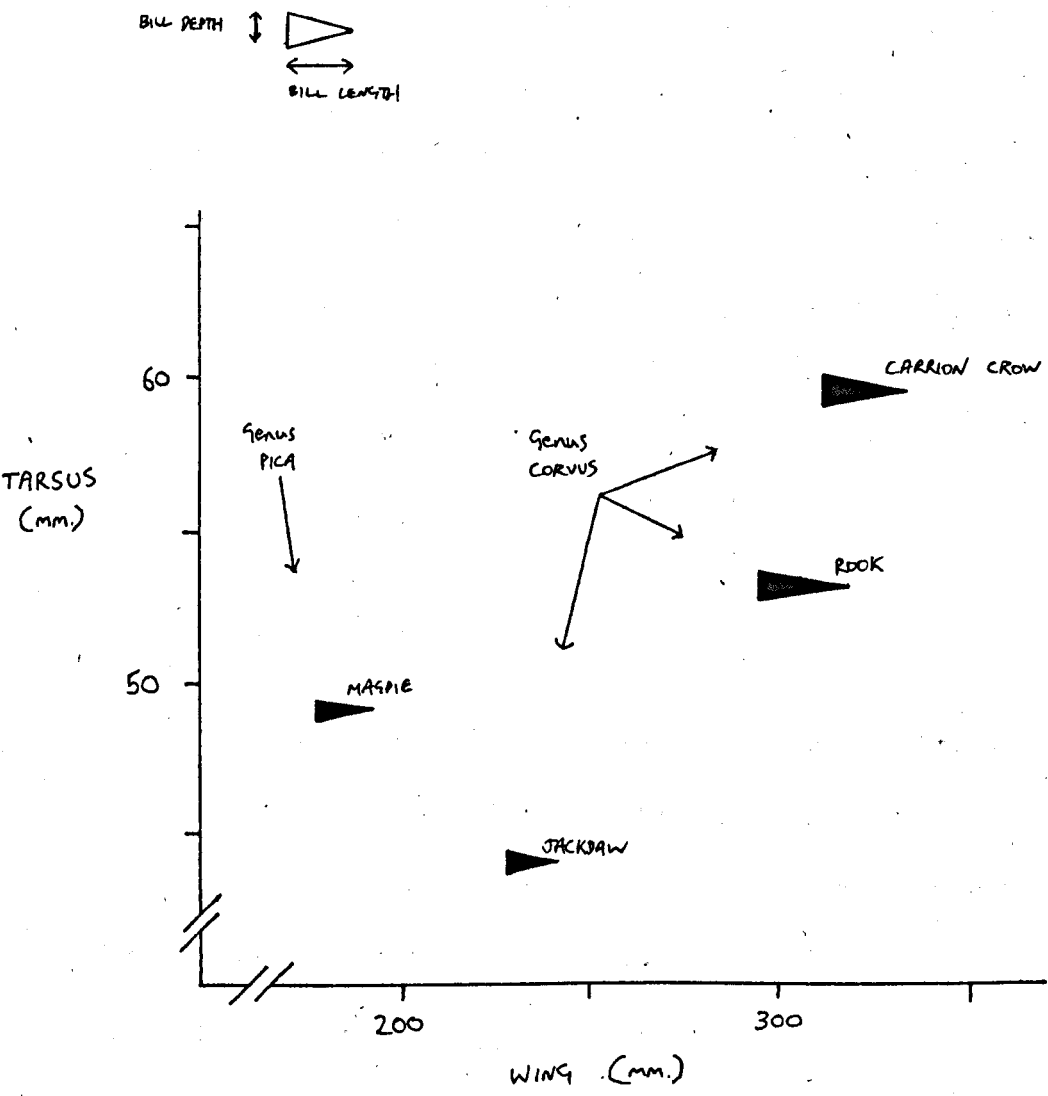
Within Britain, the Eurasian crow is represented by
its two races, <u>Corvus</u> <u>corone</u> <u>corone</u> in the south, and <u>C.</u>
<u>corone</u> <u>cornix</u> in the north and west.   There are few areas
where this species was not recorded breeding during the
period 1968-72 (figure 1.2.4b).   The 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), relation-
ships which will be analyzed later.

In the study areas these four species were sympatric
and common.   The data in this section, except where specif-
ically 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)
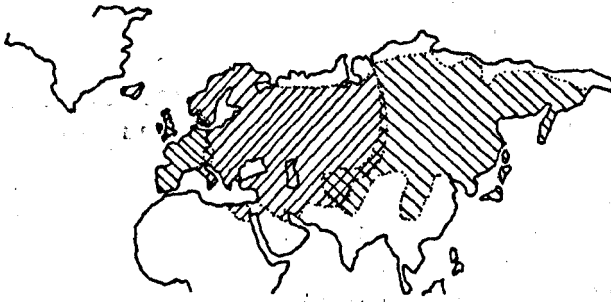
Corvus corone
CARRION/HOODED CROW
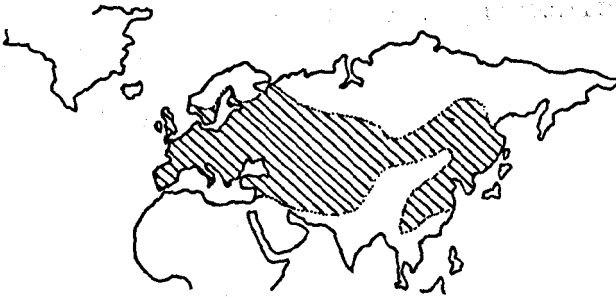
Corvus frugilegus
ROOK
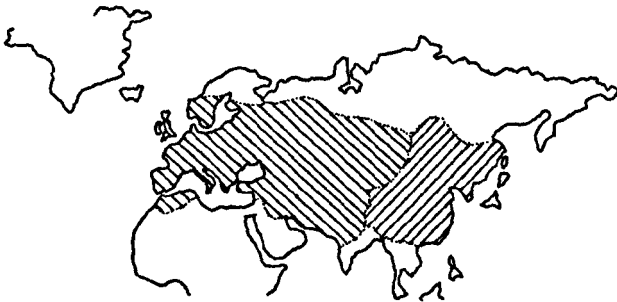
Corvus monedula
JACKDAW
(and "Daurian Jackdaw"
(Corvus dauuricus))
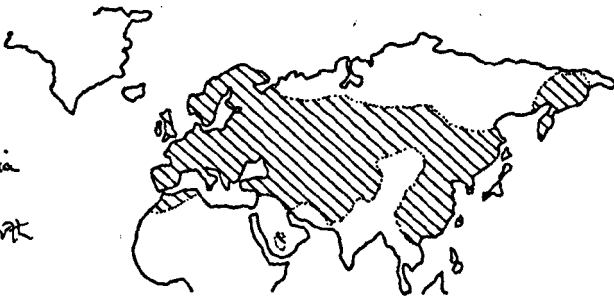
P.p. hudsonica
occurs in
western North
America at
similar
latitudes

Pica pica
MAGPIE

Figure 1.2.4

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 Shar-
rock 1976).

(c)   Location of study areas with predominant farming types
(from Anon. 1976)

WHEAT and OATS

SHEEP

DAIRY or BEEF CATTLE

(b)

Corvus corone
CARRION/HOODED CROW

Corvus frugilegus
ROOK

OVERLAP ZONE

HOODED

CARRION

H.
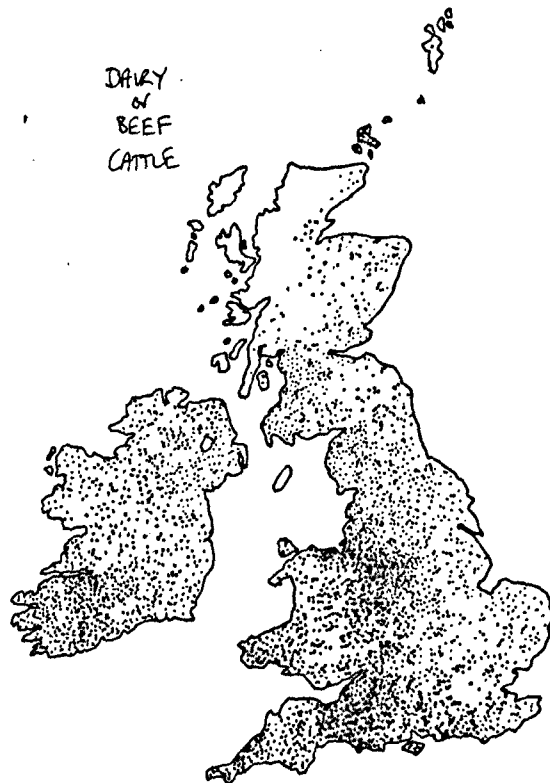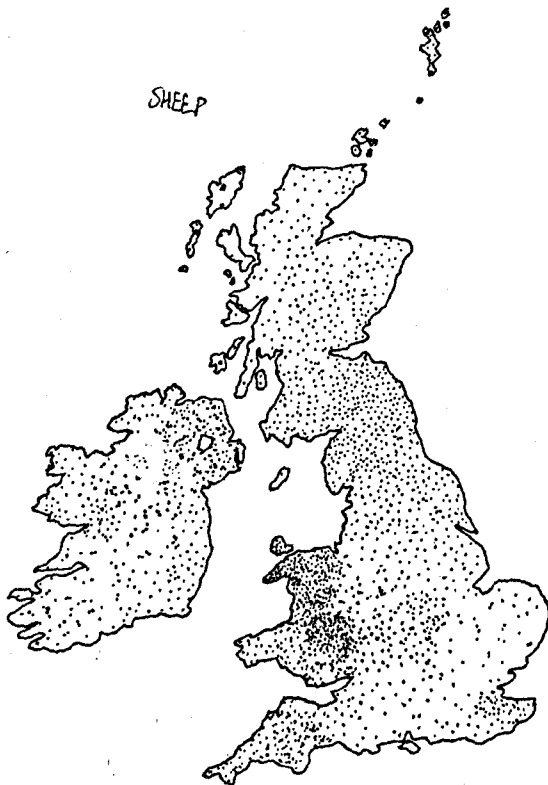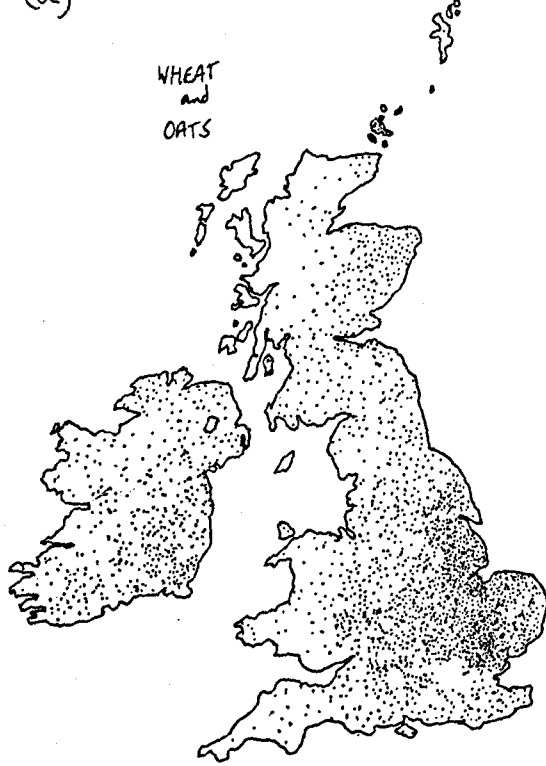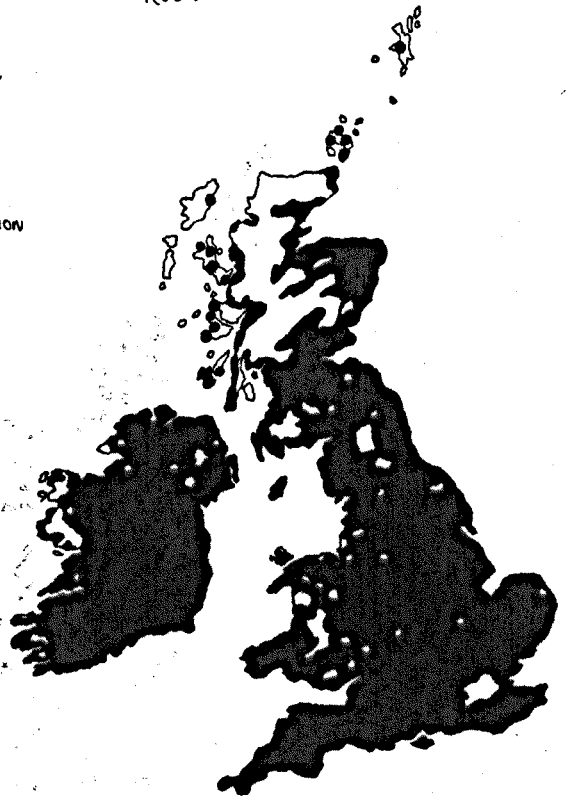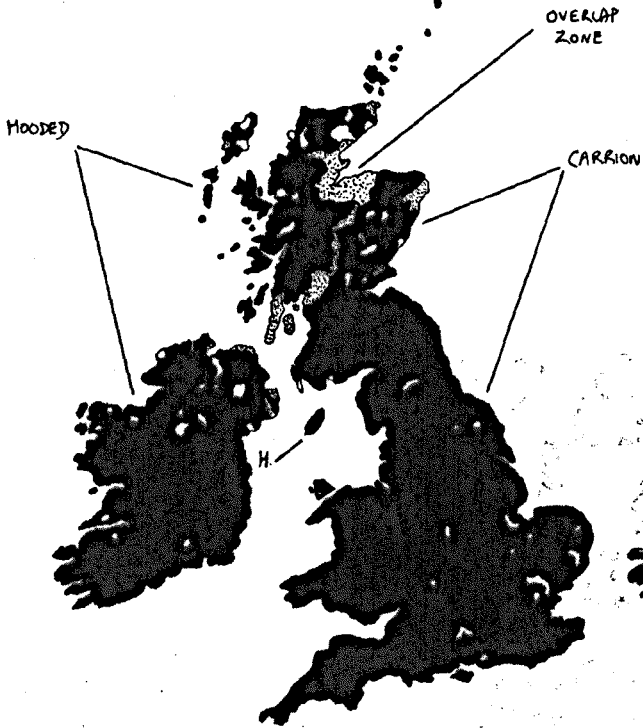
Corvus monedula
JACKDAW

Pica pica
MAGPIE

(c)

CATTLE

SHI.

CATTLE

CROFT + SHEEP

CATTLE

SHEEP OR CROFT

CROFT SHEEP

CATTLE

S.H.

I.A.

S.H.

CROFT OR SHEEP

MIXED

SHEEP

CATTLE

CROFT OR SHEEP

SHEEP

MIXED

CATTLE

SHEEP

CATTLE

MIXED

SHEEP

CATTLE

CATTLE

CROFT OR SHEEP

CATTLE

MIXED

CATTLE

S.H.

SHEEP

MIXED

HILL SHEEP

MIXED

SHEEP

MIXED

MIXED

SHEEP

CATTLE

MIXED

MIXED

SHEEP

CATTLE

MIXED

CROFT OR SHEEP

CATTLE

MIXED

CATTLE

SHEEP

CATTLE

ARABLE

MIXED

HILL SHEEP

CATTLE

MIXED

ARABLE

CATTLE

MIXED

CATTLE

CROFT OR SHEEP

CATTLE

S.H.

CATTLE

MIXED

CATTLE

SHEEP

MAIN STUDY AREA
KEELE, STAFFORDSHIRE

SUBSIDIARY STUDY AREAS
BLOREHEATH, SHROPSHIRE
FARMOOR, OXFORDSHIRE

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 unk-

nown 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 com-

munal 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 fre-

quency on arable, but most of the study area was divided

between territorial pairs or family groups (table 1.2.2 and

later discussion).

> References on which the above description is
> based: (Bohmer 1976, Charles 1972, Houston 1977a
> & b, Loman 1980, Picozzi 1975, Spray 1978, Tompa
> 1975, Wittenberg 1968, this study.)

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.

		Flock Size						Total N of Birds
		1	2	3-5	6-20	21-40	>40	
Carrion Crow	Grass	46.4	27.5	23.2	2.9	-	-	156
	Arable	48.6	35.1	5.4	10.8	-	-	85
Rook	Grass	9.3	11.6	17.4	30.2	19.8	11.6	996
	Arable	-	16.7	16.7	41.7	8.3	16.7	223
Jackdaw	Grass	10.8	16.2	16.2	35.1	16.2	5.4	441
	Arable	18.2	18.2	9.1	27.3	9.1	18.2	214
Magpie	Grass	50.0	29.6	13.0	7.6	-	-	160
	Arable	43.8	6.3	25.0	25.0	-	-	54

(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 indivi-
dually 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

1978, this study.)

Magpie

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,

Holyoak 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 metereologi-

cal 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 tempera-

tures 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.

		November	February	Nov-Feb
ARABLE	Barley Sown	0.5	0.0	0.4
	Barley Stubble	21.5	2.2	11.6
	Oat Stubble	1.9	1.3	1.4
	Wheat Sown	6.5	0.0	3.4
	Wheat Stubble	2.8	3.1	2.9
	Total Grain	33.2	6.6	19.7
	Barley Sprouted	1.9	3.5	3.4
	Wheat Sprouted	1.9	4.0	2.0
	Plough/Harrow	5.6	26.5	15.1
	Total Arable	42.6	40.6	40.2
GRASS-LAND	Non-Agricultural	9.8	10.6	10.0
	Ungrazed Ley	2.8	9.7	6.6
	Grazed Ley	14.9	11.9	17.0
	Permanent Pasture	29.9	27.0	26.3
	Total Grassland	57.4	59.2	59.9
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 12-11-80;   (b)   28-2-81

45
WHEAT STUBBLE
46
43
47 PLOUGH
44 PLOUGH
53
BARLEY STUBBLE
BARLEY STUBBLE
42 PLOUGH
41
52
54
WHEAT STUBBLE
WHEAT STUBBLE
BARLEY STUBBLE
WHEAT STUBBLE
48
WHEAT STUBBLE
49
BARLEY STUB
55
BARLEY STUBBLE
51
N.A.S.
56
BARLEY STUBBLE
NON-AGRICULTURAL GRASS
NON-AGRICULTURAL GRASS
NON-AGRICULTURAL GRASS

10
7   8
UNGRAZED LEY
11
12
GRAZED LEY
9
GRAZED LEY
PLOUGH
PERMANENT PASTURE
N.A.S. — 13
6
5
14
15
GRAZED LEY
PERMANENT PASTURE
PERMANENT PASTURE
4
GRAZED LEY
16
3
2
UNGRAZED LEY
PERMANENT PASTURE
PERMANENT PASTUAE
BARLEY STUBBLE
NON-AGRICULT. GRASS
18
UNGRAZED LEY
17
PERM. PASTURE
19

40
PERMANENT PASTURE
38
39
PERMANENT PASTURE
37
GRAZED LEY
36
GRAZED LEY
WHEAT STUBBLE
UNGRZ LEY
35
34
OAT STUBBLE
29
33
28 23
22
GRAZED LEY
PERMANENT PASTURE
32
30
24
BARLEY STUB. GRZ. LEY
20
UNGRZ. LEY
GRAZED LEY
PERMANENT PASTURE
PERMANENT PASTURE
25
31
OAT STUBBLE
SOWN WHEAT
21
GRZ. LEY
WHEAT STUBBLE
BARLEY STUBBLE

0   0.5   1 KM

(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 10cm.

(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.

(a)

(b)

DERBYSHIRE
NORTH STAFFORDSHIRE
UPLANDS
(PENNINES)

Hours

300
200
100
0

1 - 3 KT

4 - 10 KT

11 & over

(Excludes 493 hours
calm and variable)
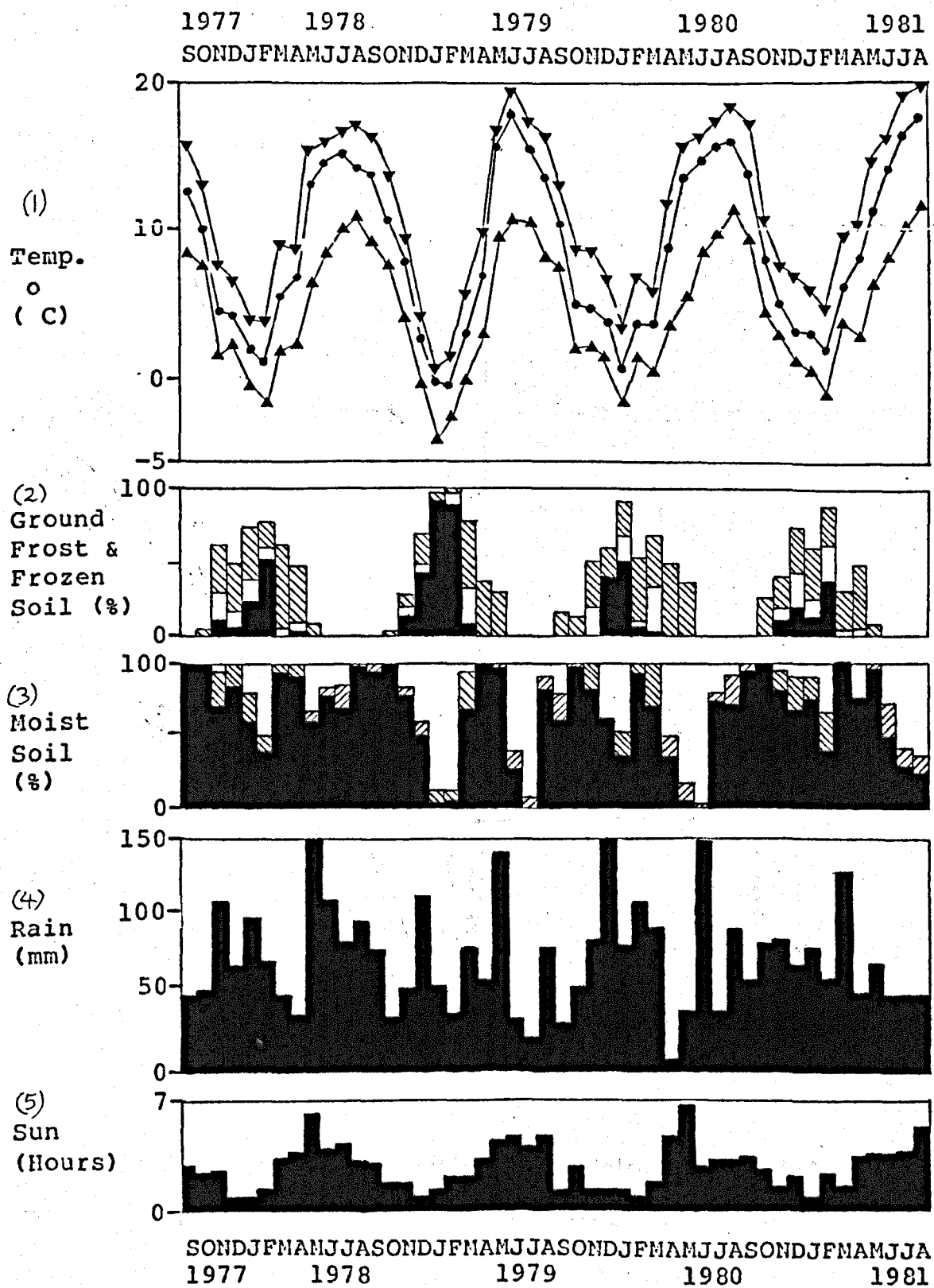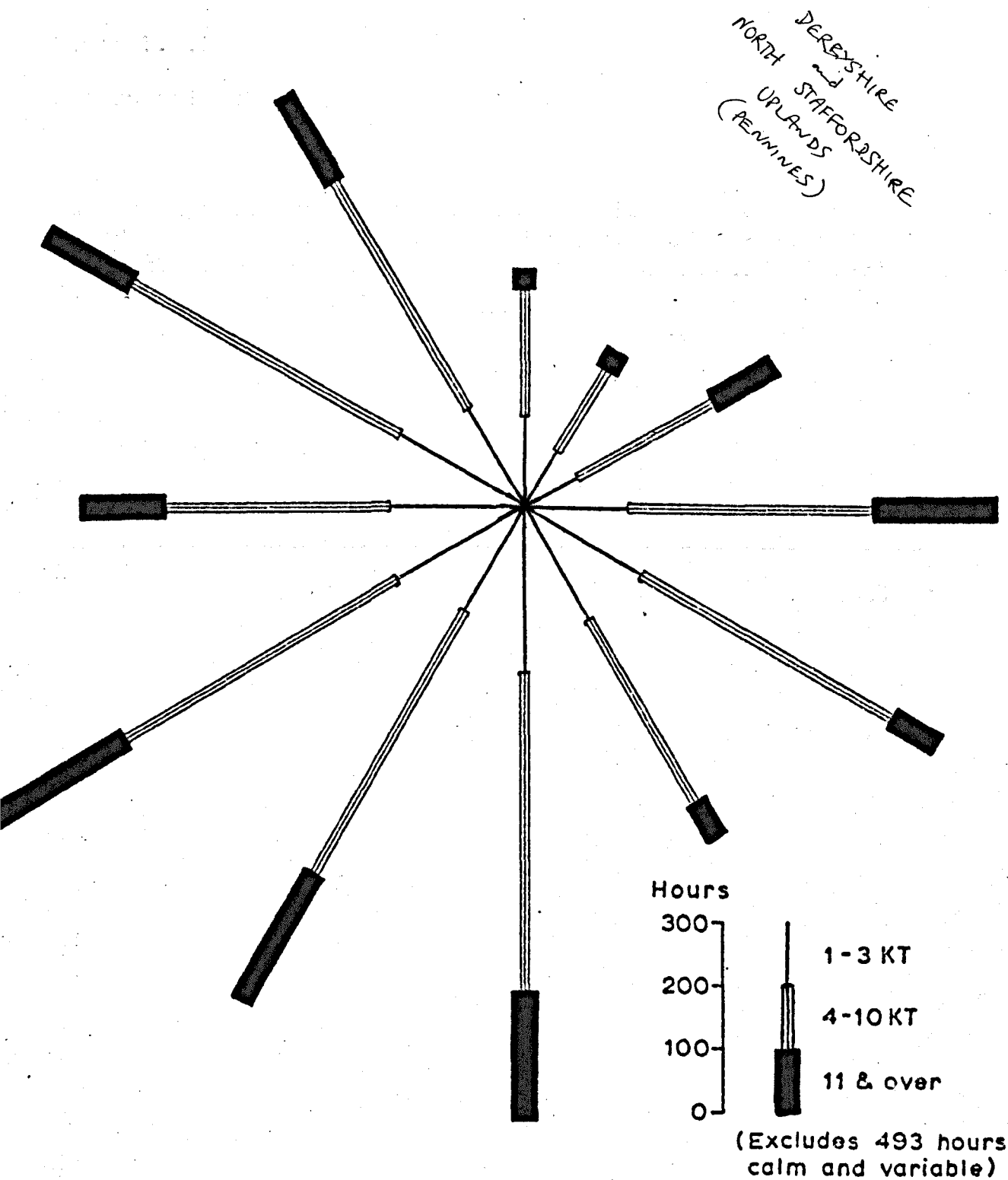
WIND. Mean Annual Direction and Velocity 1957-1969
(Based on continuous anemograph traces)

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 Beaver & Shaw 1970). Annual mean (excluding 1962-3) =
7.39.

November	December	January	February	March
0.11	2.44	4.11	3.94	0.78

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 <u>Agriolimax</u> <u>reticulatus</u>, 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 propor-
tion 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 disper-
sion, 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 aggre-
gations 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 distri-
buted 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
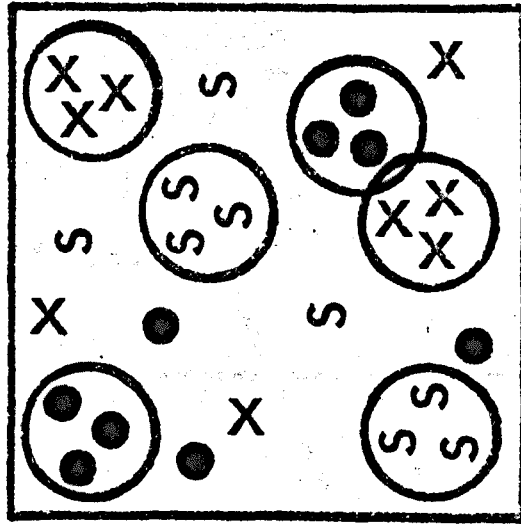
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aggregations
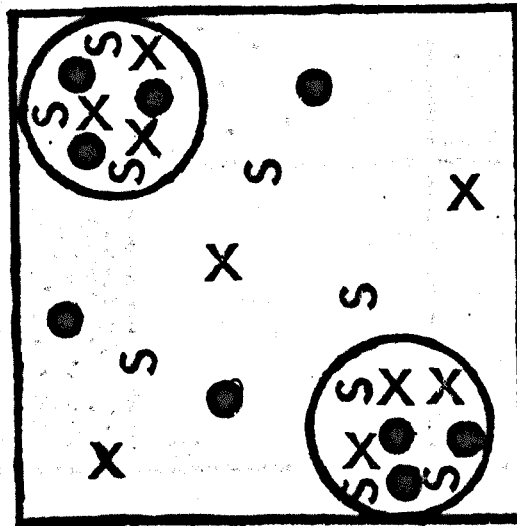
over-lapping
aggregations
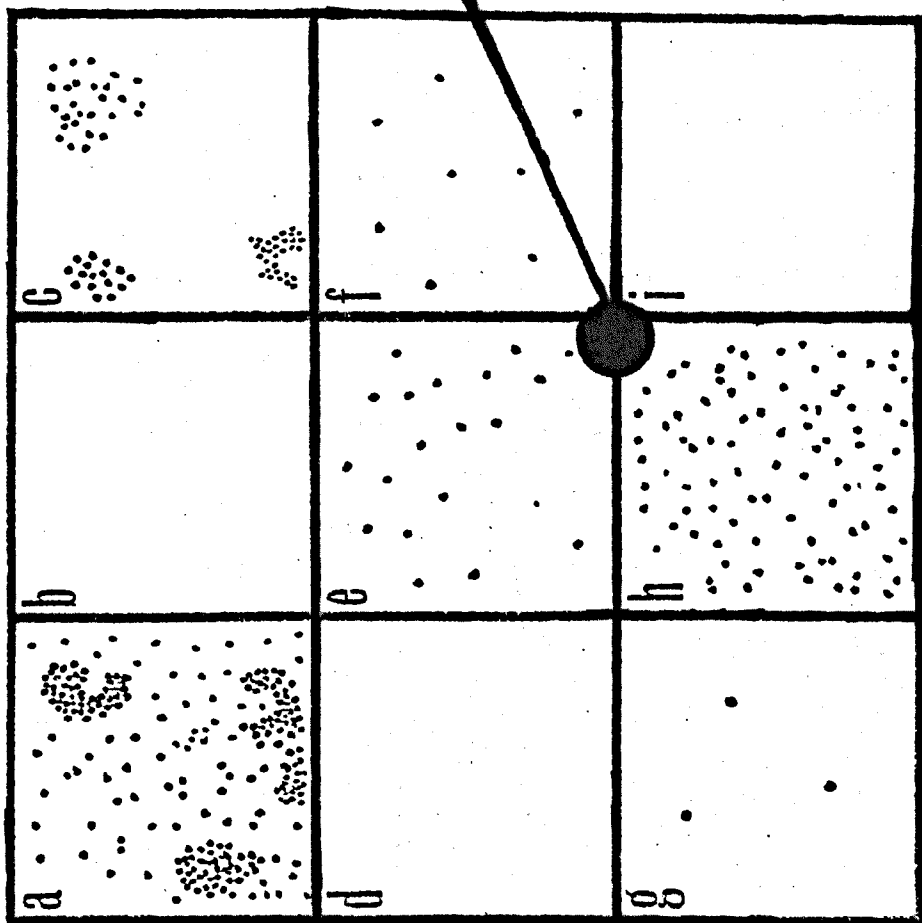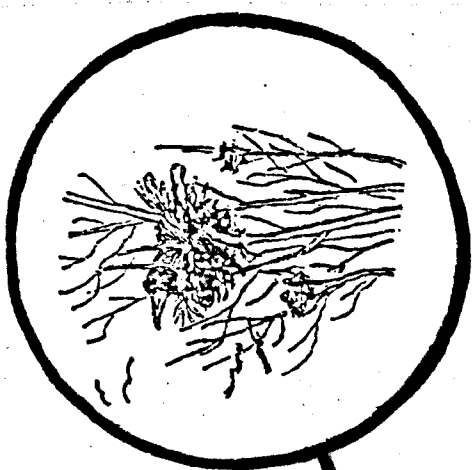
vae and Nematocera (= mainly Tipulid larvae)), with the variation in the densities of six other types being statistically independent of variation in wireworm numbers, although two of these (Arachnida and parasitic Hymenoptera) showed quite large non-significant positive relationships.

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 per-

manent pasture at Keele, but the densities of other inver-

tebrates were quite similar (appendix one).

Tables 1.3.3 and 1.3.4 summarise the relative densi-

ties 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 disper-

sion, 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 pas-
ture.

The biomass of earthworms in each separate core was meas-
ured, 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).

| | | Mean per Core | | | Ratio of Worms:Other (%) | | N of Soil Samples |
		Worms	Other: Min	Max	Min	Max	
NAG	Numbers	0.807	0.401		67:33		
	Biom(g)	0.419	0.0026	0.073	99:1	85:15	7
TLU	Numbers	0.643	0.430		60:40		
	Biom(g)	0.255	0.0030	0.079	99:1	76:24	1
TLG	Numbers	1.040	0.413		72:28		
	Biom(g)	0.386	0.0029	0.076	99:1	84:16	3
PP	Numbers	1.429	0.251		85:15		
	Biom(g)	0.544	0.0020	0.066	99:1	89:11	14
Dung	Numbers	2.700	0.351		88:12		
	Biom(g)	1.735	0.0049	0.064	99:1	96:4	2

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 M.12.2.4).

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).

| | | | Other Invertebrates: | | | |
		Earthworms	Above Soil Surface	Below Soil Surface	Either	No. of Samples
NAG	V/M	57.1	–	–	–	7
	Grid	0.0	33.3	0.0	0.0	3
TLU	V/M	(100.0)	–	(0.0)	(0.0)	1
	Grid	(100.0)	–	(0.0)	(0.0)	1
TLG	V/M	33.3	–	–	–	3
	Grid	50.0	–	50.0	50.0	2
PP	V/M	71.4	–	–	–	14
	Grid	66.7	(100.0)	16.7	16.7	6
Dung	V/M	50.0	–	–	–	2
All	V/M	68.0	–	–	–	27
	Grid	50.0	50.0	16.6	16.7	12

cussed in section M.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 M.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.

1.3.9.   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).

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 sam-

ples, though the relative numbers in each sample were not

recorded due to the excessive time-cost involved:

> Allolobophora caliginosa
> A. chlorotica
> A. longa
> A. nocturna
> A. rosea
> Lumbricus terrestris
> Octolasion cyaneum

L. terrestris, A. longa, A. nocturna and O. cyaneum 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 under-took 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 of 'all' earthworms per metre square with 'field observable': r = 0.92; 'all' with biomass (g) per square metre: r = 0.87; 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

$$r = 0.893$$
$$p < 0.001$$
$$Y = 0.338x + 13.258$$
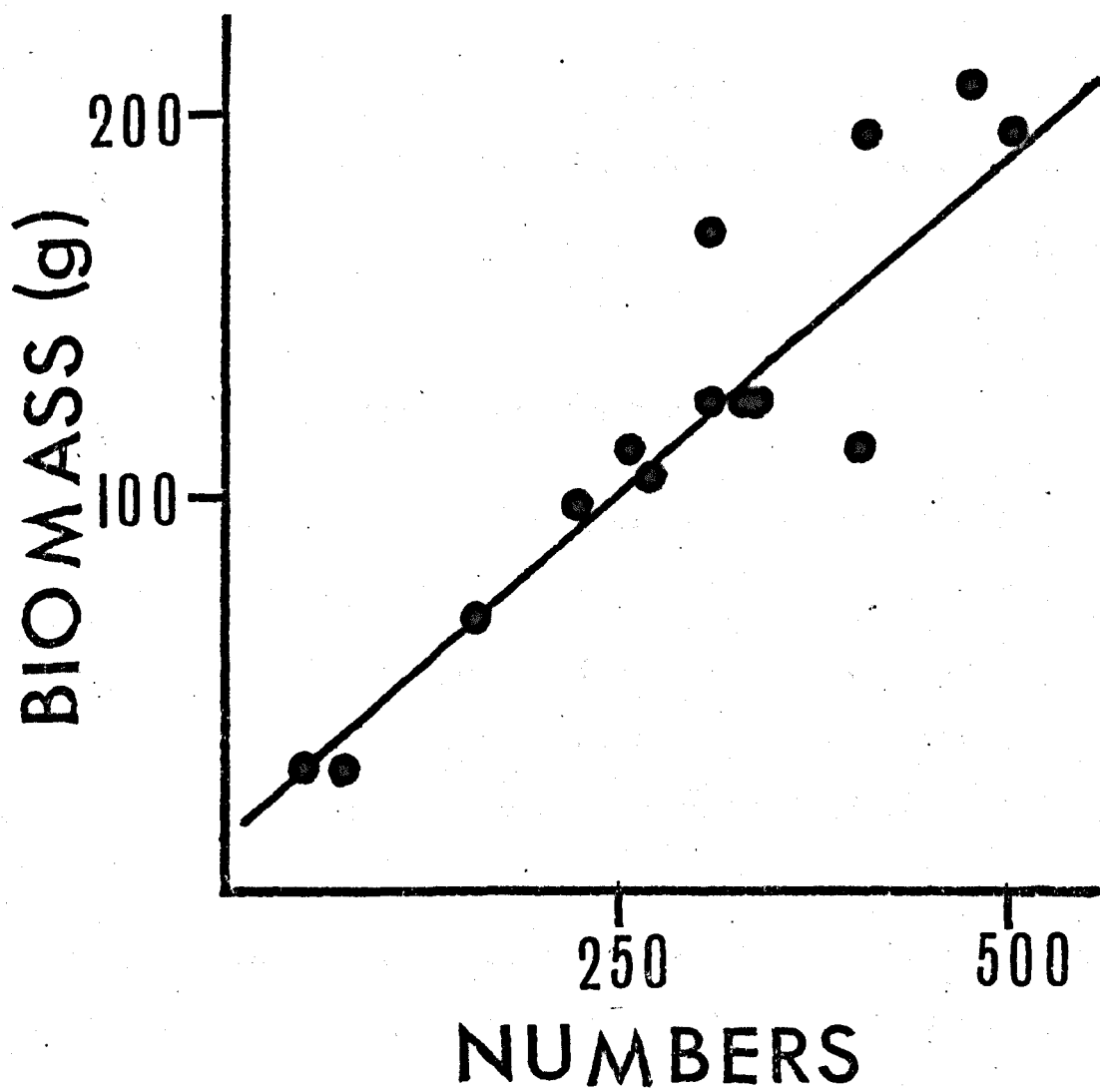
BIOMASS (g) vs NUMBERS ("FIELD OBSERVABLE")

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 M.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.

(a)
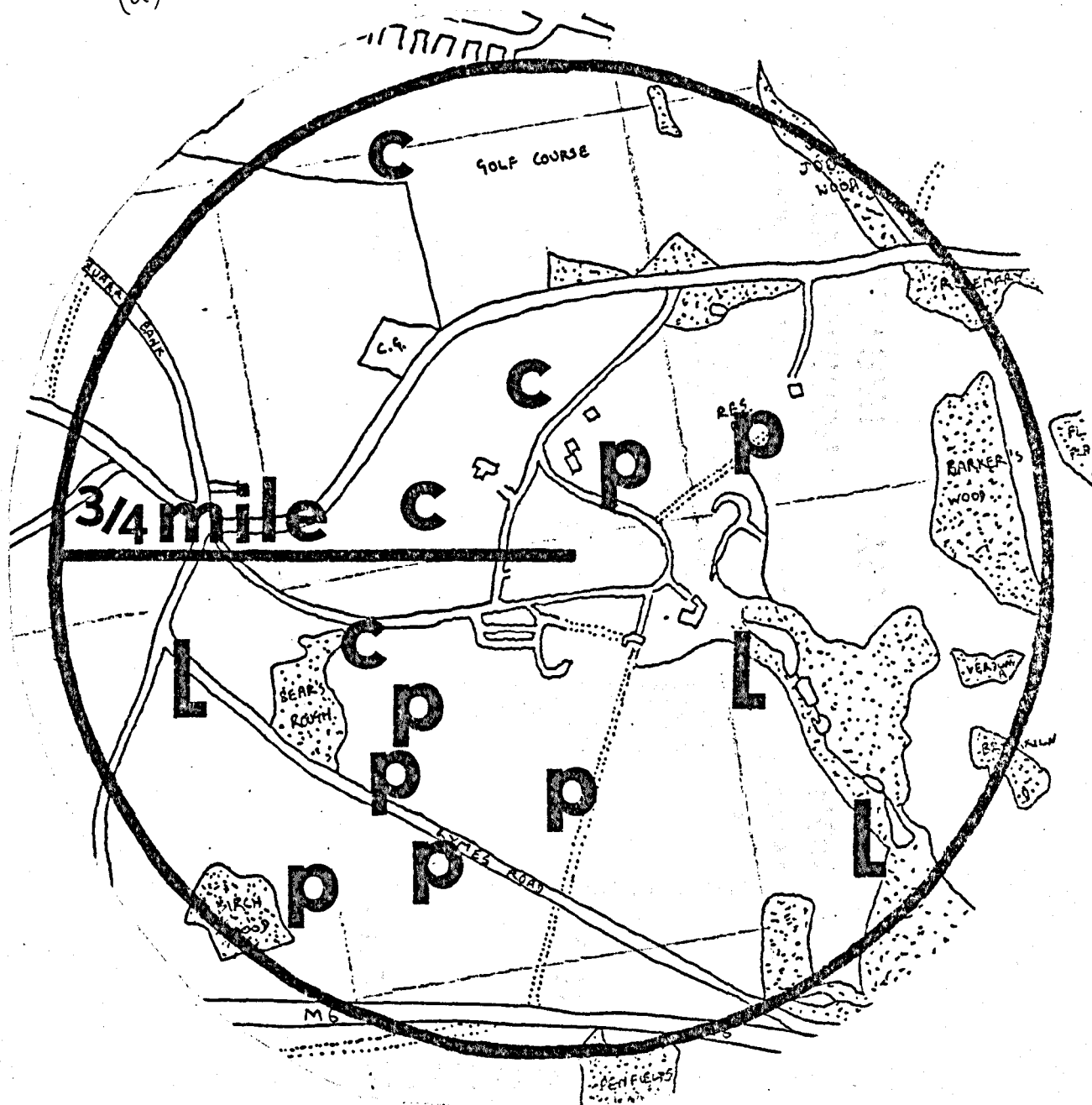
C = Non-agricultural grass
L = Temporary Ley
P = Permanent Pasture

(b)

EARTHWORM NOS./M^2

500

250

NON-FARM GRASS

LEY

PERMANENT PASTURE

(c)

(d)

0   0,5   1 km

0/m²   250/m²   500/m²
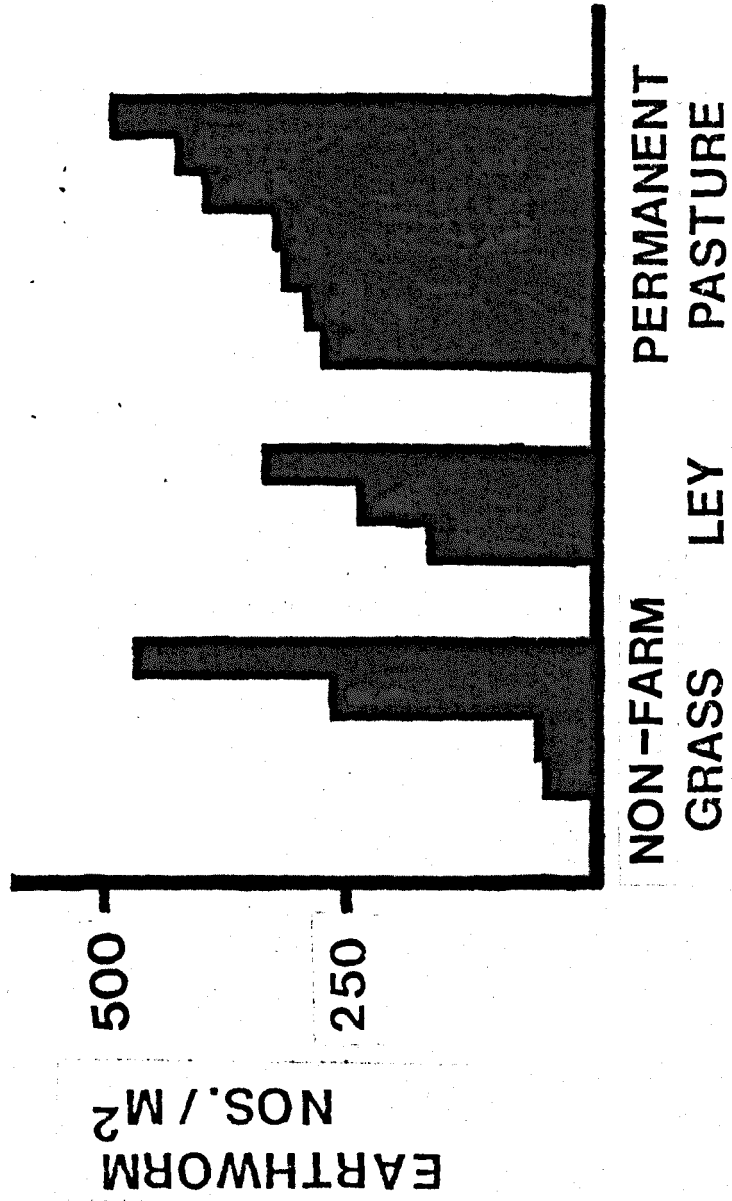
Earthworm densities
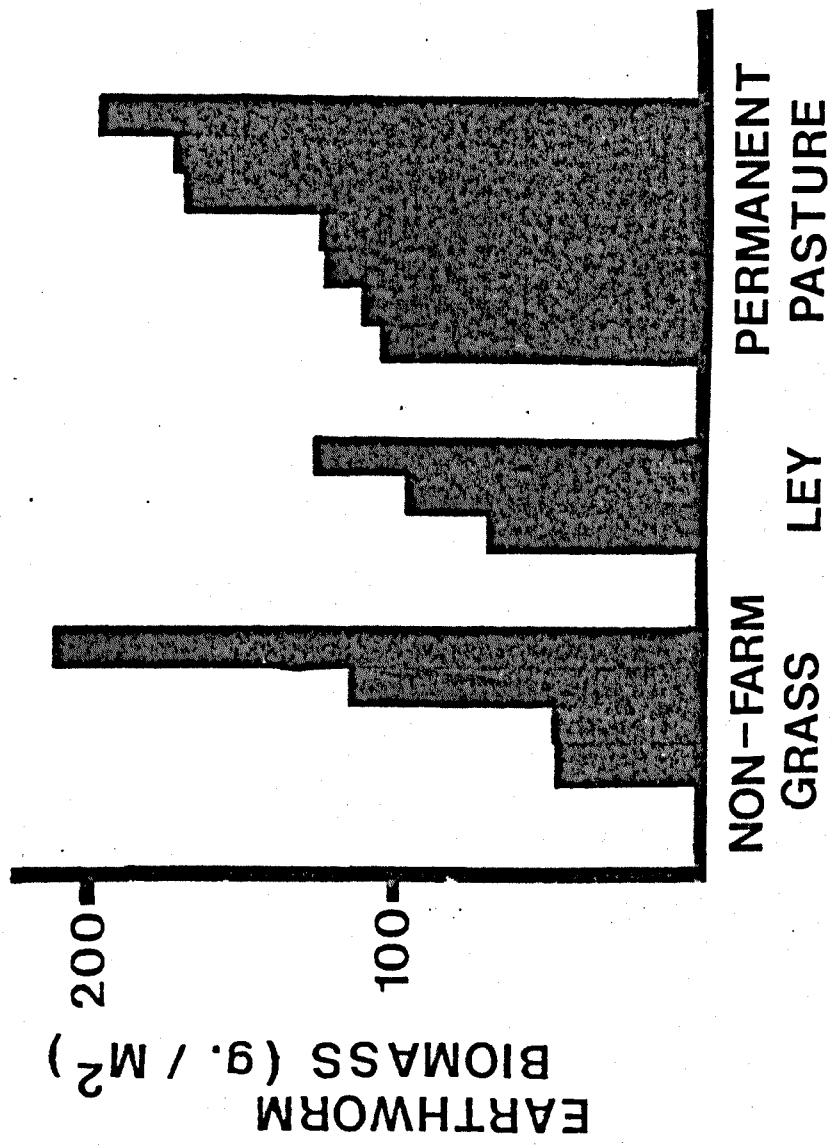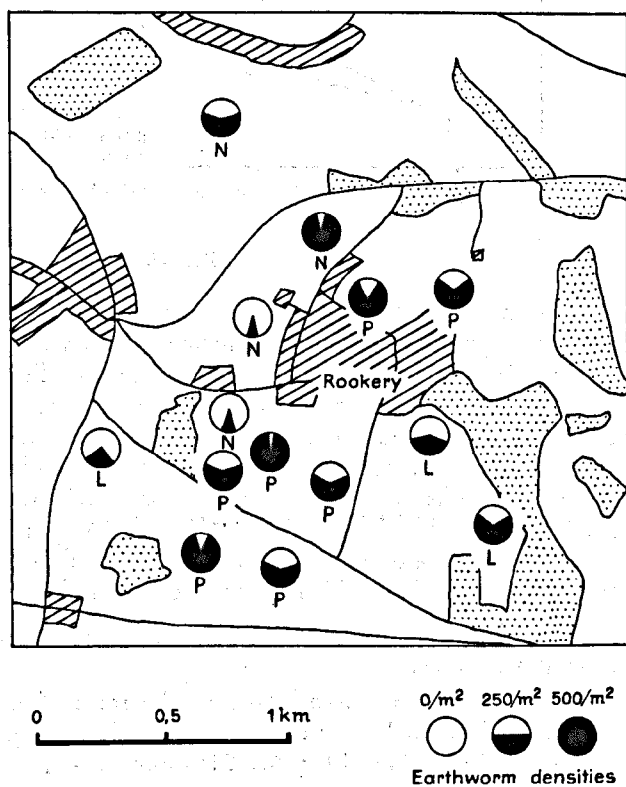
earthworm numbers and biomass (numbers - $F = 9.766$, df =

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-agriculural swards, temporary leys and permanent pas-

tures (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 pats 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 simul-

taneously (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 pat-

tern 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 — $F = 6.83$, df = 6, 582, $p < 0.001$; 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 (1967) index of mean crowding. The index is equal to 0 when the dispersion is random (Poisson; ie 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, Blore Heath and Farmoor where the sample size was 42 cores.

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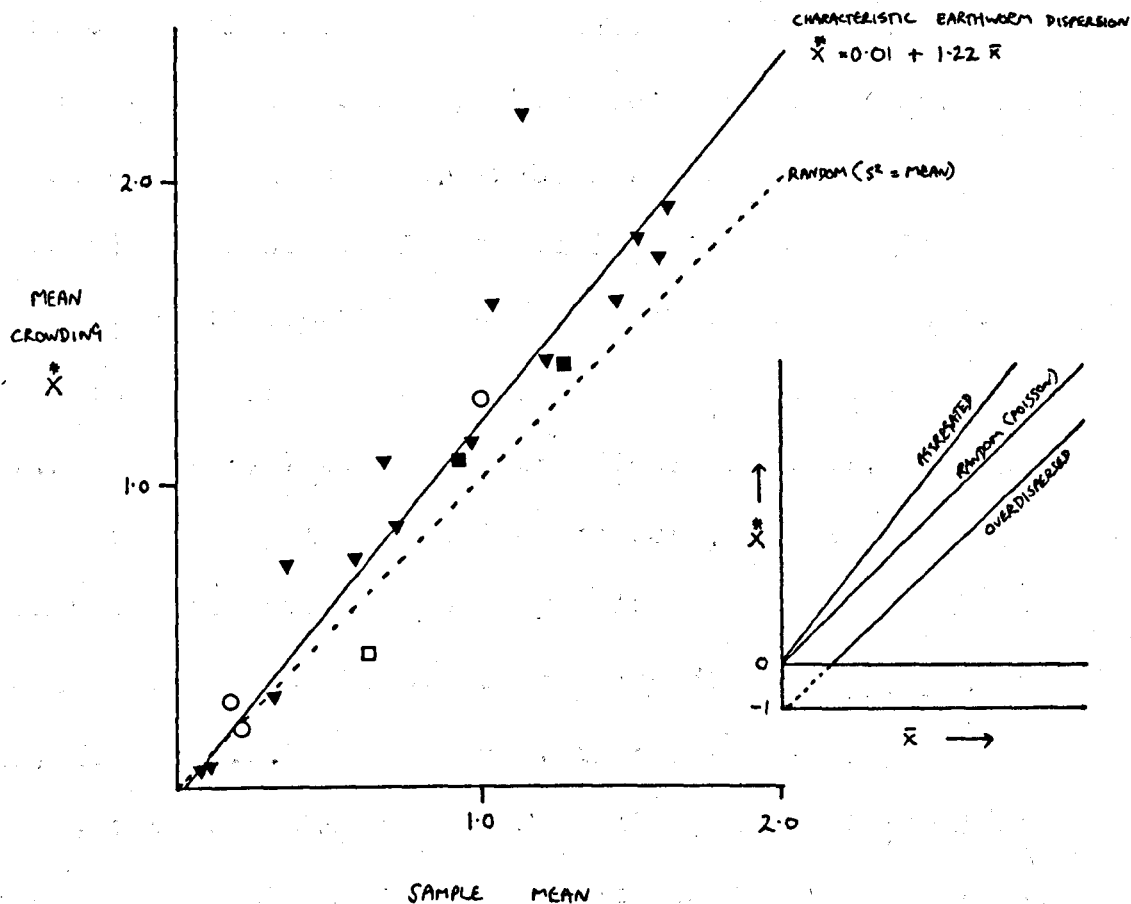
sampling dates, others were considerably so (figure 1.3.7).
The main effect of Date was not significant, probably
reflecting the fact that the second period of sampling was
a similarly mild and wet one (see figure 1.3.8c). Yet some
combination of environmental conditions had caused
earthworm densities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

FIELD X DATE
P< 0·01

biomass (g) / m²

december   february

FIELD X DATE
P< 0·001

observable no./m²

december   february
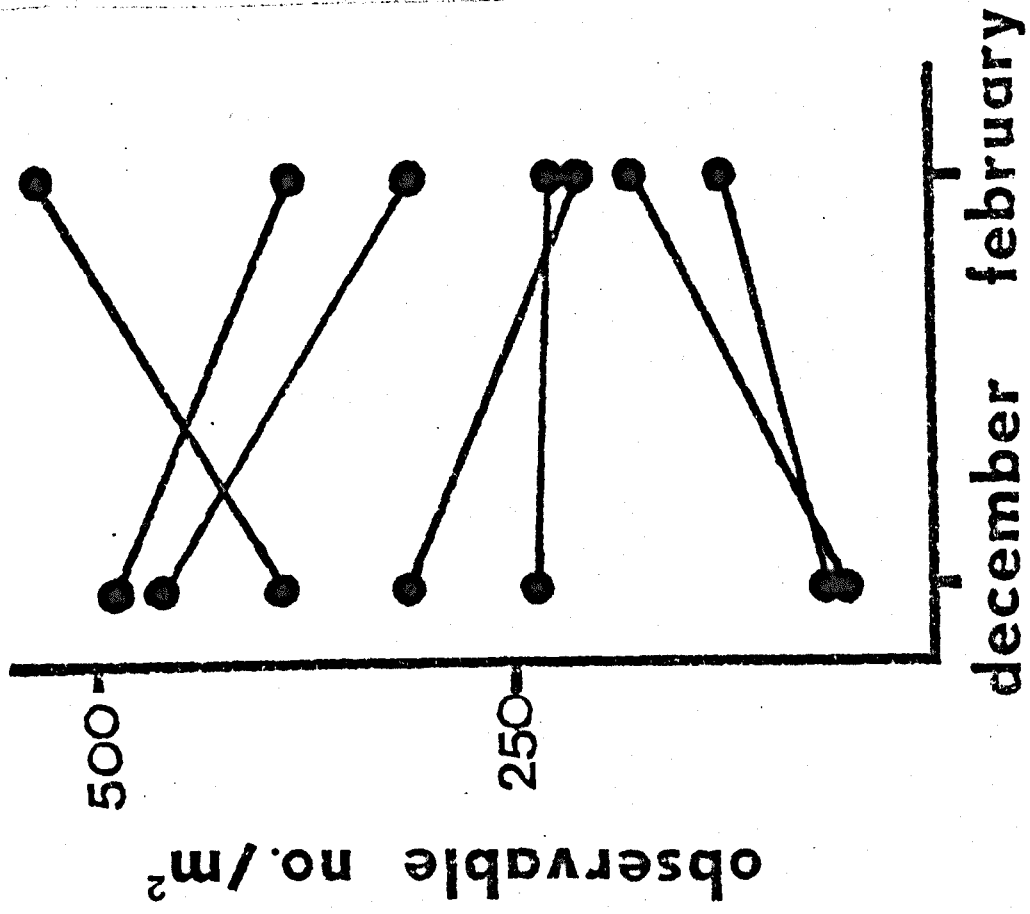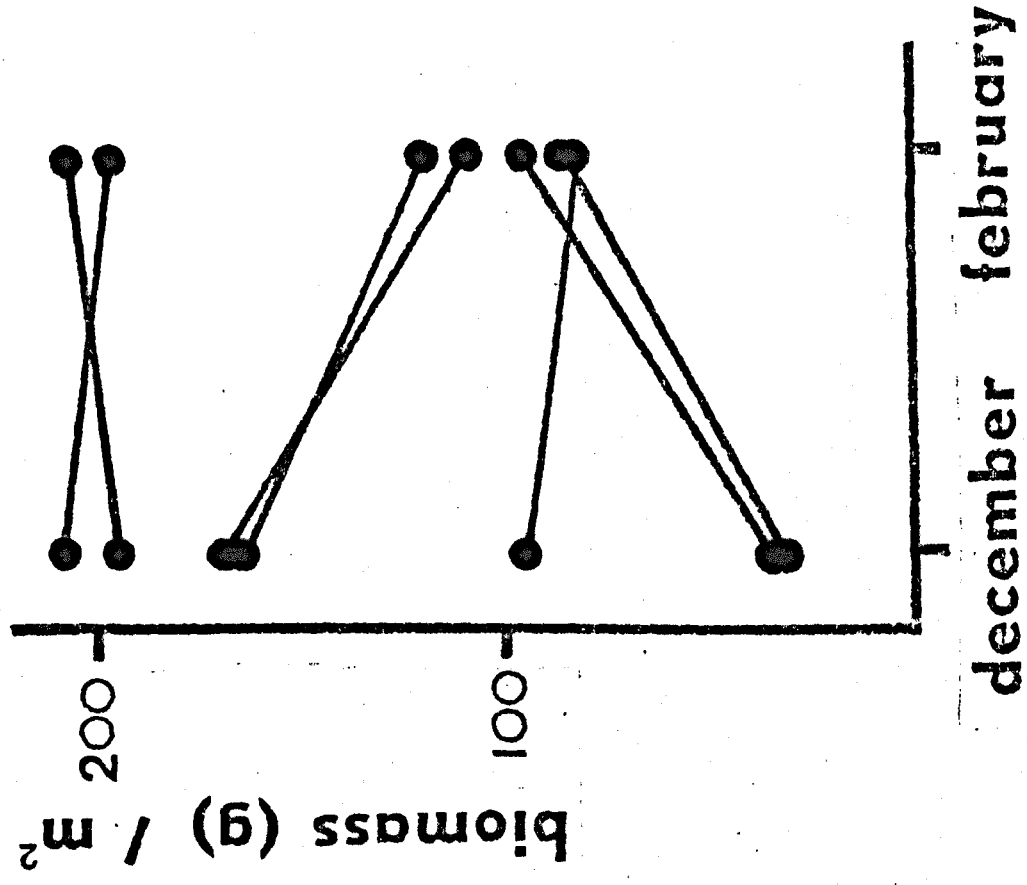
Figure 1.3.8

Shifts in earthworm densities within three grass fields

(ab) 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.

(a)

AREA X DATE
P < 0.001

observable no./m²

500

250

december   february

AREA X DATE
P = 0.056

biomass (g) / m²

200

100

december   february

(C)

SOIL TEMPERATURE AT 10 CM. (°C) □—□

CORVID USE (N OF BIRDS PER OBSERVATION PERIOD) ▽—▽

MEAN NUMBER OF INVERTEBRATES PER CORE

■—■ EARTHWORMS

OTHER INVERTEBRATES:
●—● BENEATH SOIL SURFACE
▼—▼ ABOVE " "

NOVEMBER 12ᵗʰ   DECEMBER 11ᵗʰ   JANUARY 12ᵗʰ   FEBRUARY 11ᵗʰ

1979   1980
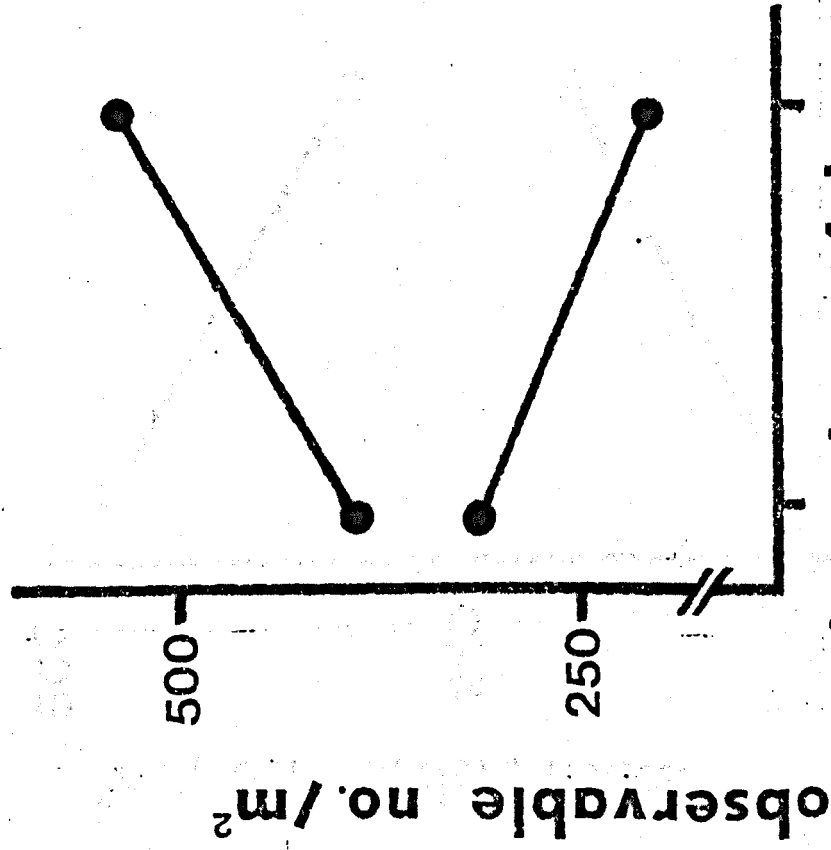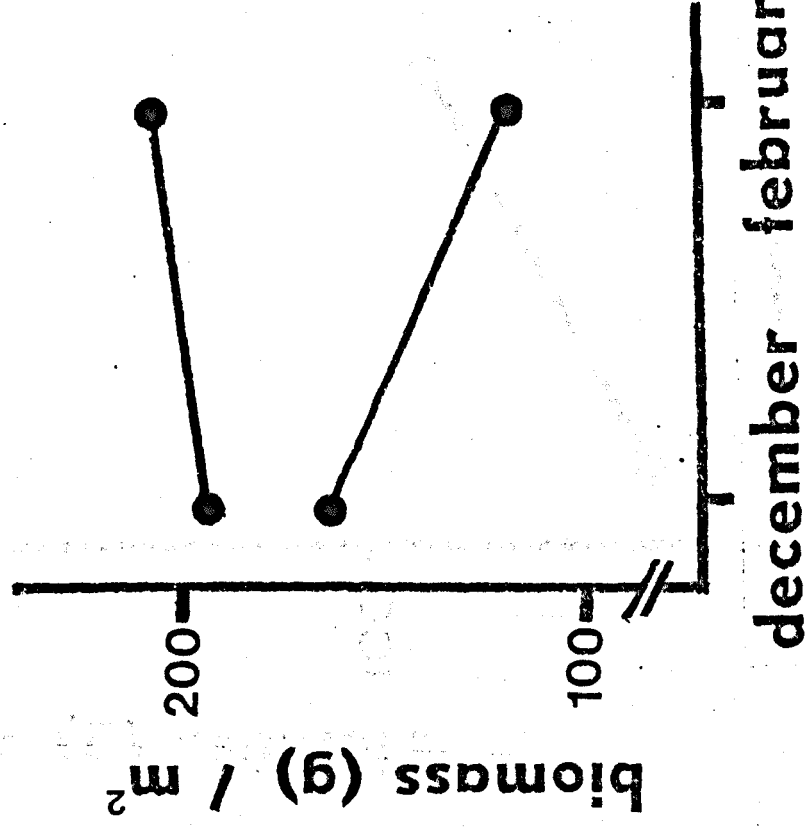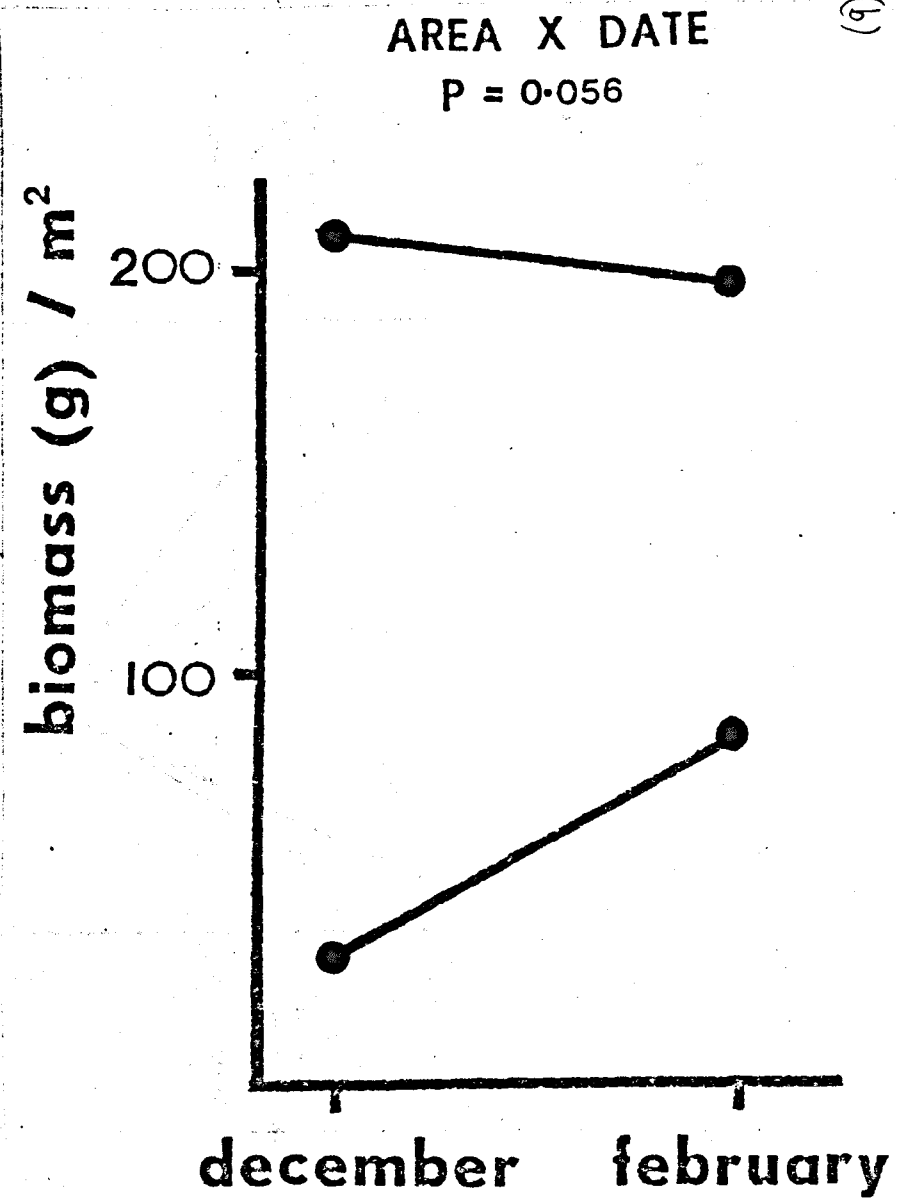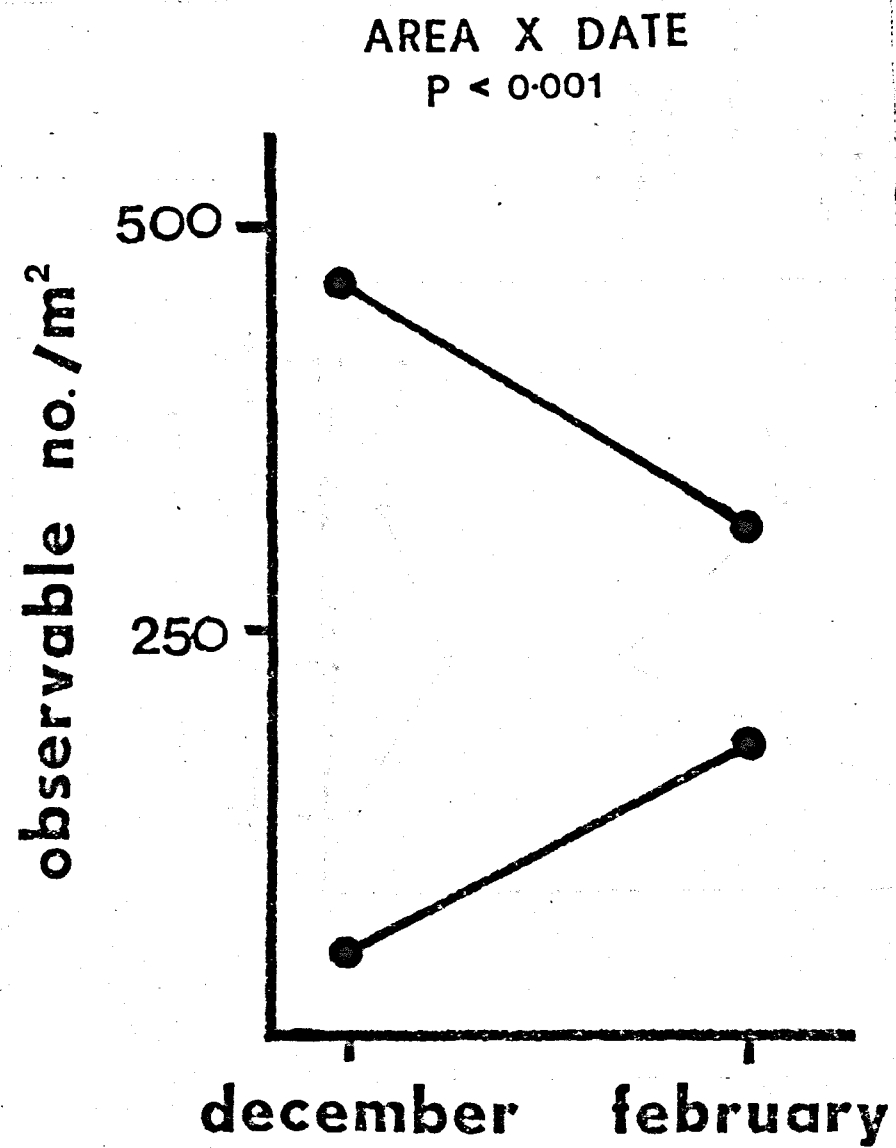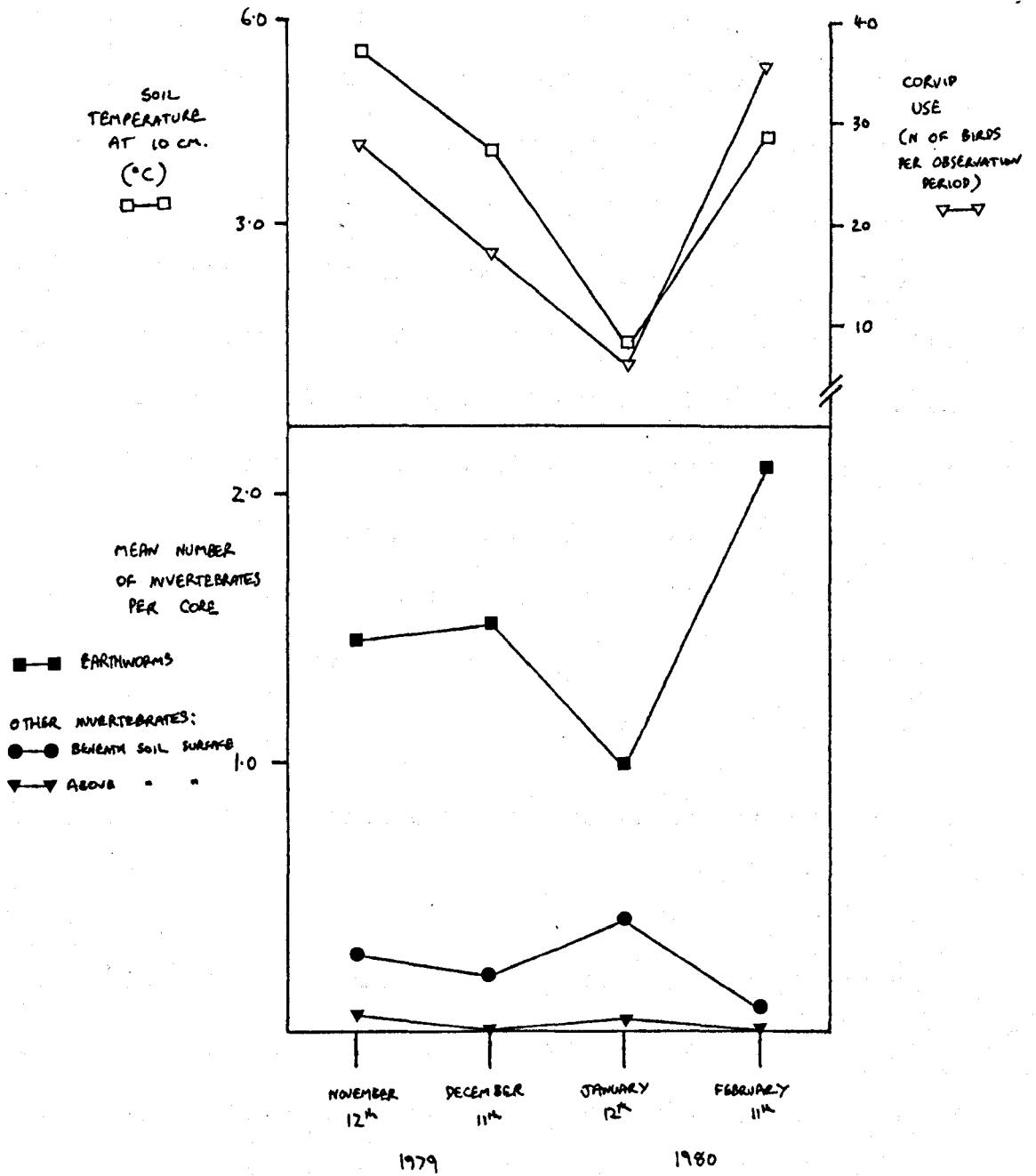
= 1.92, p = 0.168;   F = 3.78, p = 0.056).

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 ($r = -0.02$, 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
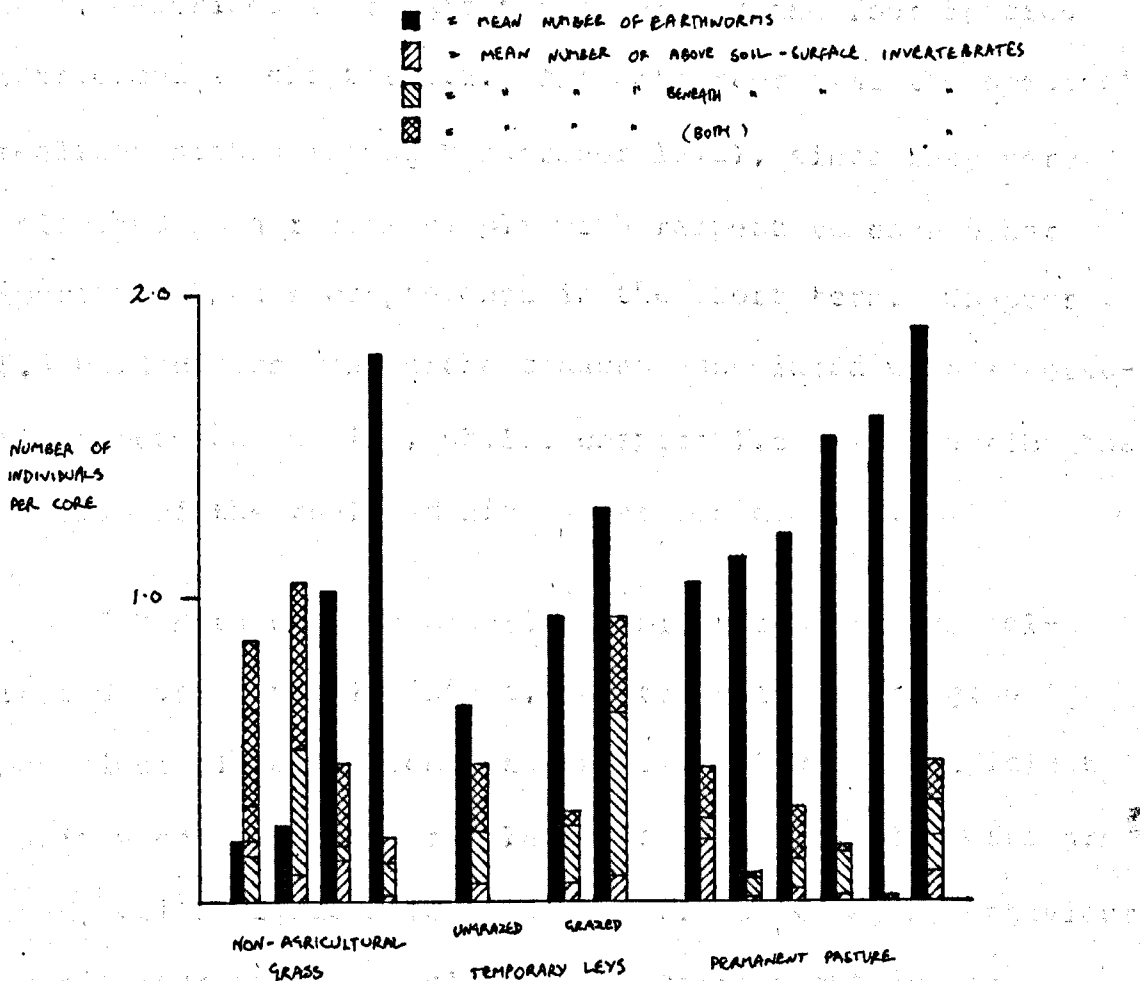
Part One Chapter Four   -   Resource Utilisation by Four

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 interac-

tions between species, whilst chapter 1.5 will describe the

overlap of the realised niches between species.

     The data used to describe habitat choice were col-

lected 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 descrip-

tion 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 ana-
lyses where recognition of individual fields was not re-
quired.

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

Symbol		Value
■	=	1
●	=	2
●	=	3-6
●	=	7-20
●	=	21-40
●	=	> 40

(a) 8-11-79

(b) 6-12-79

1 PERMANENT PASTURE
2 P.P. NON-AGRICULT. GRASS
3 P.P.
4 PERM PASTURE
5 PERM. PASTURE
6 NON-AGRICULT. GRASS
7 NON-AGR. GRASS
8 BARLEY STUBBLE
9 BARL. STUB.
10 GRAZED LEY
11 SPROUTED BARLEY
12 PERMANENT PASTURE
13 N.A.G.
14 PERM. PASTURE
15 GRAZED LEY
16 SPROUT. BARLEY
17 PERM. PASTURE
18 GRAZED LEY
19 PERMANENT PASTURE
20 GRAZED LEY
21 BARL. STUB.
22 GRAZED LEY
23 GRZ. LEY
24 PLOUGH
25 PLOUGH
28 P.P.
29 PERM. PAST.
30 P.P.
31 SPROUTED WHEAT
32 P.P.
33 P.P.
34 BARL. STUB.
35
36 SPROUTED LEY
37 GRAZED LEY
38 PERM. PASTURE
39 GRAZED LEY
40 PERM. PASTURE
41 SOWN WHEAT
42 SOWN WHEAT
43 SOWN WHEAT
44 SPROUTED WHEAT
45 BARLEY STUBBLE
46 BARLEY STUBBLE
47 BARL. STUBBLE
48 BARLEY STUBBLE
49 BARLEY STUBBLE
51 BARLEY STUBBLE
52 BARLEY STUBBLE
53 PLOUGH
54 BARL. STUB.
55 N.A.G.
56 N.A.G.

CROW
MAGPIE
ROOK
JACKDAW
R
J

0   0.5   1 KM

(C) 12-11-80

(d) 18-1-81

45 WHEAT STUBBLE
46 PLOUGH
43 PLOUGH
47 PLOUGH
53 PLOUGH
44 WHEAT STUBBLE
42 PLOUGH
41 PLOUGH
54 PLOUGH
52 PLOUGH
WHEAT STUBBLE
55 N.A.G.
48 WHEAT STUBBLE
49 PLOUGH
51 PLOUGH
56 NON-AGRICULT. GRASS
40 PERMANENT PASTURE
38 PERMANENT PASTURE
39 GRAZED LEY
37 UNGRZ. LEY
36 PLOUGH
35 PERMANENT PASTURE
34 OAT STUB.
33 PERM. PASTURE
32 PERM. PASTURE
31 PLOUGH
29 P.P.
30 PERMANENT PASTURE
28 PERM. PASTURE
23 UNGRZ. LEY
24 PLOUGH
25 SPROUTED WHEAT
22 GRAZED LEY
20 GRAZED LEY
21 UNGRZ. LEY
19 PERMANENT PASTURE
18 UNGRZ. LEY
17 P.P.
16 PLOUGH
15 GRAZED LEY
14 PERMAN. PASTURE
13 N.A.G.
2 NON-AGRICULT. GRASS
3 P.P.
4 GRZ. LEY
5 PERM. PASTURE
6 NON-AGRICULT. GRASS
1 PERMANENT PASTURE
7 NON-AGRICULT. GRASS
8 UNGRZ. LEY
9 UNGRZ. LEY
10 UNGRZ. LEY
11 PLOUGH
12 PERMANENT PASTURE

MAGPIE
JACKDAW
MAGPIE
CROW
MAGPIE
R
J
R
MAGPIE
CROW
JACKDAW
R
MAGPIE
J
M
CROW
CROW
CROW
MAGPIE
CROW
MAGPIE
CROW
MAGPIE
ROOK
CROW

0   0.5   1 KM

(c) 23-2-81

(5) 28-2-81

whole area reflecting their (mainly) A-type ter-
ritoriality (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 avai-
lability, the other three species all selected grassland
over arable. All four species were found at higher densi-
ties 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) - signficant selection of crops over
availability is indicated by asterisks;   (b)   density as
numbers of birds per hectare within each species.

(a)	Crop Availability		Proportional Use by Species			
	N of Fields	Total Area	Rook	Jackdaw	Crow	Magpie
GRASS	59.8	61.5	81.7	67.3	63.9	74.8
			***	*	NS	***
ARABLE	40.2	38.5	18.3	32.7	36.1	25.2
Sample N	411		1219	655	244	214

(b)		Number of Birds per Hectare			
		Rook	Jackdaw	Crow	Magpie
GRASS		137.9	79.7	26.3	26.4
ARABLE		36.0	36.4	9.5	10.2
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 insigni-
ficant 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). Exami-
nation of expected frequencies reveals that for the rook
and jackdaw this was due to a strong selection for per-
manent pasture coupled with strong avoidance of ungrazed
fields and a weaker avoidance of ungrazed leys. The dis-
tribution 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


```
0   %  100    0   %  100
```

Area of   Rook   Jackdaw   Crow   Magpie
Crop
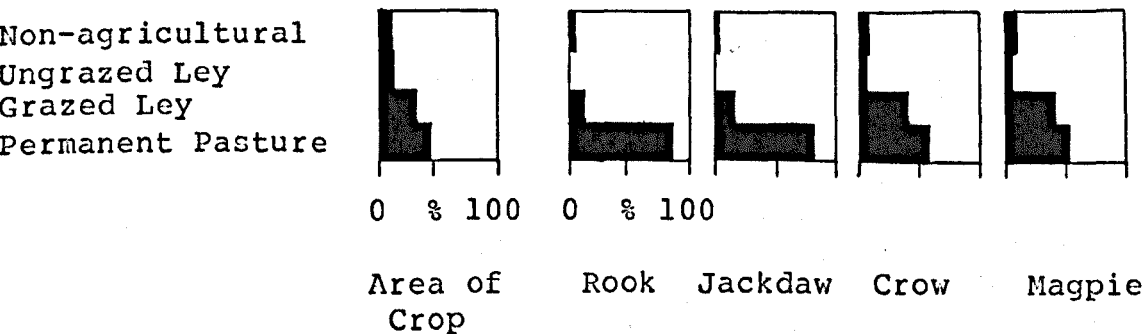
(b) Habitat Use - preference/avoidance or use as available?

Non-agricultural
Ungrazed Ley
Grazed Ley
Permanent Pasture

Electivity Index


```
-1   0   1
```

Rook   Jackdaw   Crow   Magpie
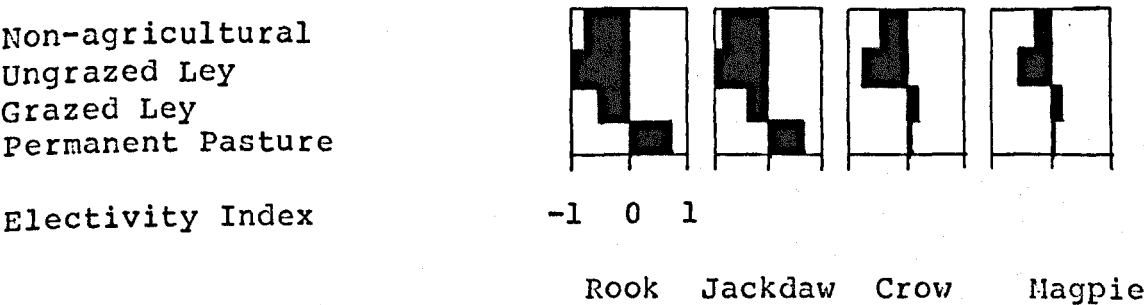
Figure 1.4.3

Habitat selection by four Corvid species in relation to habi-
tat 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
                    M = Magpie
                    R = Rook

(a) Theoretical Values

High
Proportion

BIRDS
(n/N)

Low
Proportion

Low ← Availability → High

HABITATS
(n/N)
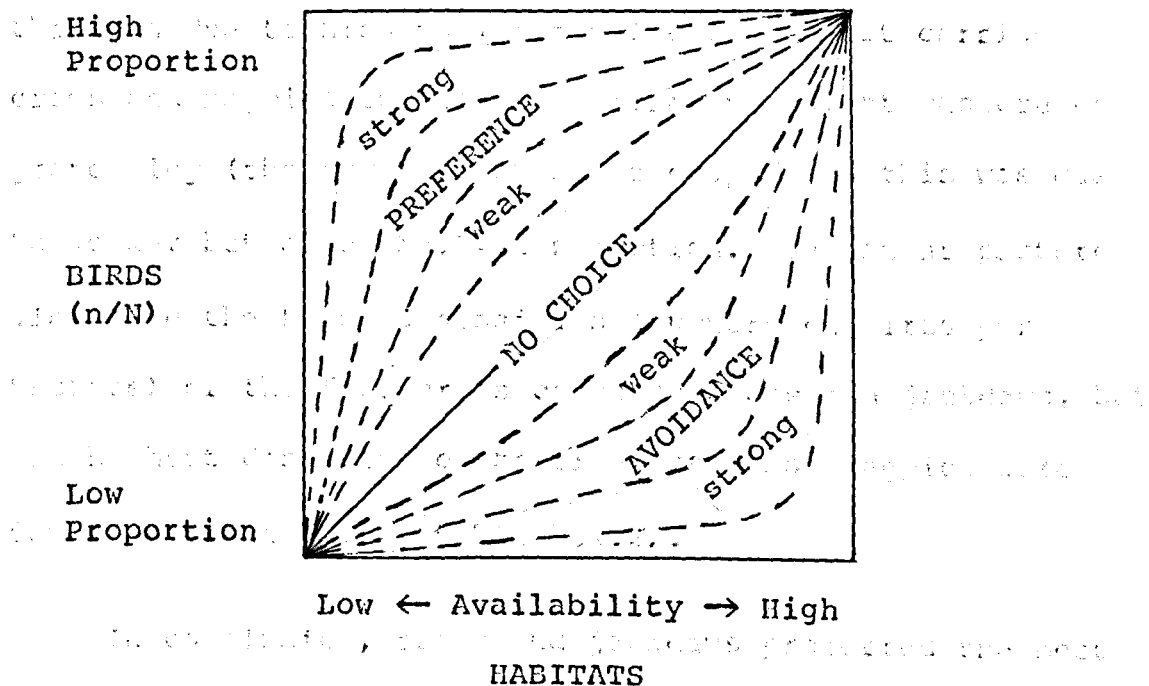
(b) Recorded Use of Four Grass Crops

BIRDS

Non-agricultural

Ungrazed Ley

Grazed Ley

Permanent Pasture

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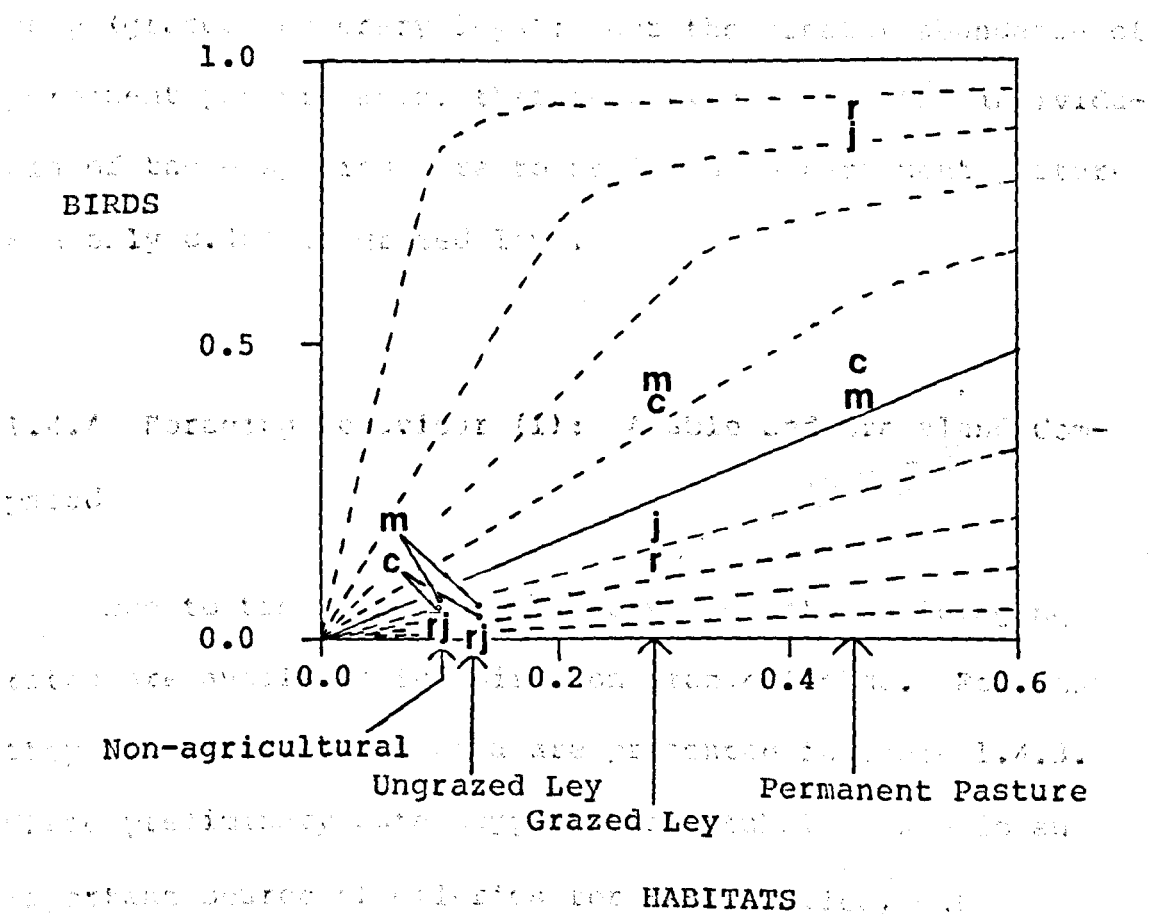
this was due to high positive selection. Most carrion crows and magpies occurred on either permanent pasture or grazed ley (the two most abundant crops) and this was due to weaker but also positive selection. Permanent pasture also held the highest densities (numbers of birds per hectare) of the four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

| | Number of Birds per Hectare | | | |
	Rook	Jackdaw	Crow	Magpie
Non-agricultural	1.5	0.3	1.6	0.8
Ungrazed Ley	-	-	0.5	2.4
Grazed Ley	22.5	17.7	14.2	14.5
Permanent Pasture	113.9	61.4	9.9	8.6
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 avail-
able 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 nitro-
genous 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

	Stubble Grain	Stubble Inverts.	Plough Inverts.	Grass Inverts.
Carrion Crow	(0.144) N = 1	(0.088) N = 1	(0.260) N = 6	0.279 N = 90
Rook	(0.501) N = 8	(0.027) N = 8	(0.456) N = 1	0.240 N = 69
Jackdaw	(0.308) N = 4	(0.000) N = 4	(0.026) N = 1	0.051 N = 60
Magpie	No Data	No Data	No Data	0.082 N = 70

(b) Protein intake rate (g) per minute

	Stubble Grain	Grassland Invertebrates
Rook	(0.0083) N = 8	0.0401 N = 69
Jackdaw	(0.0051) N = 4	0.0070 N = 60

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 parti-

tioning 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 calcu-

lated only for actions which resulted in the capture of a

prey item, since Waite 1978 has shown peck rate to corre-

late 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 propor-

tions 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 success-
ful 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 frequen-
cies (p < 0.01) from every other species (separate pairwise
comparisons by chi-square on original data).

(a)

Feeding Action	Crow	Rook	Jackdaw	Magpie
Surface Pick	41.6	17.0	41.4	56.0
Pounce	8.5	0.5	-	8.5
Jump	-	-	5.2	-
Surface Probe	8.5	2.8	5.2	9.2
Clod/Stone Turn	8.3	6.6	12.1	11.3
Dung Turn	25.1	6.6	34.5	12.1
Dung Crumble	0.2	-	-	-
Deep Probe	2.7	36.3	-	0.7
Dig	1.9	7.1	-	2.1
Jab	3.2	18.4	1.7	-
N Actions	411	212	174	282
N Birds	90	69	60	70

(b)

Micro Habitat	Crow	Rook	Jackdaw	Magpie
Above Soil Surface	58.6	25.0	51.7	73.8
Beneath Clods/Stones	8.3	6.6	12.1	11.3
Within/ Beneath Dung	25.3	6.6	34.5	12.1
Beneath Soil Surface	7.8	61.8	1.7	2.8
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 dif-
ferent 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

		Earthworms:			Total Worms	Other Invertebrates:		Total Other	Number of: Items	Birds
		Small	Medium	Large		Small	Medium			
Car-	N	13.9	5.2	6.5	24.2	34.0	41.8	75.8	403	90
rion	C	13.7	9.3	33.9	56.9	1.3	42.0	43.3		
Crow	P	15.7	10.6	38.7	65.0	1.1	34.3	35.4		
Rook	N	38.6	6.1	4.5	49.2	31.1	19.7	50.8	208	69
	C	38.6	14.4	26.3	79.3	1.2	19.5	20.7		
	P	41.0	15.3	28.0	84.3	1.0	14.7	15.7		
Jack-	N	3.1	–	–	3.1	88.6	8.3	96.9	174	60
daw	C	20.6	–	–	20.6	22.5	56.3	78.8		
	P	27.1	–	–	27.1	21.4	51.4	72.8		
Mag-	N	5.2	–	–	5.2	69.4	25.4	94.8	274	70
pie	C	16.6	–	–	16.6	7.7	76.2	83.9		
	P	21.8	–	–	21.8	7.3	71.8	78.1		

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

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(*) 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

| | Earthworm Size Category: | | | |
	Small	Medium	Large	N Worms
Availability in Soil Core Samples	75.4	17.0	7.7	825
Predation by: Rook	80.9	13.5	5.6	89
Carrion Crow	56.2	26.6	17.2	64
Magpie	100.0	0.0	0.0	20

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

| | | Earthworm Size Category: | | | |
		Small	Medium	Large	N Worms
Rook	Above Soil Surface	100.0	0.0	0.0	16
	Beneath	76.7	16.4	6.8	73
Carrion Crow	Above	49.0	31.4	19.6	51
	Beneath	84.6	7.7	7.7	13

(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 tem-

porary leys and permanent pastures. Magpies caught small

invertebrates by Surface Picking faster on permanent pas-

ture 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 M.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 Scheffé's test will, of course, have reduced 'experimentwise' error to acceptable bounds.

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
    M = Magpie
    R = Rook
    * = >1 species with same

    s = Small Invertebrate
    m = Medium Invertebrate
    1 = 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


```
                            0.92 -| J          |          |          |          |
                                / |¦           |          |          |          |
                                  | ¦          |          |          |          |
                                  | M          |          |          |          |
                            0.60 -|            |          |          |        ( |
                                  |            |          |          |          |
                                  |            |          |          |          |
                            0.50 -|            |          |          |          |
                                  |            |          |          |          |
                                -|            | J        |          |          |
                                  |            | ¦        |          |          |
Number of                   0.40 -|            | ¦        |          |          |
Prey Items                        |            | ¦        |          |          |
Ingested                       -| C          | ¦        |  J       |    R     |
per Minute                        |            | ¦        |  ¦       |    ¦     |
                            0.30 -| C          | ¦        |  ¦       |    ¦     |
                                  | ¦          | ¦        |  ¦       |    ¦     |
                                -| ¦          | ¦   C    |  ¦       |    ¦     |
                                  | ¦          | M  ¦     |  ¦       |    ¦     |
                            0.20 -| ¦          | ¦  ¦     |  ¦       |  R ¦     |
                                  | M          | ¦  ¦     |  ¦       |  R ¦     |
                                -| R ¦        | ¦  ¦     |  ¦       |  ¦ ¦     |
                                  | ¦ ¦        | ¦  ¦     |  ¦       |  ¦ ¦     |
                            0.10 -| ¦ ¦ * C    | ¦  CM    |  M       |  ¦ ¦ C R |
                                  | ¦ JM¦ ¦    | ¦  ¦¦    |  ¦       |  ¦ ¦ ¦ ¦ |
                                -| ¦ JC ¦    | R  CC   | *MR      |  ¦ ¦ ¦ R |
                                  | R ¦¦ ¦    | ¦ *RR   | *CC      | **CCC ¦  |
                            0.00 -|_¦¦¦_**____|_¦¦_**___|_¦¦_**____|_¦_***____|
```

Prey Type: | sml23 | sml2 | sml2 | sml23 |
                 | | | | |
                 | Above |Beneath- | Stone- | Beneath |
Micro-habitat: | Soil |Within | Clod | Soil |
                 | Surface |Dung | Turn | Surface |

(b) Mean species' ingestion rates as calorific value of
    intake

```
           .092 -|        C  |           |           |           |
                 /           |           |           |           |
           .065 -|           |  |         |         |       R   |
                 /           |           |           |       |   |
           .063 -|           |  |         |         |       |  R |
                 /           |           |           |       |  | |
           .053 -|        C  |  |         |         |       |  |  |- |
                 /           |  |         |           |       |  |  |
           0.04 -|        |  |  |      C  |         |       |  |  |
                 |        |  |  |      |  |         |       |  |  |
Calorific        |        |  |  |      |  |         |    R  |  |  |
Intake           |        H  |  |      |  |         |    |  R  |  |
(Kcal      0.03 -|        |  |  |      |  |         |    |  |  |  |
per Minute)      |        |  |  |      |  |         |    |  |  |  |
                 |        |  |  |      |  |         |    |  |  |  |
                 |        |  C |       |  |         |    |  |  |  |
           0.02 -|        C  | |       |  H         |    |  |  C  |
                 |        R  | |       |  |         |    |  |  |  |
                 |        |  | |       |  |         |    |  |  |  |
                 |        JH | |       |  |         |    |  |  |  |
           0.01 -|        |  J |       |  C         |  H |    C  |
                 |        |  | |       |  |         |  C |    |  |
                 |     J  |    |    J  |  |      JR |    |  J |  |
                 |     HR |    | JJRR  |  |   JR |  |    |RH *CC |
                 |     *  |    | *R C  |  |   *  |*C|    | *  |**|
           0.00 -|__|____|__**__|__|_|_**__|__|_|__*___|__|_|____|
Prey Type:       |  sml23  |  sml2   |  sml2   |  sml23  |
                 |         |         |         |         |
                 | Above   |Beneath- | Stone-  | Beneath |
Micro-habitat:   | Soil    |Within   | Clod    | 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.

Micro-Habitat:	Above Soil Surface	Beneath-Within Dung	Stone-Clod Turn	Beneath Soil Surface
Prey Type:	sml23	sml2	sml2	sml23
	JC C HH	JC HH	J R C	RRRRR
Ingestion Rate per Minute (Ranks only)	H J			
	C C RJJ CJHHH RRJRR	CC HHRR CJJJ RRHH	H C HCCJ CJJH RRHR	CCCCC HJJJJ JHHHH

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.

Figure 1.4.5

Ingestion rates by four corvid species of prey types taken by different feeding actions

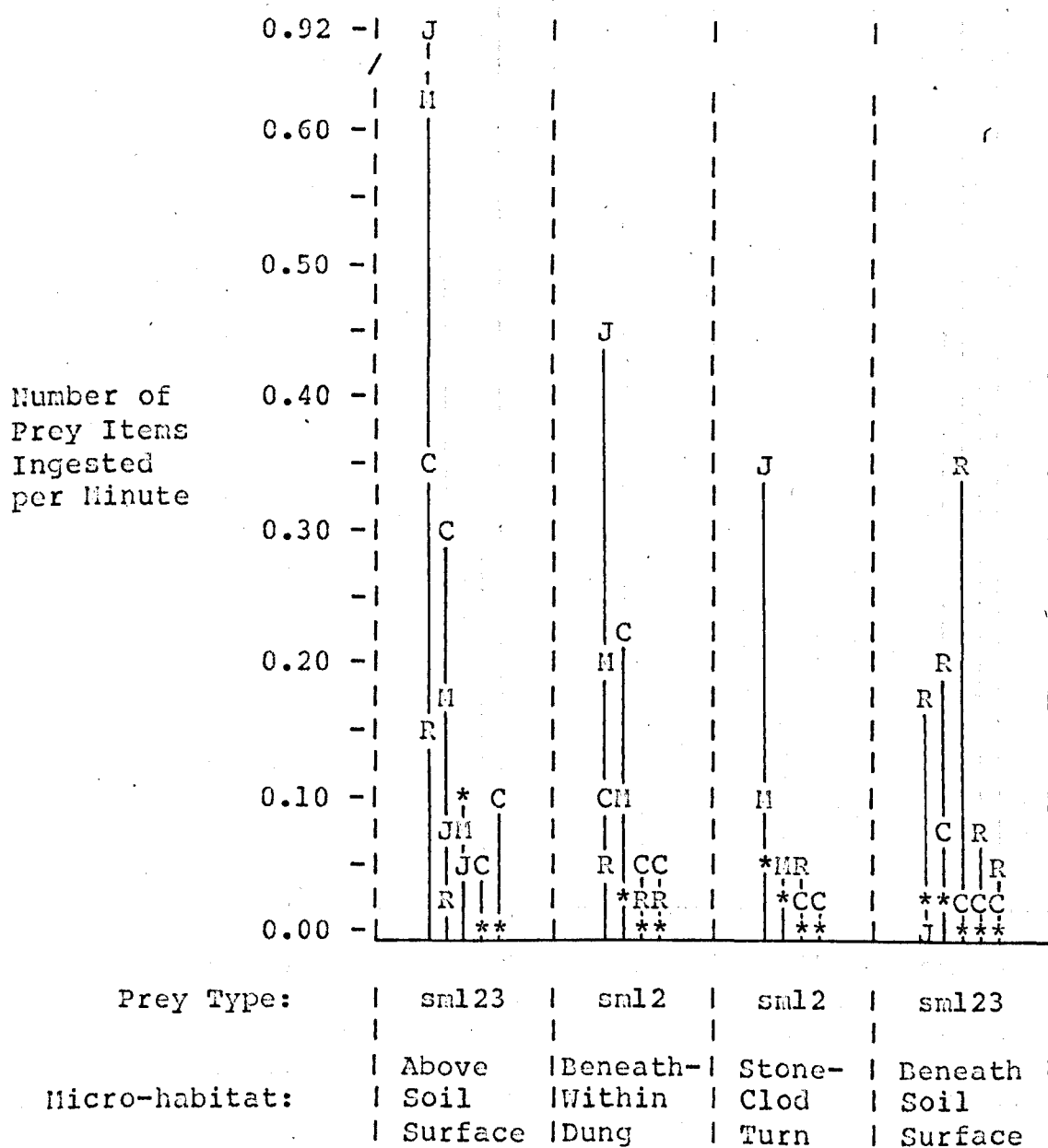(a) Mean ingestion rates as number of prey items taken per minute.

Pick = Surface Pick
Pnce = Pounce
 Jmp = Jump
  SP = Surface Probe
  ST = Stone/Clod Turn
  DT = Dung Turn
  DC = Dung Crumble
  DP = Deep Probe
 Dig = Dig
 Jab = Jab

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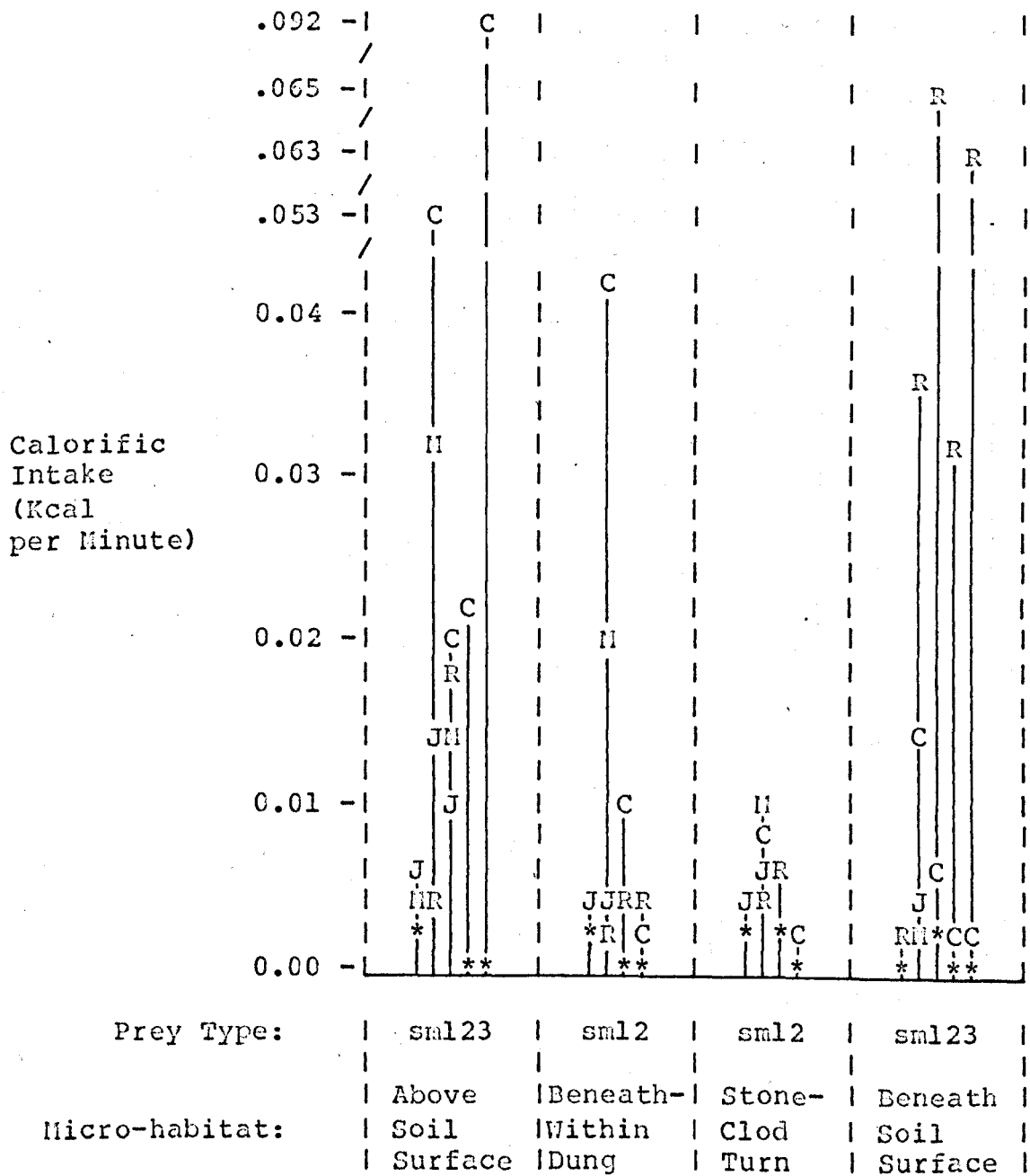   1 = Small Earthworm
   2 = Medium Earthworm
   3 = Large Earthworm

C = Carrion Crow
J = Jackdaw
M = Magpie
R = Rook
* = >1 species with same
        ingestion rate

(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

Number of Prey Items Ingested per Min.

```
        J
0.6 -|
    -|
0.5 -| H                                          J
    -|
    -|                                          J
0.4 -|
    -|
    -|                        J              C
0.3 -| C
    -|                                       H
    -|          J                                    R
0.2 -|   C                                                      R
    -| R                                  CH              R
0.1 -|   H                        HC   H                    R        RC      R
    -|   C          H    C        J    *H   R C       R R   R        R       R
    -| JH       H  *R           C**C  *RC  *RC    C  *CR  C*R    ***CR
0.0 -| R  CC  CR*C    *   RRJ*  R**     **   *  * *** * *     M  **
          **  *JJ**
```

Prey Type: | sml23   sml23   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

```
        .084 -|             C        |        |        |               |
             /             |         |        |        |               |
        .054 -|            |         |        |        |        R      |
             /             |         |        |        |        |      |
        .042 -|            |         |        | C      |        |      |
             /             |         |        | |      |        |      |
        .035 -|  C         |         |        | |      |  R     |      |
             /   |         |         |        | |      |  |     |      |
              -| H         |         |        | |      |  |   R |      |
              -|           |         |        | |      |  |   R |      |
              -|           |         |        | |      |  |   | |      |
        0.02 -|           |         |        | H      |  |   | |      |
              -|           |         |        |        |  |   | |      |
Kcal          -|           |         |        |        |  |   | |      |
Ingested      -|  C        |    C    |        |        |  |   | |      |
per Min.      -|  |        |    |     |        | C      |  | R | |      |
              -|  R        |    |     |        | |      |  | | | |      |
        0.01 -| JJC       | C   |     |  M     | |      |  R | | R  R  |
              -|  H        | |   |     |  |     | |      |  | | C | | C|
              -|   C       | R   |     |  C     | C      | R| | | | | R|
              -| J |       | CC  |  J  |  J     | JR     | C| | | | JC|
              -| HR        | HM  |  |  | R RR   | JR|   | *| | | |RJC|
              -| C R       |M* J**|  |  |*RCC  |J* *C | *R*C  |RJ* **|J|*| M |*C|
        0.00 -| R  **     |*J**  |* |  |J*    |* *   *| |* ** |J| * |  |**|
```

Prey Type: | sml23   sml23   s   sml2 | sml2 | sml2   s | sml123   sml   sml23 |

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.

Feeding Action:	Pick	Pnce	Jmp	SP	ST	DT	DC	DP	Dig	Jab
Prey Type:	sml23	sml23	s	sml2	sml2	sml2	s	sml23	sml	sml23
Ingestion Rate per Minute (Ranks Only)	HC C JH	H		J J H	C	J R C	JC HH		RRRRR J H	R J	R RR
	C C JJJ CJRHH RRHRR	CRCC CHCJJ JRHHH RJJRR	C H R	H CC JJHJ CHRH RRJR	H C HCCJ CJJH RRHR	CC C MHRR J CJJJ H RRHH R		CCCJC JHJHJ HJHCH	RR CCJ HHC JJH	R C CCCCR JJJJJ HHHHH

Part One Chapter Five - Overlap and Partitioning of
Resource Utilization

The last chapter described individual resource utilisation 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

Figure 1.5.1

Individual species' niche breadths, community matrices (where A = [alpha(i,j)]) and community dendograms for four basic resource states

(a) Habitat - N = 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 censuses 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).
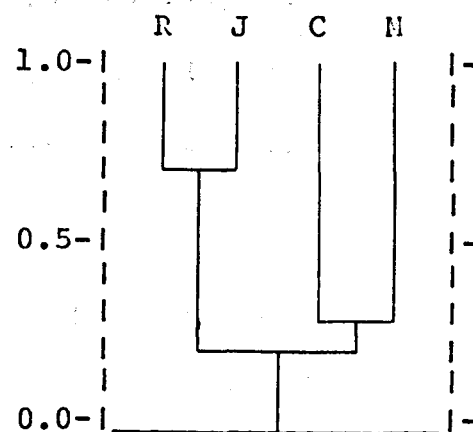
(a) Habitat (Between Grass Crops)

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.10	–			
Carrion Crow	.39	.69	–		
Jackdaw	.14	.95	.73	–	
Magpie	.45	.68	.95	.72	–
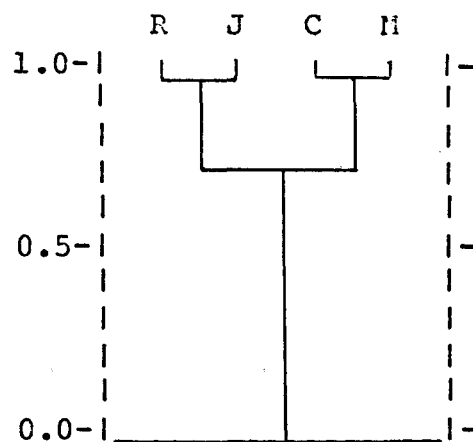
(b) Time/Space

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.19	–			
Carrion Crow	.34	.28	–		
Jackdaw	.08	.65	.18	–	
Magpie	.30	.15	.27	.15	–

(c) Prey Type

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.61	–			
Carrion Crow	.54	.73	–		
Jackdaw	.06	.42	.45	–	
Magpie	.20	.56	.65	.81	–
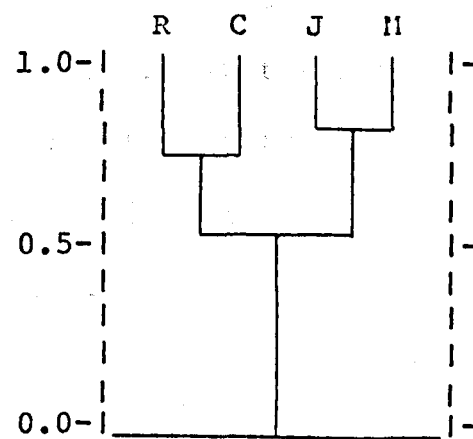
(d) Foraging Technique

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.41	–			
Carrion Crow	.33	.43	–		
Jackdaw	.31	.32	.73	–	
Magpie	.24	.35	.84	.78	–
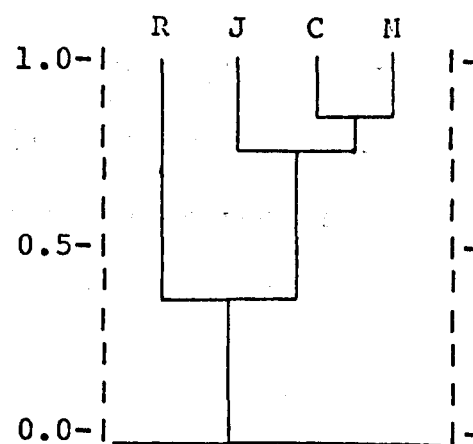
considers overlap in prey type (different sized earthworms and other invertebrates), but this time it is carrion crow-rook (0.73) and jackdaw-magpie (0.81) who make up the two groups, with average overlap between these two groups of 0.52 (figure 1.5.1c). Finally, yet another different pattern emerges 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

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.09	–			
Carrion Crow	.36	.65	–		
Jackdaw	.18	.84	.73	–	
Magpie	.29	.65	.82	.68	–
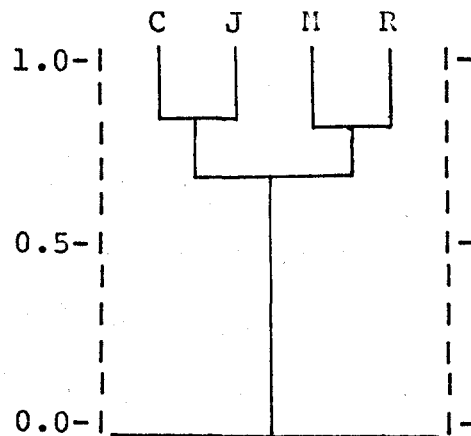
(b) Grass Crop Types Only

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.10	–			
Carrion Crow	.39	.69	–		
Jackdaw	.14	.96	.73	–	
Magpie	.45	.68	.95	.72	–
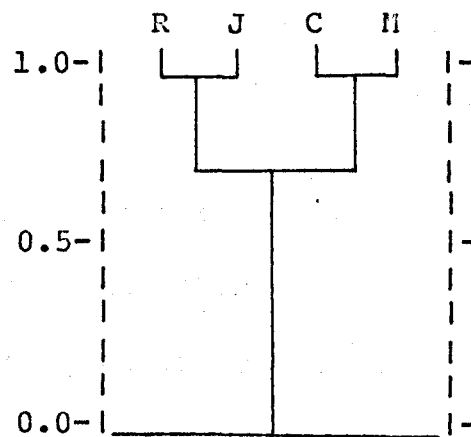
higher than foraging technique overlap, but this was not the case in every pair-wise comparison, and in any case the measure provided only an **extremely** gross estimate of taxonomy.

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 significance of this is discussed in chapter seven.

1.5.1.2 Niche Breadth

Asymetry 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 break-

down 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 habi-

tat 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 representa-

tion of the study area maps of figure 1.4.1 which illus-

trates 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 dif-

ferent 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
M = Magpie(s) present
R = Rook(s) present

Vertically, each rectangle represents a different field; hor-
izontally, the same field at a different time.

Habitat Field   ←— TIME —→

SPACE (vertical axis on right)

Habitat	Field	Time 1	Time 2	Time 3	Time 4	Time 5	Time 6
NAG	2	R M			M		
	6		M		RJCM		
	7	M			M	C	M
	13						
	55			M			C
	56	C			M		
	57				M	C	
TLU	4						
	8						
	9	M		M			
	10				C	M	M
	21						
TLG	4		R CM	M		M	
	14	C				M	M
	15	CM	C				
	18		C		C		
	20		R	C	CM		M
	22			C			C
	23		C	CM		M	
	37			C		RJC	
	39	R	C	R			
PP	1	R CM		M			RJ M
	3				M		
	5	R M	R C	M			
	12	C	C				M
	17	M		C			
	19	CM	CM	R CM			
	27	RJ	C	C			
	28		RJ	RJC			C
	29	RJ	R	RJ	C	C	R C
	30	RJ	RJ		M		
	32	RJ	RJ	RJC	CM	CM	R CM
	33	RJ M	RJ	RJ			R CM
	35	RJ	RJ	RJ	R C		R C
	38	RJCM		RJCM	RJ M	RJC	R
	40	RJ		RJC			

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.
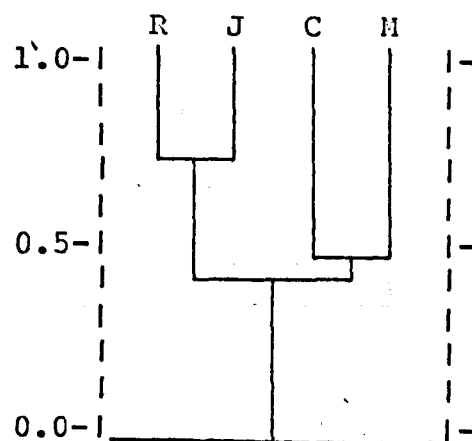
(d)   Use of 27 arable fields ignoring time.

(a) Field Use at One Time

	Niche Breadth	Overlap Indices			
Species	(B st.)	R	C	J	M
Rook	.19	–			
Carrion Crow	.34	.28	–		
Jackdaw	.08	.65	.18	–	
Magpie	.30	.15	.27	.15	–
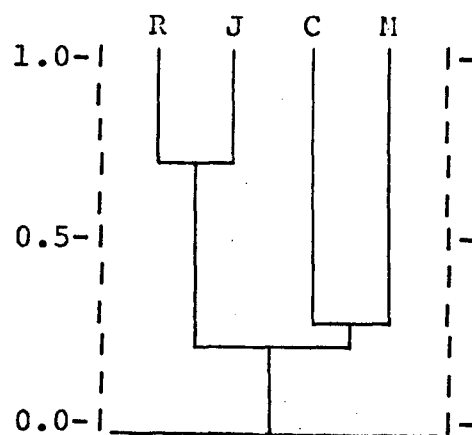
(b) Field Use Ignoring Time

	Niche Breadth	Overlap Indices			
Species	(B st.)	R	C	J	M
Rook	.21	–			
Carrion Crow	.47	.43	–		
Jackdaw	.17	.73	.38	–	
Magpie	.30	.37	.48	.42	–

(c) Field Use at One Time

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	H
Rook	.11	-			
Carrion Crow	.39	.28	-		
Jackdaw	.05	.64	.35	-	
Magpie	.18	.20	.23	.31	-
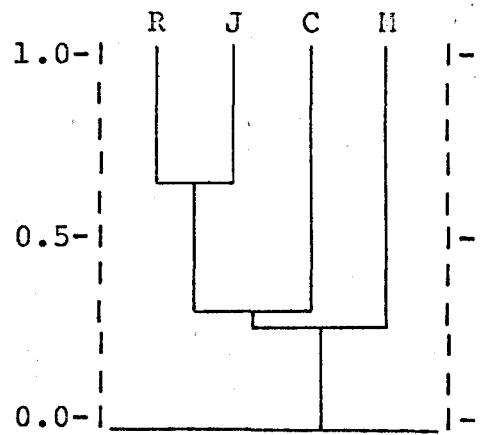
(d) Field Use Ignoring Time

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	H
Rook	.20	-			
Carrion Crow	.27	.41	-		
Jackdaw	.08	.66	.47	-	
Magpie	.21	.34	.32	.32	-
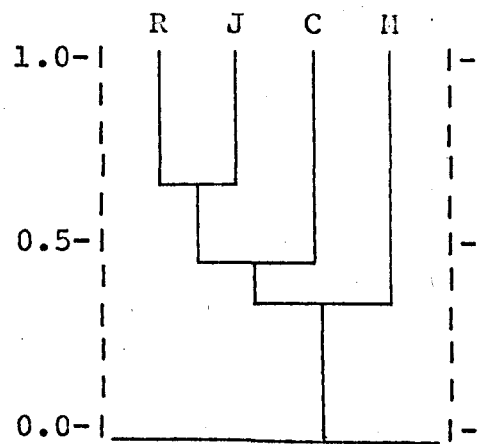
this is highlighted by the fact that if one calculates

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 particu-

lar 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
996 rooks, 441 jackdaws, 156 carrion crows and 160 magpies.

Species Absent or Present		Proportion of Subject Species Seen Without or in the Presence of Other Corvids — Subject Species:			
		Rook	C.Crow	Jackdaw	Magpie
Rook	Absent	--	62.9	5.4	63.5
Flock	1- 5	--	18.6	18.9	17.5
Size	6-20	--	11.4	35.1	9.5
	21-40	--	5.7	29.7	7.9
	> 40	--	1.4	10.8	1.6
Crow	Absent	53.6	--	51.3	74.6
Flock	1- 5	44.6	--	45.9	6.3
Size	6-20	1.8	--	2.7	11.1
	21-40	0.0	--	0.0	7.9
	> 40	0.0	--	0.0	0.0
Jack-	Absent	37.5	74.3	--	50.8
daw	1- 5	26.8	8.6	--	47.6
Flock	6-20	25.0	12.9	--	1.6
Size	21-40	8.9	4.3	--	0.0
	> 40	1.8	0.0	--	0.0
Magp-	Absent	58.9	55.7	56.8	--
pie	1- 5	37.5	38.6	35.1	--
Flock	6-20	3.6	5.7	8.1	--
Size	21-40	0.0	0.0	0.0	--
	> 40	0.0	0.0	0.0	--
Any	Absent	16.1	41.4	0.0	41.3
Corvid	1- 5	41.1	30.0	18.9	27.0
Species	6-20	30.4	14.3	32.4	14.3
Flock	21-40	8.9	7.1	32.4	6.3
Size	> 40	3.6	7.1	16.2	11.1

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 particu-
lar 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). How-
ever, 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 esti-

mates for separate resources are combined by the simple

mathematical operation of summation and averaging, or mul-

tiplication (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 deter-

mines (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, Wall-

work 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 feed-
ing 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 over-
lap may be illustrated by the following simple case. Con-
sider 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):

(a)   Feeding Action   (b)   Feeding Action

                 A   B   A   B

         A   .25   .25 | .50   A   .50   .00 | .50
Prey | Prey |
Type | Type |
         B   .25   .25 | .50   B   .00   .50 | .50
             ----------------|-----   ----------------|-----
               .50   .50 | .50   .50 |
                             | |

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 rela-

tionship 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 nutri-

tive 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
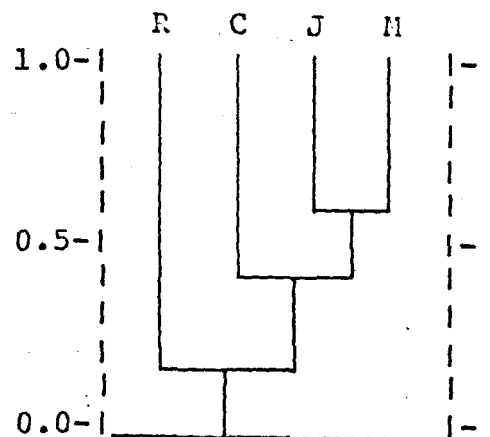   (grams of protein-containing material).

(a) Numbers

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.37	–			
Carrion Crow	.27	.43	–		
Jackdaw	.10	.26	.41	–	
Magpie	.12	.31	.62	.66	–
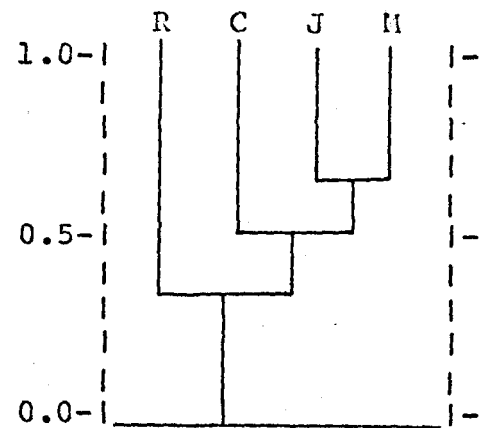
(b) Calorific Intake

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.23	–			
Carrion Crow	.16	.23	–		
Jackdaw	.19	.11	.34	–	
Magpie	.13	.15	.47	.59	–

(c) Protein Intake

Species	Niche Breadth (B st.)	Overlap Indices R	C	J	M
Rook	.22	–			
Carrion Crow	.15	.23	–		
Jackdaw	.16	.10	.30	–	
Magpie	.14	.14	.40	.59	–
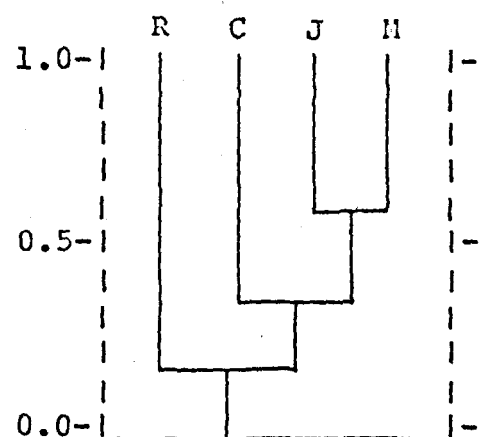
M.11.1.3).

Having shown that the two dimensions are mainly sta-
tistically 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 inver-
tebrate 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).

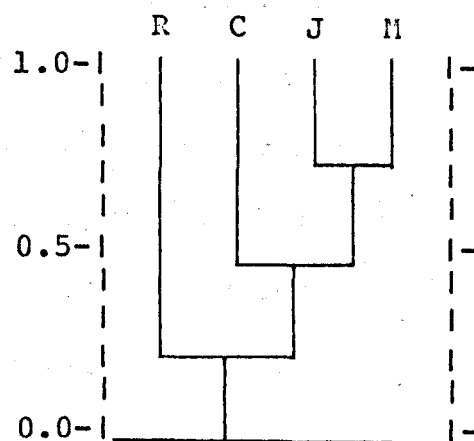(c)   Proportional use as relative nutritive value of items (grams of protein-containing material).

(a) Numbers

Species	Niche Breadth (B st.)	Overlap Indices			
		R	C	J	M
Rook	.36	–			
Carrion Crow	.40	.42	–		
Jackdaw	.13	.27	.43	–	
Magpie	.16	.29	.62	.79	–
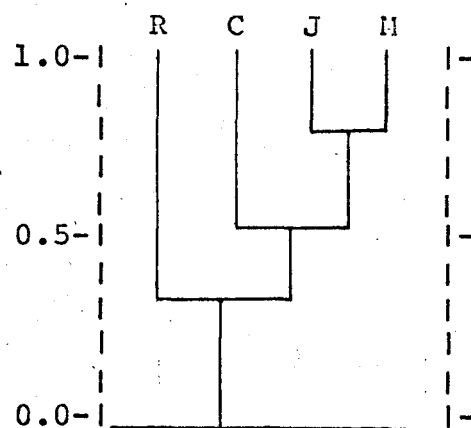
(b) Calorific Intake

Species	Niche Breadth (B st.)	Overlap Indices			
		R	C	J	M
Rook	.25	–			
Carrion Crow	.26	.23	–		
Jackdaw	.28	.22	.41	–	
Magpie	.17	.15	.48	.72	–

(c) Protein Intake

Species	Niche Breadth (B st.)	Overlap Indices			
		R	C	J	M
Rook	.23	–			
Carrion Crow	.24	.23	–		
Jackdaw	.26	.20	.37	–	
Magpie	.18	.14	.41	.73	–
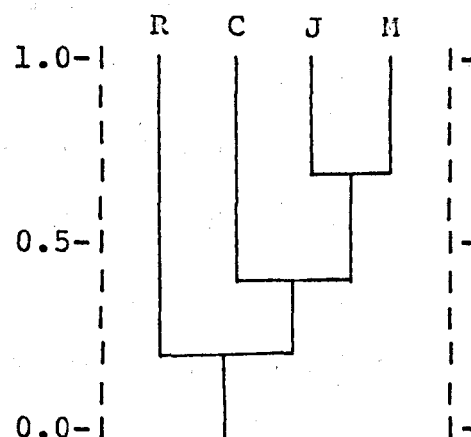
may not belong to different populations as such, but the
predatory behaviour, feeding apparatus and flocking tenden-
cies which differ between the species (discussed elsewhere)
make them separate prey populations to some extent.
Earthworms below the soil surface may not be available to
carrion crows, 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 conserva-
tive, 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 descrip-
tion of the data is limited since it does not reveal
whether each species occupies a unique area of niche hyper-
space 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 signifi-
cantly from one another in resource use. Finally, the
relative importance of the different elements of the par-
ticular 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 discrimi-
nation between species in terms of the rate of ingestion
(*) of the different prey types from the different microha-
bitats, 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 vari-
able, 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).

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

Actual Species	N	Predicted Species Membership			
		Carrion Crow	Rook	Jackdaw	Magpie
Carrion Crow	90	51.1%	6.7	4.4	37.8
Rook	69	4.3	58.0	5.8	31.9
Jackdaw	60	5.0	0	65.0	30.0
Magpie	70	22.9	0	25.7	51.4

(b)

Micro-habitat	Prey Type	DF1	DF2	DF3
Beneath Soil Surface	Small Invertebrate	.47		
	Small Earthworm	.62		
	Medium Earthworm	.20		
	Large Earthworm	.34		
Above Soil Surface	Small Invertebrate	-.48	-.71	
	Medium Invertebrate		.75	
Within-beneath Dung	Small Invertebrate		-.30	.80
	Medium Invertebrate		.75	-.32
Within-beneath Stones/Clods	Small Invertebrate			.78
	Small Earthworm	.21		
Eigenvalue		.830	.477	.009
Explained Variance (%)		63.1	36.2	0.7
Cumulative Variance (%)		63.1	99.3	100.0
With 3 Discriminant Functions Included:				
Wilk's Lambda		.367		
df		30		
p		***		
With DF1 removed:				
Wilk's Lambda			.671	
df			18	
p			***	
With DF1 and DF2 removed:				
Wilk's Lambda				.991
df				8
p				p=.96

tats. The final, non-significant, function is character-
ised by tendencies to catch small invertebrates from dung
or beneath other surface litter, and to avoid taking medium
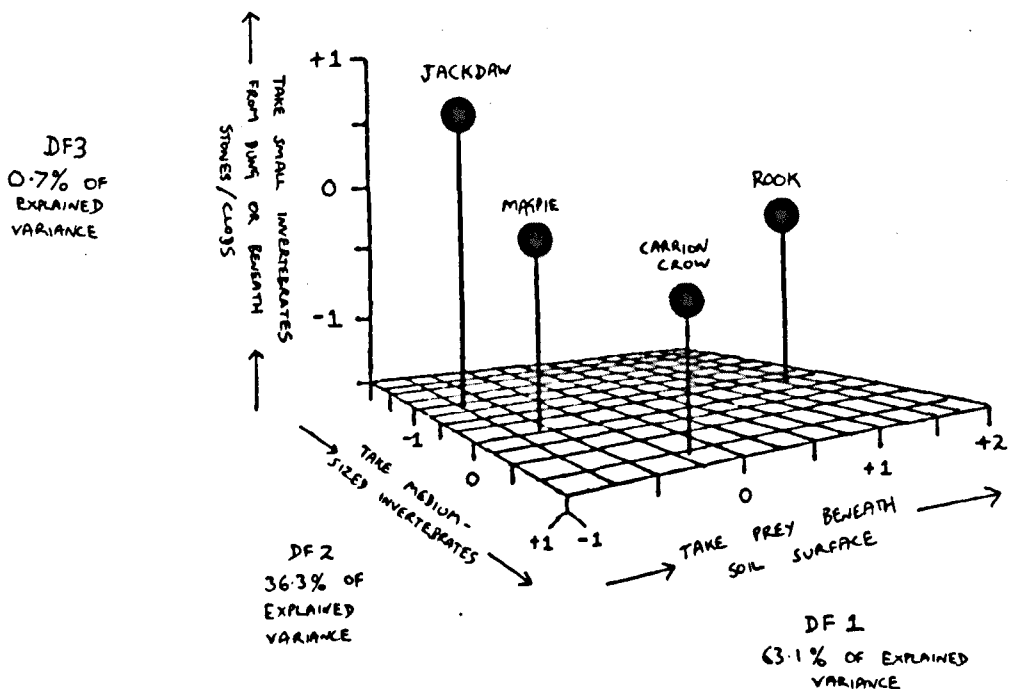invertebrates from dung.

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 distri-
bution 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
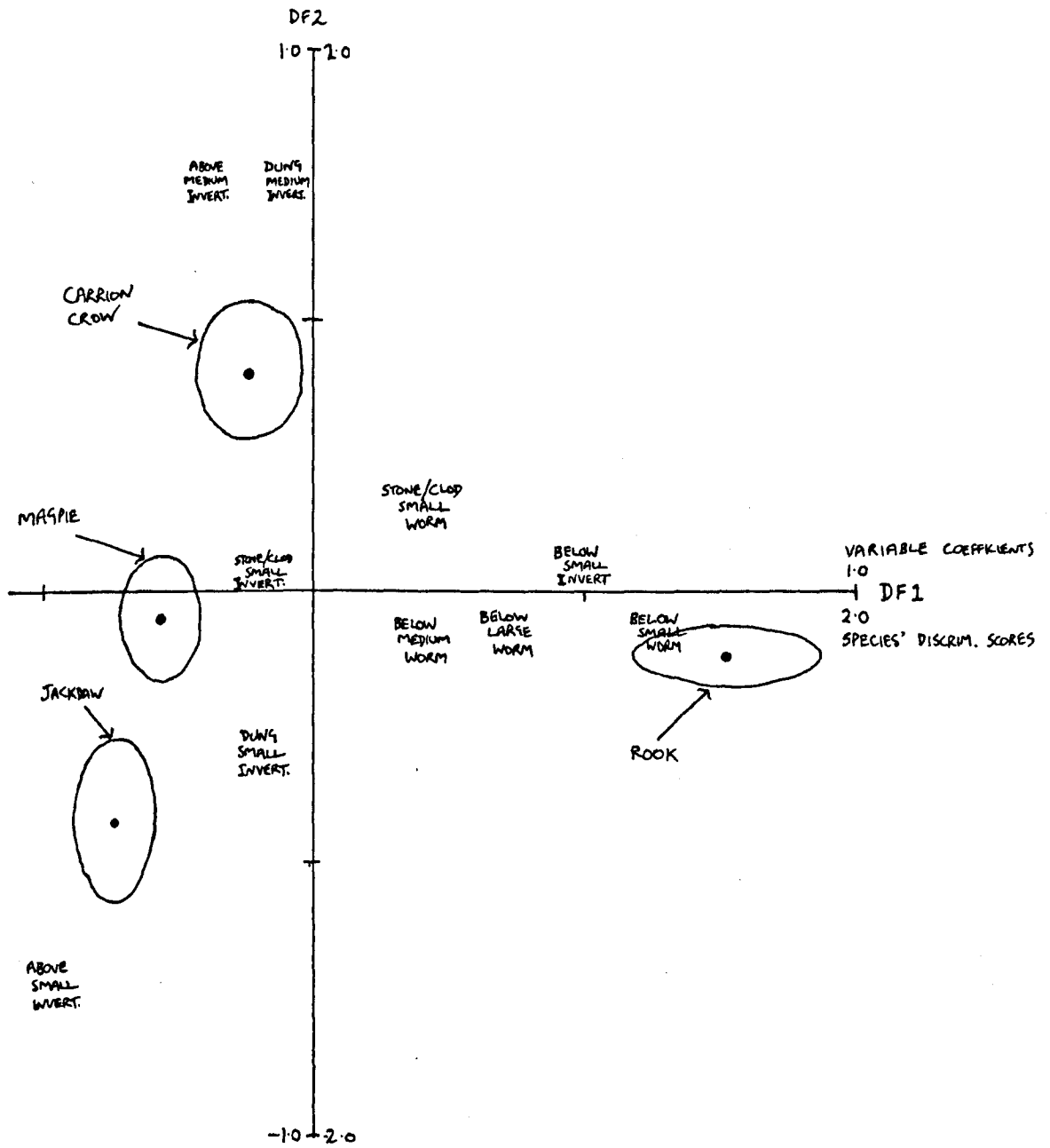above the soil surface but were more intermediate in their

Figure 1.5.7

Summary figures of four Corvid species' positions in discrim-
inant 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 func-
      tions (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 separa-
      tion 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 observa-
      tions for each species fall within each ellipse, hence
      their greater size than the confidence ellipses based on
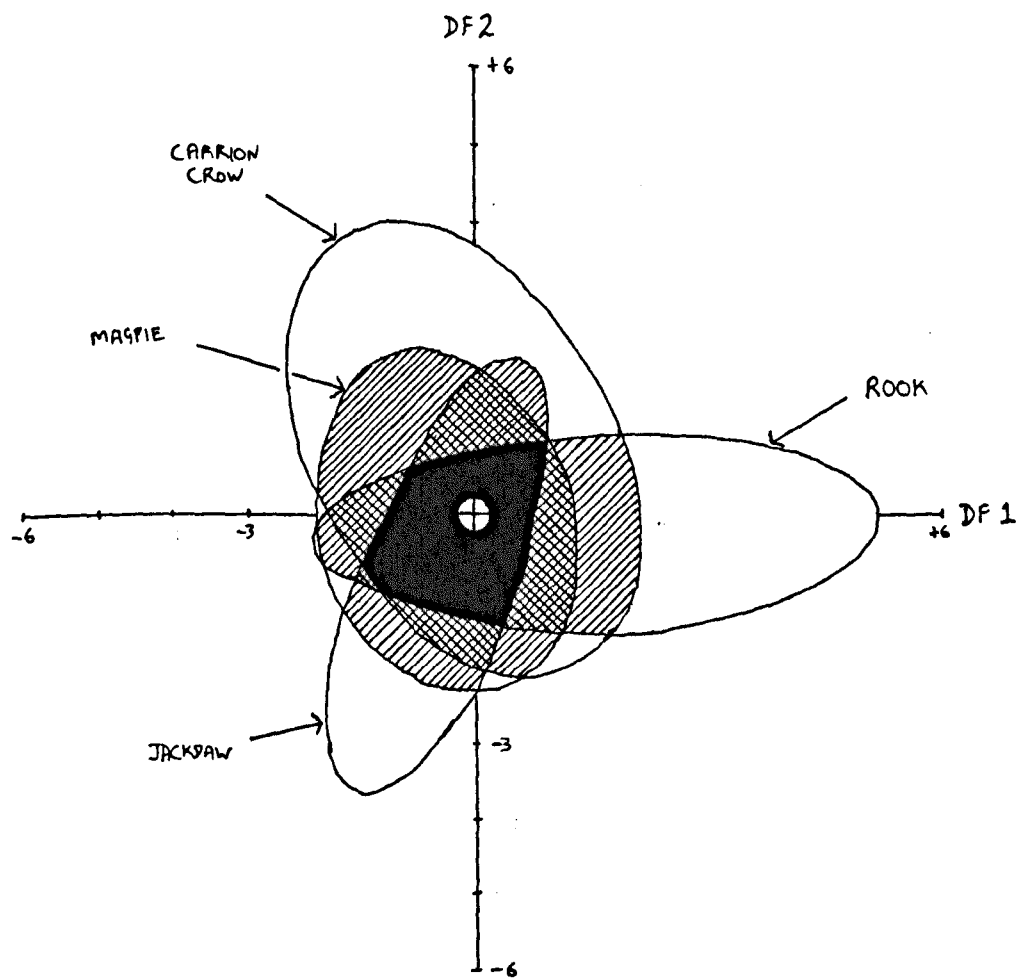   the standard errors of the mean figured in (a).

(a)

(b)

(c)

DF2
+6

CARRION
CROW

MAGPIE

ROOK

-6   -3

DF1
+6

JACKDAW

-3

-6

choice of different sized invertebrates from other microha-
bitats compared to carrion crows and jackdaws.

Although species were significantly separated from one
another in discriminant space, there was still a consider-
able 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 varia-
tion in niche breadths between species was not very great.
These patterns are quantified more precisely in the clas-
sification table which shows that overall 55.7% of indivi-
dual 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 meas-
ured 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 impor-
tant (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%

Actual Species	N	Predicted Species Membership			
		Carrion Crow	Rook	Jackdaw	Magpie
Carrion Crow	90	51.1%	5.6	6.7	36.7
Rook	69	2.9	52.2	5.8	39.1
Jackdaw	60	5.0	0	65.0	30.0
Magpie	70	22.9	0	20.0	57.1

(b)

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

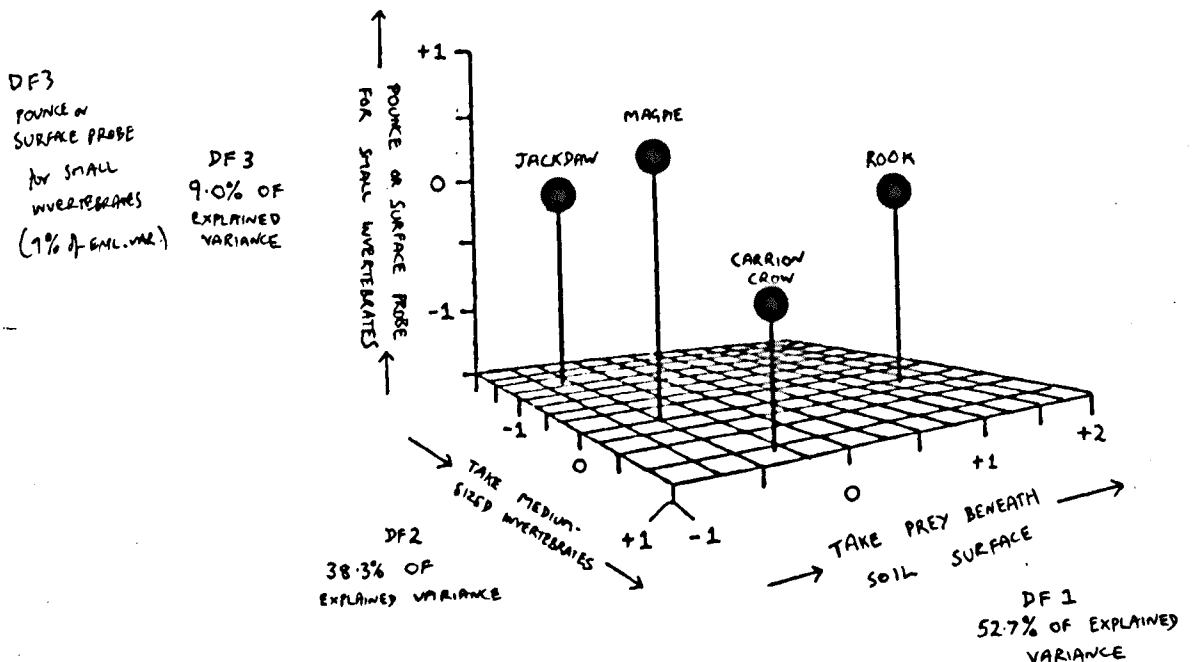|	DF1	DF2	DF3
Eigenvalue	.636	.462	.108
Explained Variance (%)	52.7	38.3	9.0
Cumulative Variance (%)	52.7	91.0	100.0
With 3 Discriminant Functions Included:			
Wilk's Lambda	.377		
df	48		
p	***		
With DF1 removed:			
Wilk's Lambda		.617	
df		30	
p		***	
With DF1 and DF2 removed:			
Wilk's Lambda			.902
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.
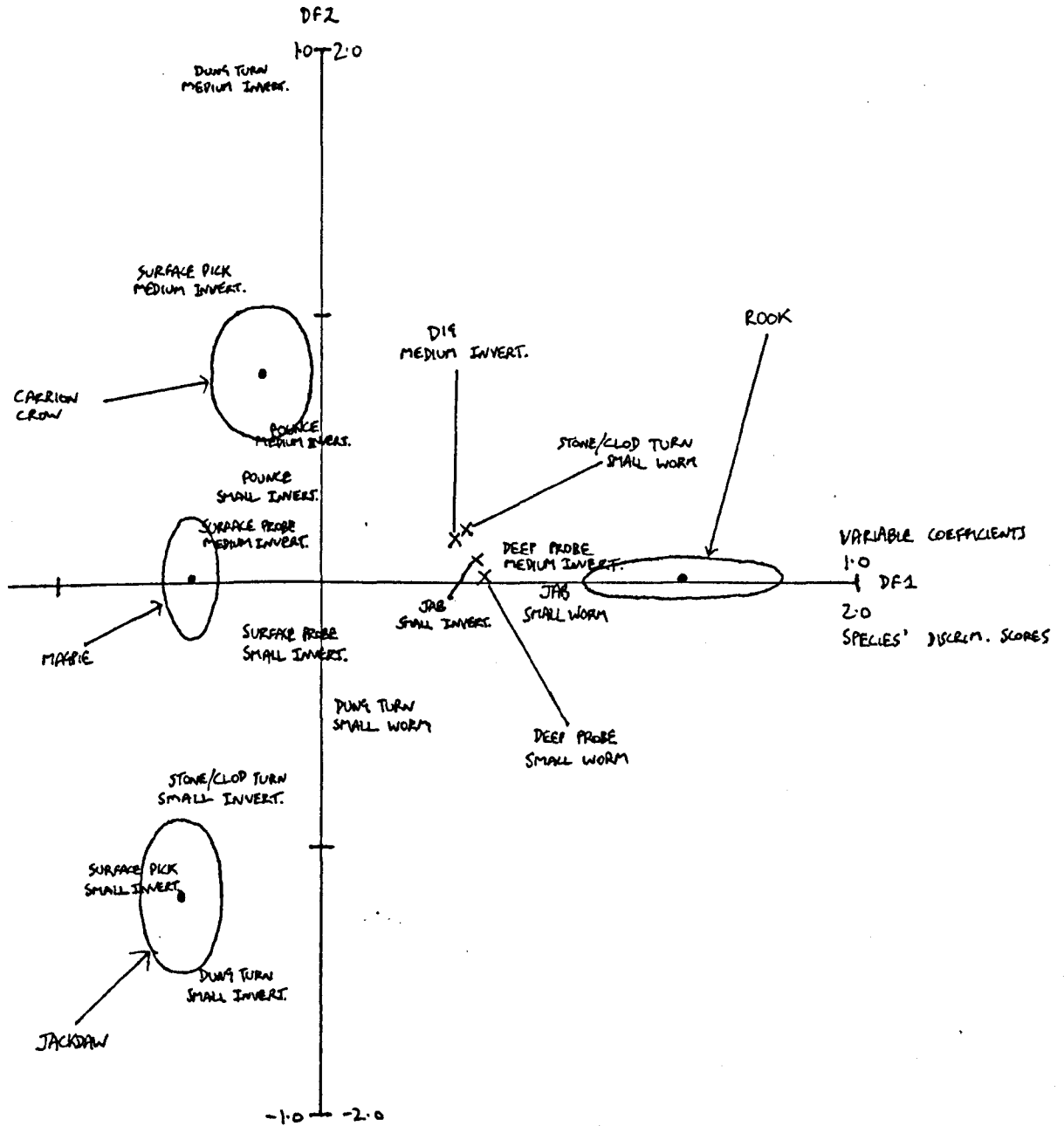
Figure 1.5.8

Summary figures of four Corvid species' positions in discrim-
inant 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 func-
      tions (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 separa-
      tion 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 observa-
      tions for each species fall within each ellipse, hence
      their greater size than the confidence ellipses based on
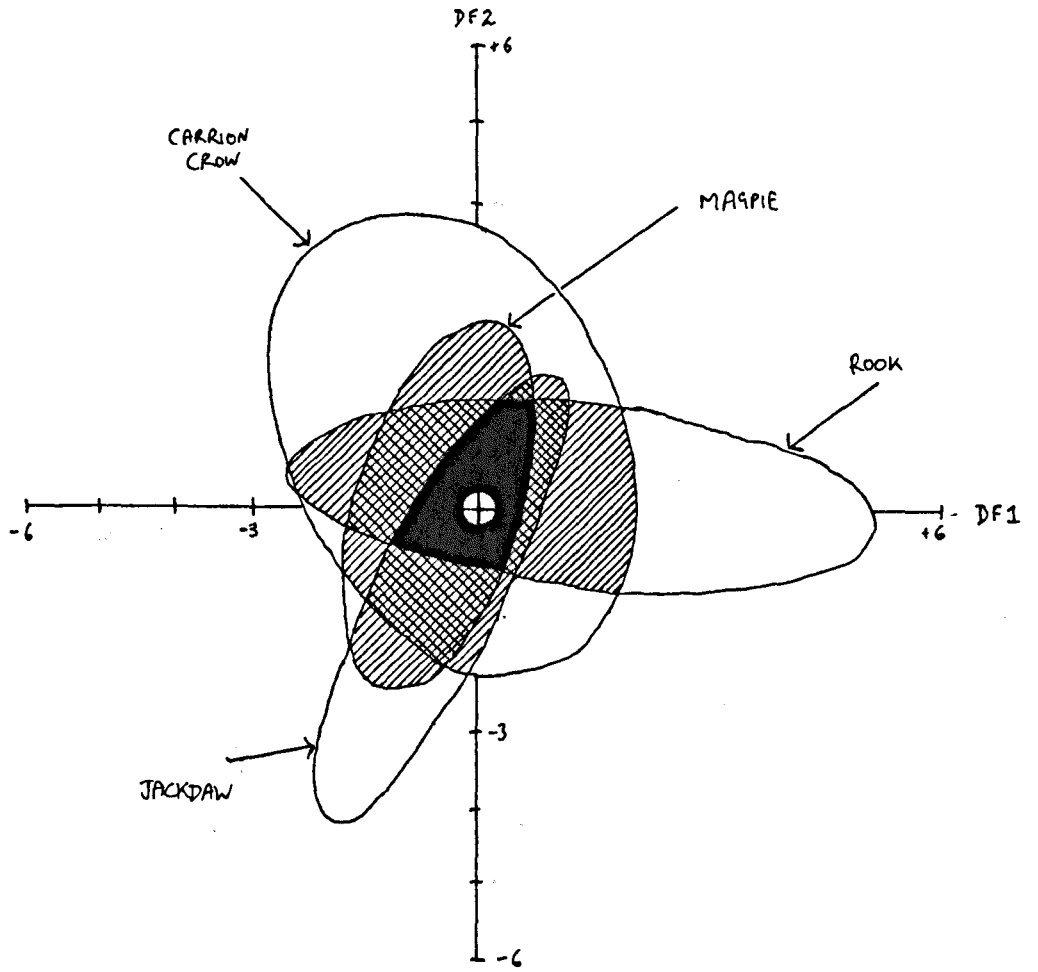   the standard errors of the mean figured in (a).

(a)

(b)

DF2

+0 ⊤ 2·0

DUNG TURN
MEDIUM INVERT.

SURFACE PICK
MEDIUM INVERT.

DIG
MEDIUM INVERT.

ROOK

CARRION
CROW

POUNCE
MEDIUM INVERS.

STONE/CLOD TURN
SMALL WORM

POUNCE
SMALL INVERT.

SURFACE PROBE
MEDIUM INVERT.

DEEP PROBE
MEDIUM INVERT.

VARIABLE COEFFICIENTS
1·0

DF1

MAGPIE

SURFACE PROBE
SMALL INVERT.

JAB
SMALL INVERT.

JAB
SMALL WORM

2·0
SPECIES' DISCRIM. SCORES

DUNG TURN
SMALL WORM

DEEP PROBE
SMALL WORM

STONE/CLOD TURN
SMALL INVERT.

SURFACE PICK
SMALL INVERT.

DUNG TURN
SMALL INVERT.

JACKDAW

−1·0 ⊥ −2·0

(C)

Part One Chapter Six - Effects of Other Corvid Species on Prey Intake Rates

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

considers the data available to describe partial and funda-

mental niches.

1.6.1 Changes in Prey Intake Rate

Figure 1.6.1 presents mean intake rates in the pres-
ence and absence of other Corvid species. Few significant
effects were found, but in many cases the number of obser-
vations 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 vari-
ance: $p = 0.108$), whilst the mean for magpies was based on
only six observations. Jackdaws had an opposite, facilita-
tive 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 cir-
cumstantial 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
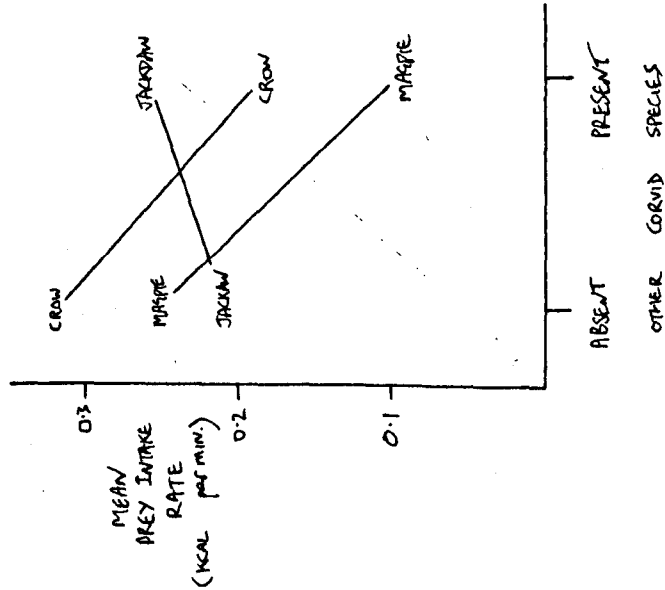prey intake rates

(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) car-
rion crow intake rates, (d) jackdaw intake rates, and (e)
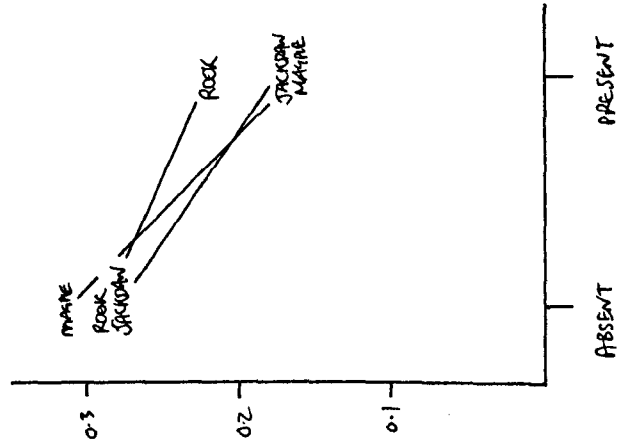magpie intake rates.

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
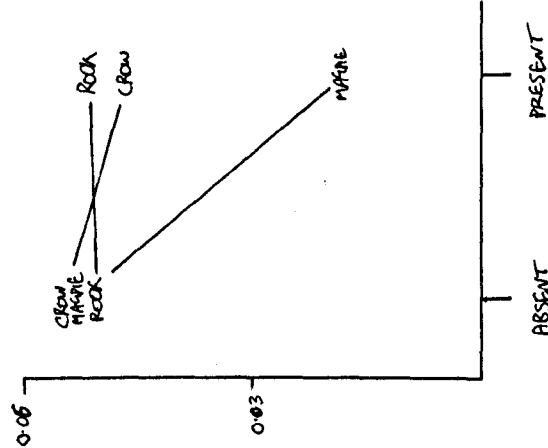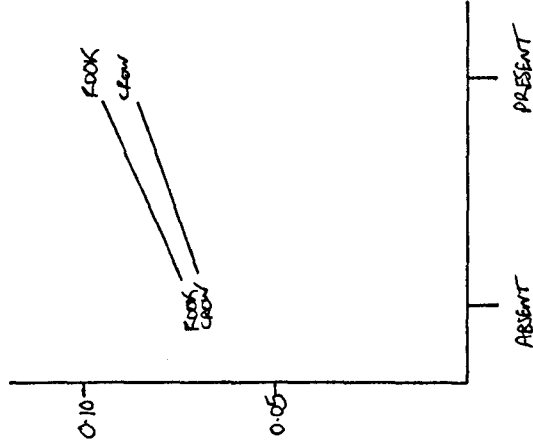(anova: $p < 0.05$) are flagged by asterisks.

(a)

SUBJECT SPECIES:

ROOK   CARRION CROW   JACKDAW   MAGPIE

MEAN PREY INTAKE RATE (Kcal per min)

ROOK panel: 0.3, 0.2, 0.1 — CROW, JACKDAW, MAGPIE, JACKDAW — ABSENT PRESENT — OTHER CORVID SPECIES

(MAGPIE PRESENT: N only = 6)

MAIN EFFECT OF CARRION CROW ABSENCE-PRESENCE:
$p = 0.108$

INTERACTION EFFECT OF CARRION CROW AND JACKDAW ABSENCE-PRESENCE:
$p < 0.05$

CARRION CROW panel: 0.3, 0.2, 0.1 — MAGPIE, ROOK, JACKDAW, ROOK, JACKDAW MAGPIE — ABSENT PRESENT

NO SIGNIFICANT EFFECTS

(ROOK PRESENT: N = only 8)
(JACKDAW " " : " " 5)
(MAGPIE " " : " " 16)

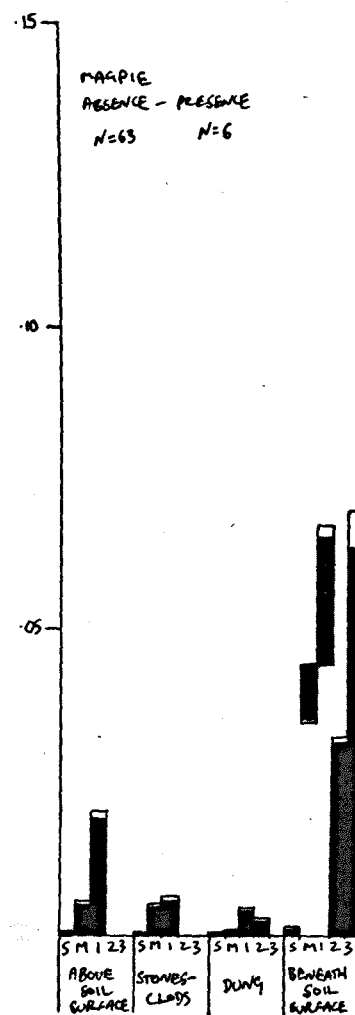**JACKDAW panel:** 0.06, 0.03 — CROW MAGPIE ROOK, ROOK, CROW, MAGPIE — ABSENT PRESENT

NO SIGNIFICANT EFFECTS

(MAGPIE PRESENT: N = only 5)

MAGPIE panel: 0.10, 0.05 — ROOK CROW, ROOK, CROW — ABSENT PRESENT

NO SIGNIFICANT EFFECTS

(JACKDAW PRESENT: N = 0)

MEAN
PREY
INTAKE RATE
OF ROOKS

((KCAL)/MIN.)

ANY OTHER CORVID SPECIES
ABSENCE — PRESENCE
N=14   N=55

CARRION CROW
ABSENCE — PRESENCE
N=30   N=39

JACKDAW
ABSENCE — PRESENCE
N=32   N=37

MAGPIE
ABSENCE — PRESENCE
N=63   N=6

PREY TYPE →   S M 1 2 3   S M 1 2 3   S M 1 2 3   S M 1 2 3

MICRO — HABITAT →   ABOVE SOIL SURFACE   STONES- CLODS   DUNG   BENEATH SOIL SURFACE

MEAN PREY INTAKE RATE OF CARRION CROWS ((KCAL)/MIN.)

(c)

ANY OTHER CORVID SPECIES
ABSENCE - PRESENCE
N = 63   N = 27

ROOK
ABSENCE - PRESENCE
N = 82   N = 8

JACKDAW
ABSENCE - PRESENCE
N = 85   N = 5

MAGPIE
ABSENCE - PRESENCE
N = 74   N = 16

PREY TYPE →   S M 1 2 3

MICRO-HABITAT →   ABOVE SOIL SURFACE   STONES-CLODS   DUNG   BENEATH SOIL SURFACE

MEAN PREY INTAKE RATE OF JACKDAWS (KCAL per MIN.)

ANY OTHER CORVID SPECIES
ABSENCE - PRESENCE
N= 17   N=43

ROOK
ABSENCE - PRESENCE
N=36   N=24

CARRION CROW
ABSENCE - PRESENCE
N=28   N= 32

MAGPIE
ABSENCE - PRESENCE
N=55   N=5

PREY TYPE →
MICRO - HABITAT →

S M 1 2 3   S M 1 2 3   S M 1 2 3   S M 1 2 3
ABOVE SOIL SURFACE   STONES-CLODS   DUNG   BENEATH SOIL SURFACE

(e)

MEAN
PREY
INTAKE - RATE
OF MARINES
(Kcal per min.)

PREY TYPE →
MICRO-HABITAT →

ANY OTHER CORVID SPECIES
ABSENCE - PRESENCE
N=22   N=45

ROOK
ABSENCE - PRESENCE
N=41   N=27

CARRION CROW
ABSENCE - PRESENCE
N=32   N=38

JACKDAW
ABSENCE -   PRESENCE
N=70   (NO DATA)

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 ne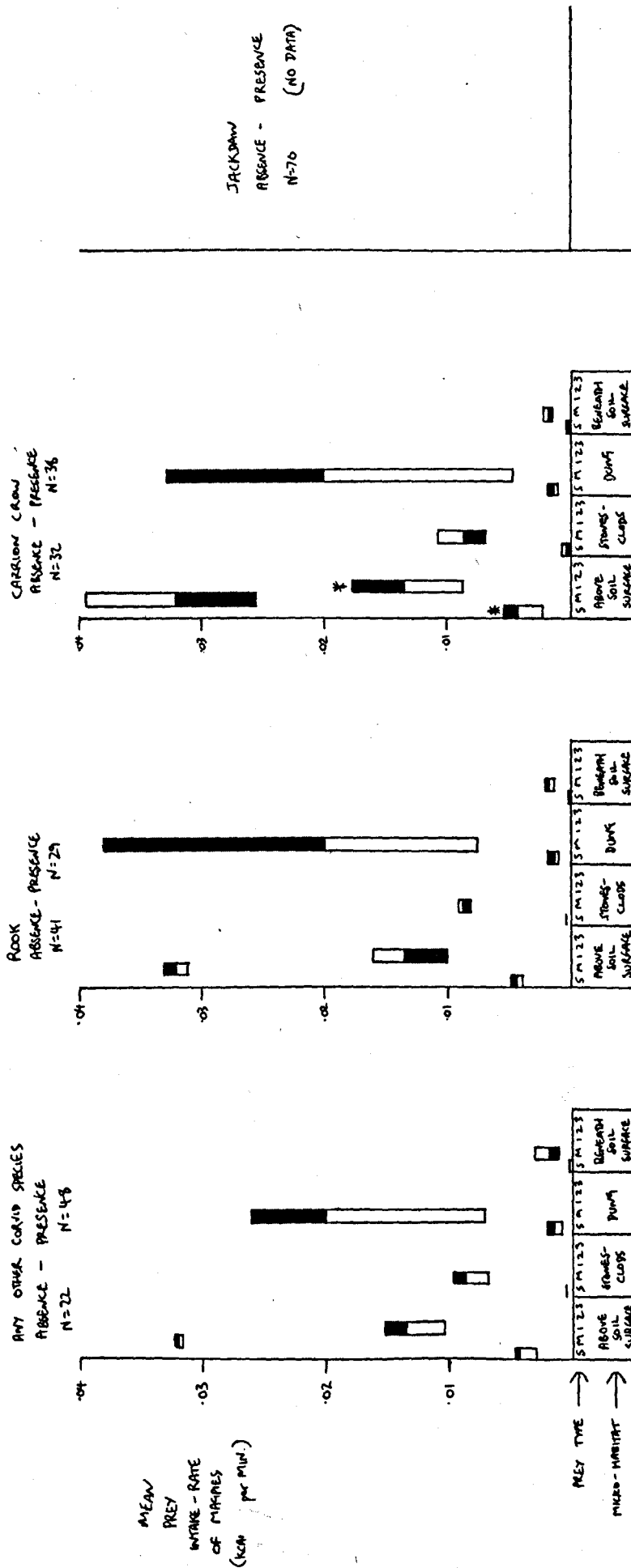gative effect. Magpies were associated with a more substantial reduction in jackdaw prey intake rate, but there were only five observations in the presence of magpies. Rooks and carrion crows had weak (non-significant) facilitative effects on magpie intake rate, whilst there were no data when jackdaws 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 nega-
tive correlations (binomial test p<0.05).

Proportion of positive-to-negative correlations;
Intake rates correlated with flock size of:

Species	C.Crow +	−	Rook +	−	Jackdaw +	−	Magpie +	−	All +	−
Carrion Crow	---		3*29		7*25		10*22		2*30	
Rook	14:13		---		15:12		2*25		15:12	
Jackdaw	6:5		3:8		---		3:8		2*9	
Magpie	8:8		7:9		No Data		---		8:8	

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 microha-
bitats, 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

presence of these species (5 and 16 respectively).

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 obser-

vations 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 calcula-
tions 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 forag-
ing 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.

		In Absence or Presence	In Absence of One Another	In Presence of One Another
C. Crow	Breadth	0.26	0.25	0.18
	Overlap	0.48	0.55	0.46
Magpie	Breadth	0.17	0.10	0.18
Rook	Breadth	0.25	0.17	0.21
	Overlap	0.22	0.14	0.28
Jackdaw	Breadth	0.28	0.18	0.25

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 nega-
tive 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 sug-
gests 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:

	rho	p
small earthworms:	-0.474	***
medium and large earthworms:	-0.253	*
all earthworms:	-0.385	***
small ew calorific value:	-0.474	***
med./lge. ew calorific value:	-0.246	*
all ew calorific value:	-0.329	**

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

	rho	p
earthworms:	-0.385	***
other invertebrates:	-0.176	NS
all invertebrates:	-0.246	*
ew calorific value:	-0.329	**
other inv. calorific value:	-0.197	NS
all invert. calorific value:	-0.354	**

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.

(a)

NUMBER OF
EARTHWORMS
INGESTED
PER MINUTE

0.50

0.25

ALL EARTHWORMS
SMALL EARTHWORMS
MEDIUM AND LARGE EARTHWORMS

CALORIFIC VALUE
INGESTED PER MINUTE
(KCAL / g)

0.15

0.10

0.05

FLOCK SIZE OF
CARRION CROWS
AND ANY OTHER
CORVID SPECIES:

1   2   3-5   6-20   > 20

SAMPLE SIZE: 11   19   27   14   9

(b)

NUMBER OF INVERTEBRATES INGESTED PER MINUTE

ALL PREY ITEMS

INVERTEBRATES OTHER THAN EARTHWORMS

EARTHWORMS

CALORIFIC VALUE INGESTED PER MINUTE (KCAL / G)

ALL PREY ITEMS

INVERTEBRATES OTHER THAN EARTHWORMS

EARTHWORMS

FLOCK SIZE OF CARRION CROWS AND ANY OTHER CORVID SPECIES:

| 1 | 2 | 3-5 | 6-20 | >20 |

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). Alterna-
tively, 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 car-
rion 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 sug-
gest 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 observa-
tions 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 particu-
lar 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.

Chapter Seven - Competition and Coexistence: Predictions
and Observations about Short-term Behavioural Options

1.7.1 Long-term Behaviour and Coexistence: Testing the
Null Hypothesis

Chapter 1.4 described the use of macro- and microhabi-
tats, 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 indivi-
dual 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 <u>Pica</u> <u>pica</u> to be more in overlap with
the three <u>Corvus</u> 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 possi-
ble 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 exploi-
tation 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 effi-
ciencies 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 struc-
ture is generated by filling a matrix with randomly gen-
erated (*) numbers, where the number of columns equals the
number of species and the number of rows equals the number

(*)   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 pro-
gram used for the present simultions 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 partic-
ular resource in question. Differences between observed
and randomly generated alphas could be tested for signifi-
cance by the t-test for the comparison of a single observa-
tion 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 utilisa-
tion 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 pro-

vide 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 pro-

duce 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 = Observed, N = Null value; significant differences are
flagged by an asterisk.

Overall Matrix Mean Overlaps:

Grass Crop Use   - O > N
Prey Type and Size   - O < N
Foraging Technique   - O < N
Prey from Different
    Microhabitats   - O < N *
Time/Space   - O < N *

	Grass Crop Use			
Species	R	C	J	M
Rook	-			
C.Crow	O>N	-		
Jackdaw	O>N*	O>N	-	
Magpie	O>N	O>N*	O>N	-

	Time/Space			
Species	R	C	J	M
Rook	-			
C.Crow	O<N*	-		
Jackdaw	O<N	O<N*	-	
Magpie	O<N*	O<N*	O<N*	-

	Prey Type and Size			
Species	R	C	J	M
Rook	-			
C.Crow	O>N	-		
Jackdaw	O<N*	O<N*	-	
Magpie	O<N	O<N	O>N	-

	Foraging Technique			
Species	R	C	J	M
Rook	-			
C.Crow	O<N*	-		
Jackdaw	O<N*	O>N	-	
Magpie	O<N*	O>N*	O>N*	-

	Microhabitat/Prey (Numbers of Prey)			
Species	R	C	J	M
Rook	-			
C.Crow	O<N*	-		
Jackdaw	O<N*	O<N*	-	
Magpie	O<N*	O<N	O>N	-

	Microhabitat/Prey (Calorific Value)			
Species	R	C	J	M
Rook	-			
C.Crow	O<N*	-		
Jackdaw	O<N*	O<N*	-	
Magpie	O<N*	O<N*	O>N	-

ficantly 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 indi-
viduals of any one particular species still further, some-
times 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 subor-
dinate 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 com-
petition 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 dif-
      ferent 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

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 (<u>Corvus</u>). 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 differ-
ence 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 <u>Corvus</u> 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 <u>Corvus</u>
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 <u>Corvus</u> species evolved from
some more jay-like form in the course of adaptation to life
in more open country (Goodwin 1976). The <u>Corvus</u> 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 differ-

ences 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 unique-

ness 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 con-
> vergent adaptations to ground feeding in rela-
> tively 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

guild despite the overlap revealed.

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.

(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 with-
      stand carrion crow aggression better than smaller
      ones, and should feed for longer in carrion crow
      presence.

(11b)Rook - jackdaw. Rooks should either ignore or associ-
      ate 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).

(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 dis-

     turbable 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 relation-
      ships 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 esta-
      blished 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 effi-

ciencies 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 addi-

tion, 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
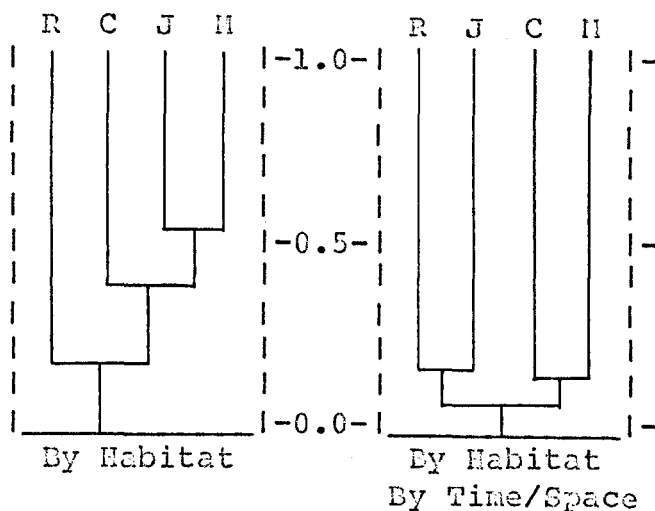original matrices may be found in chapter 1.5.

(a) Numbers

| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.08	.16	.03
Carrion Crow	.29	–	.06	.16
Jackdaw	.25	.31	–	.09
Magpie	.20	.59	.57	–

By Habitat

By Habitat
By Time/Space
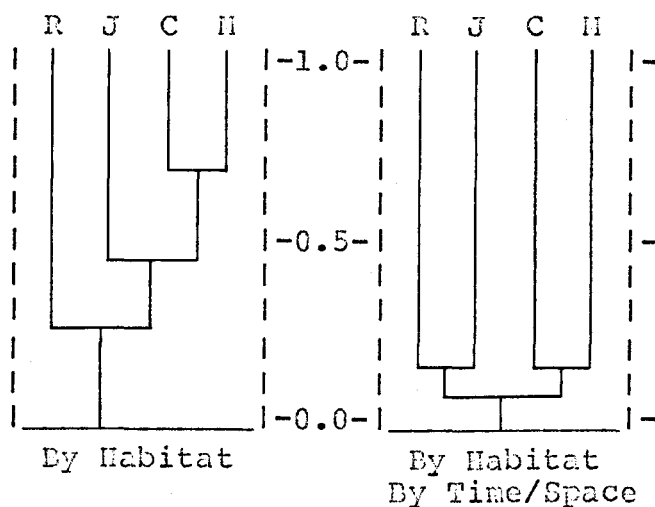
(b) Calorific Intake

| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.04	.13	.01
Carrion Crow	.16	–	.05	.12
Jackdaw	.21	.30	–	.08
Magpie	.10	.45	.52	–

By Habitat

By Habitat
By Time/Space

(c) Protein Intake

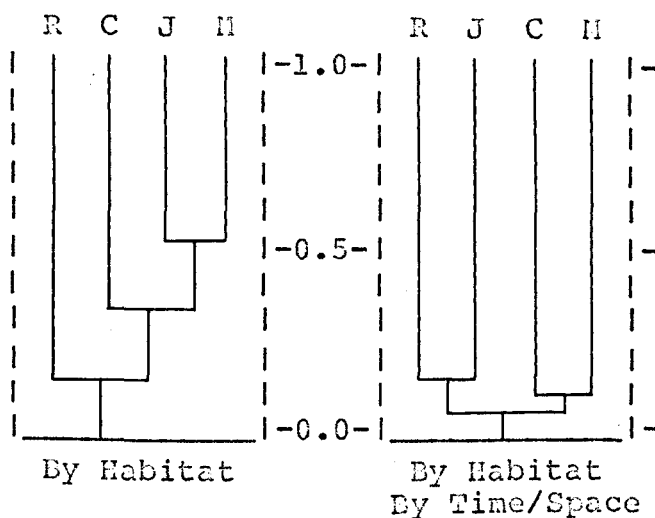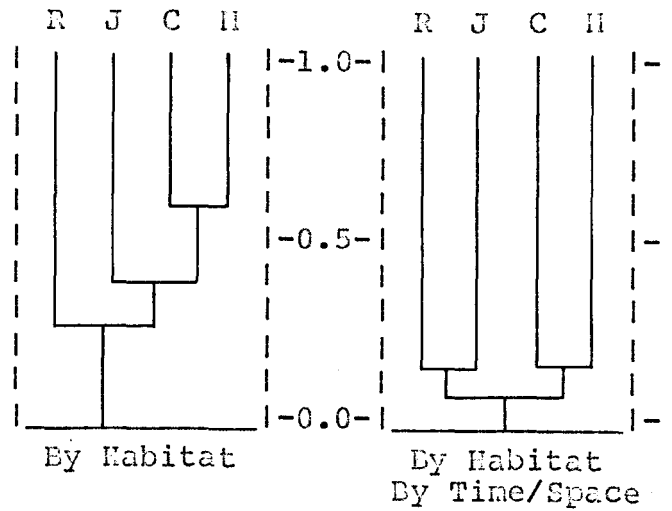| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.04	.13	.01
Carrion Crow	.16	–	.05	.10
Jackdaw	.19	.27	–	.08
Magpie	.09	.39	.52	–

By Habitat

By Habitat
By Time/Space

Figure 1.7.2

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
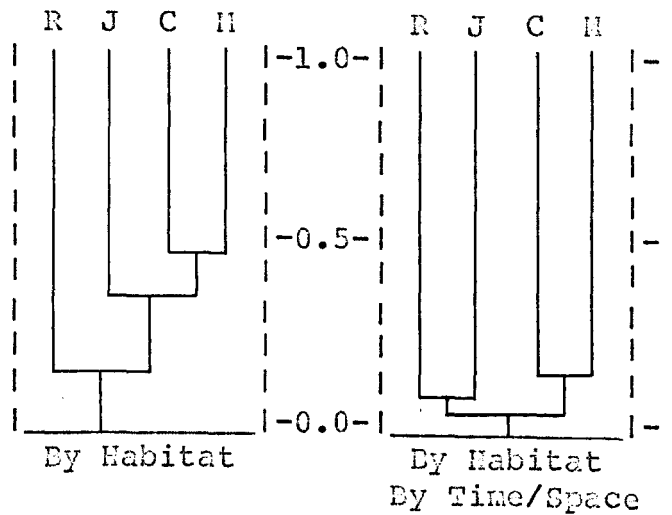original matrices may be found in chapter 1.5.

(a) Numbers

| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.08	.15	.06
Carrion Crow	.30	–	.06	.16
Jackdaw	.25	.30	–	.07
Magpie	.21	.59	.47	–

By Habitat

By Habitat By Time/Space

(b) Calorific Intake

| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.04	.07	.02
Carrion Crow	.16	–	.01	.12
Jackdaw	.10	.25	–	.06
Magpie	.10	.45	.43	–

By Habitat

By Habitat By Time/Space

(c) Protein Intake

| | Overlap Indices | | | |
Species	R	C	J	H
Rook	–	.04	.05	.01
Carrion Crow	.16	–	.04	.10
Jackdaw	.07	.22	–	.06
Magpie	.10	.38	.42	–

By Habitat

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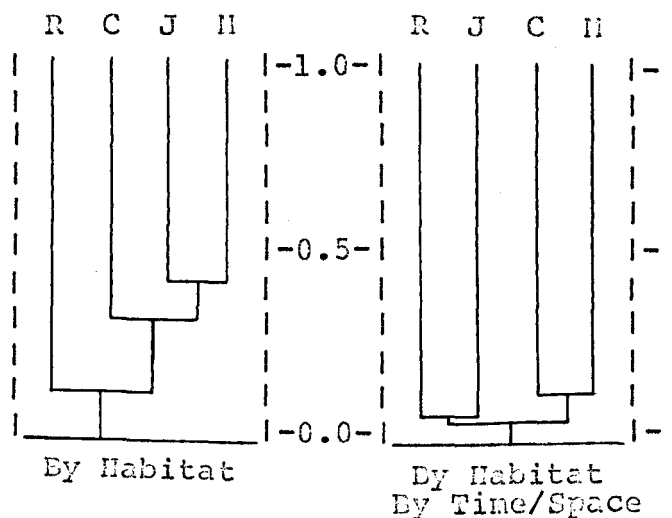
densities of different types of invertebrate between dif-
ferent grass crop types), and thus choosing a different
crop type in an attempt to reduce overlap with another
species may not be an economic possibility if individuals
of the species then found themselves foraging on much lower
levels of prey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

Other Species

Species	Crow Ab Pr	Rook Ab Pr	Jackdaw Ab Pr	Magpie Ab Pr
Carrion Crow	---	63 65	71*49	53*80
Rook	84*77	---	84 81	83 79
Jackdaw	75*58	30*74	---	72*63
Magpie	65*79	67*92	73 79	---

(b) Percentage of birds on permanent pasture

Other Species

Species	Crow Ab Pr	Rook Ab Pr	Jackdaw Ab Pr	Magpie Ab Pr
Carrion Crow	---	41*81	55 57	47 64
Rook	92*76	---	97*85	83*96
Jackdaw	90*72	0*88	---	79 86
Magpie	36*56	24*97	39*74	---

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 fort-

night 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 fre-
quently in larger flocks than magpies, but the opposite to
what would be predicted if carrion crows were using aggres-
sion 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 observa-
tions 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 (N 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 percen-
      tage 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:

	1- 2	3- 5	6-20	21-40	>40	Mean
1. Flocks Attacked	32.0	52.6	55.5	92.9	100.0	59.4
2. Flocks Leaving	75.0	60.0	61.0	46.1	75.0	61.9
3. Attack Rate	166.1	59.9	26.0	95.5	69.7	79.1
4. N Observations	25	19	36	14	12	106
5. Crow Present	23.1	26.9	30.8	15.4	3.8	--
6. Crow Absent	16.7	13.3	30.0	23.3	16.7	--
7. With Crow	54.5	63.6	47.0	36.4	16.7	46.4
8. N Observations	11	11	17	11	6	56

Jackdaw Flock Size:

	1- 2	3- 5	6-20	21-40	Mean
1. Flocks Attacked	13.8	66.7	76.5	85.7	47.7
2. Flocks Leaving	25.0	75.0	38.5	50.0	48.4
3. Attack Rate	2.6	55.8	102.4	145.2	53.9
4. N Observations	29	12	17	7	65
5. Crow Present	27.8	5.5	50.0	16.7	--
6. Crow Absent	26.3	26.3	26.3	21.0	--
7. With Crow	50.0	16.7	64.3	42.8	48.6
8. N Observations	10	6	14	7	37

Magpie Flock Size:

	1- 2	3- 5	6-20	Mean
1. Flocks Attacked	30.4	40.0	50.0	32.1
2. Flocks Leaving	42.9	50.0	100.0	47.1
3. Attack Rate	24.6	8.2	69.2	24.8
4. N Observations	46	5	2	53
5. Crow Present	61.3	25.8	12.9	--
6. Crow Absent	96.9	3.1	0.0	--
7. With Crow	38.0	88.9	100.0	49.2
8. N Observations	50	9	4	63

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 jack-

daws 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 obser-

vations that the only way to collect sufficient data was to

do so opportunistically - i.e. whenever the author hap-

pened 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 interac-
tions 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

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 fre-
quently. 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 distur-
bance 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 Bossema 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 pres-
ence - 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, how-
ever, 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 reduc-
ing 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 fre-
quently (row 1, though no test of the significance of this
trend may be made due to violation of assumptions), con-
trary to an interference competition hypothesis but con-
sistent 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 car-
rion 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 nega-
tive 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 predict-
able.   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
congeners we might expect, if they are part of a stably
structured community, to show a positive linear relation-
ship between overlap in body size and overlap in prey
type/microhabitat/grass habitat use. This is because pre-
dator 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 popula-
tions.

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
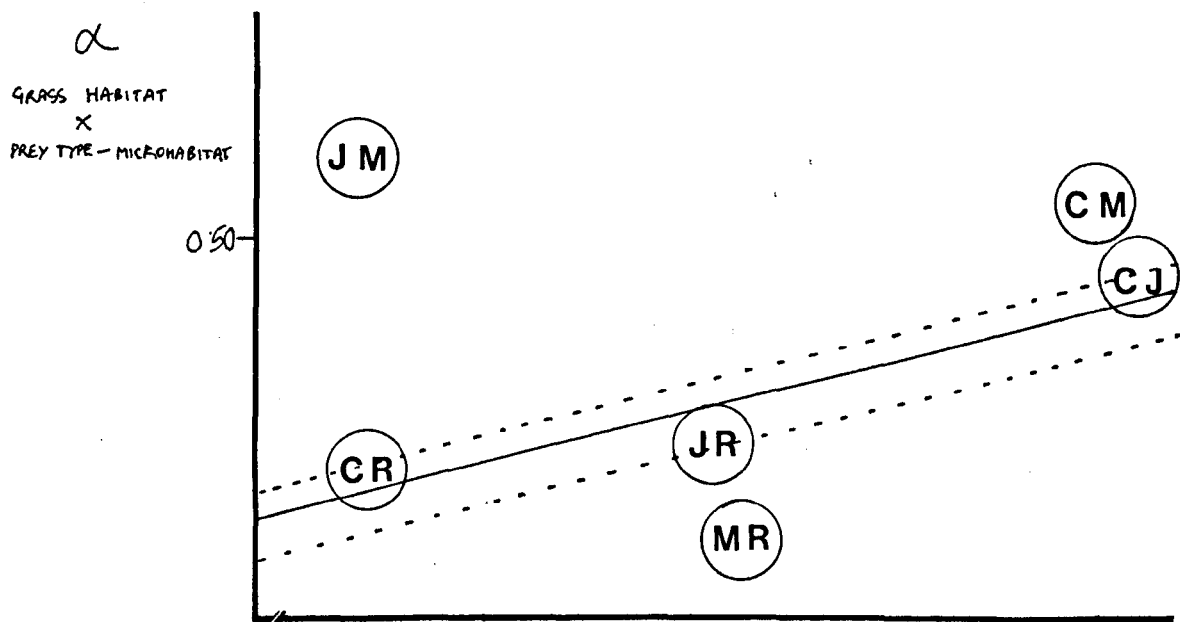adaptation and long-term behaviour, magpies were not part

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
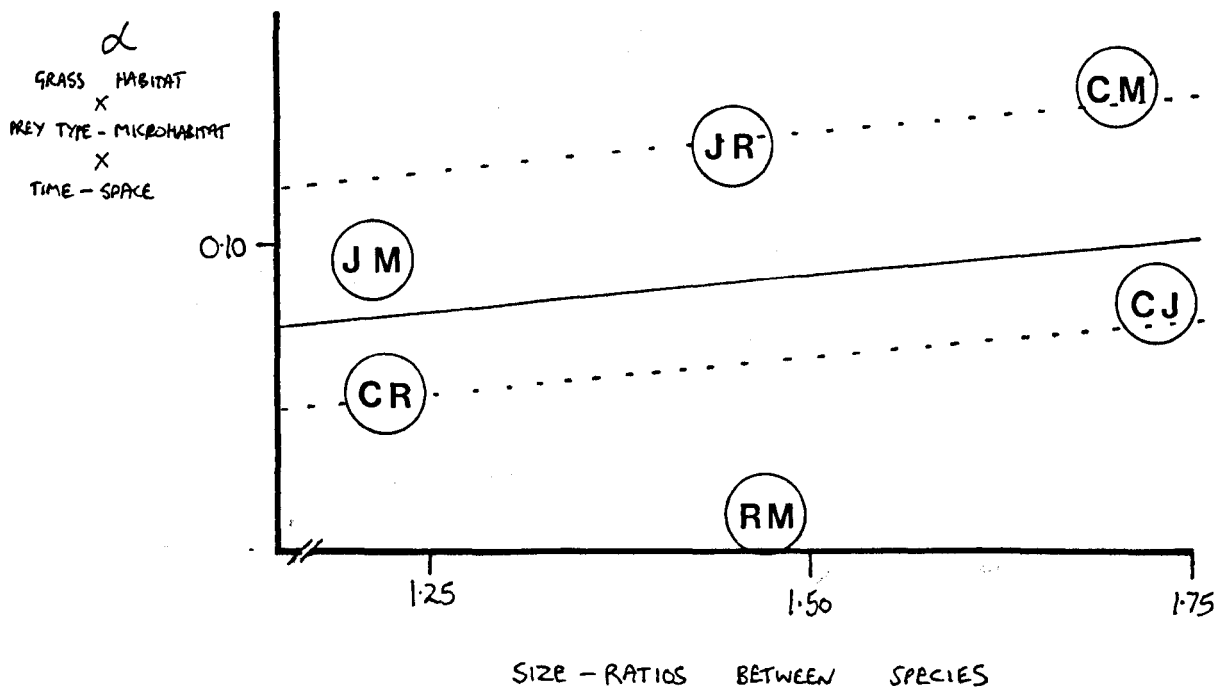type/microhabitat x use of space in time.

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)

α

GRASS HABITAT
×
PREY TYPE – MICROHABITAT

0·50 —

J M   C M   C J

C R   J R   M R

(b)

α

GRASS   HABITAT
×
PREY TYPE – MICROHABITAT
×
TIME – SPACE

0·10 —

C M   J R   C J

J M   C R   R M

1·25   1·50   1·75

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 habi-

tats 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 competi-
tors compared to the other species for certain prey items).

      Yet another short-term behaviour which may help mag-
pies 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

| | Overlap in Time-Space | Grass Habitat x Diet/Microhabitat x Time-Space | |
		Numbers	Calories
Carrion Crow	0.24	0.10	0.07
Rook	0.36	0.09	0.06
Jackdaw	0.33	0.10	0.09
Magpie	0.19	0.09	0.07

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:

$$L = \text{alpha}_{i,j} \cdot x_j$$
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.

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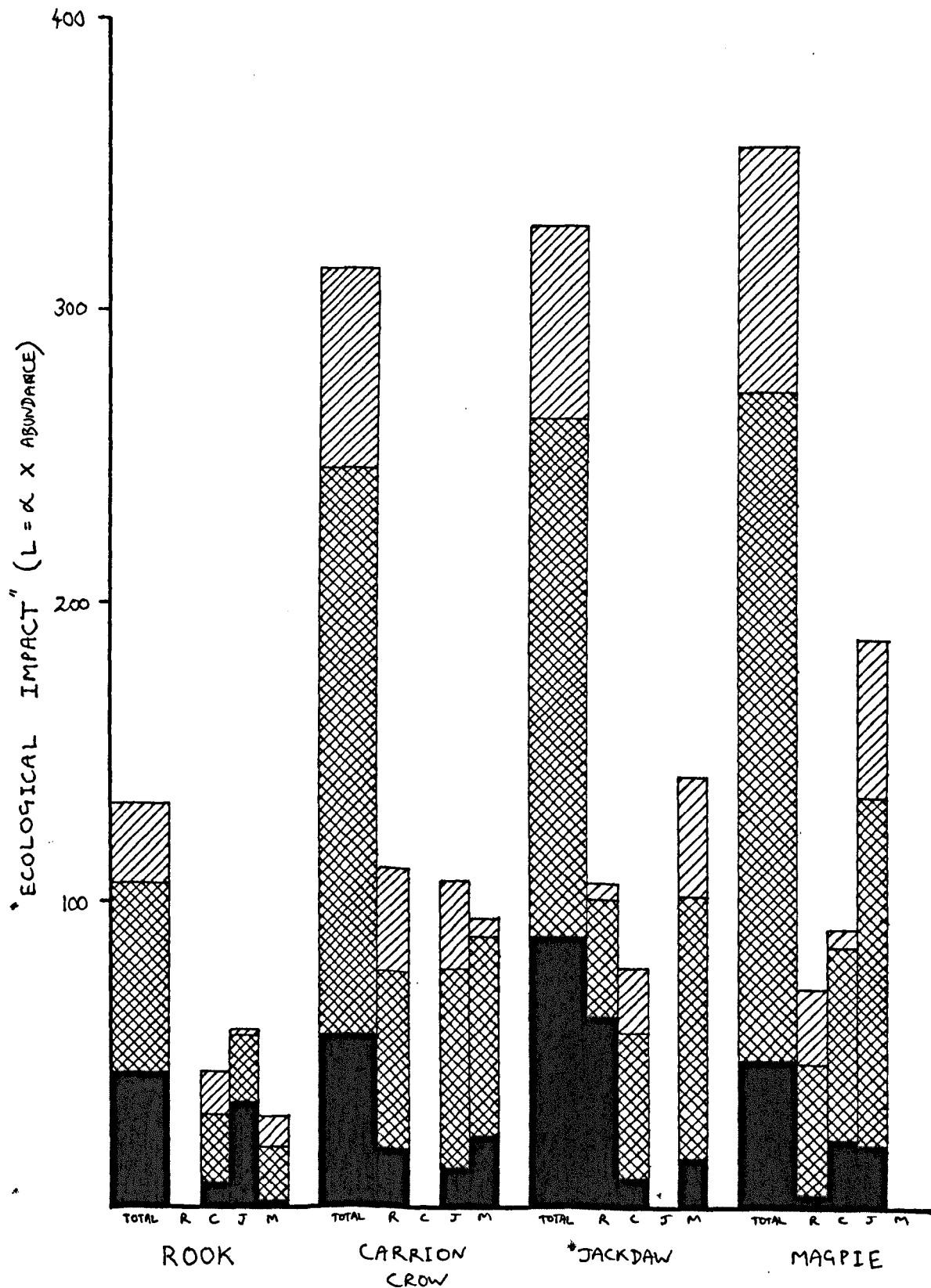
Figure 1.7.4

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: pro-
duct alpha = diet/micrhabitat x habitat x use of space in
time.

(a)

"ECOLOGICAL IMPACT" (L = α × ABUNDANCE)

400

300

200

100

TOTAL R C J M   TOTAL R C J M   TOTAL R C J M   TOTAL R C J M

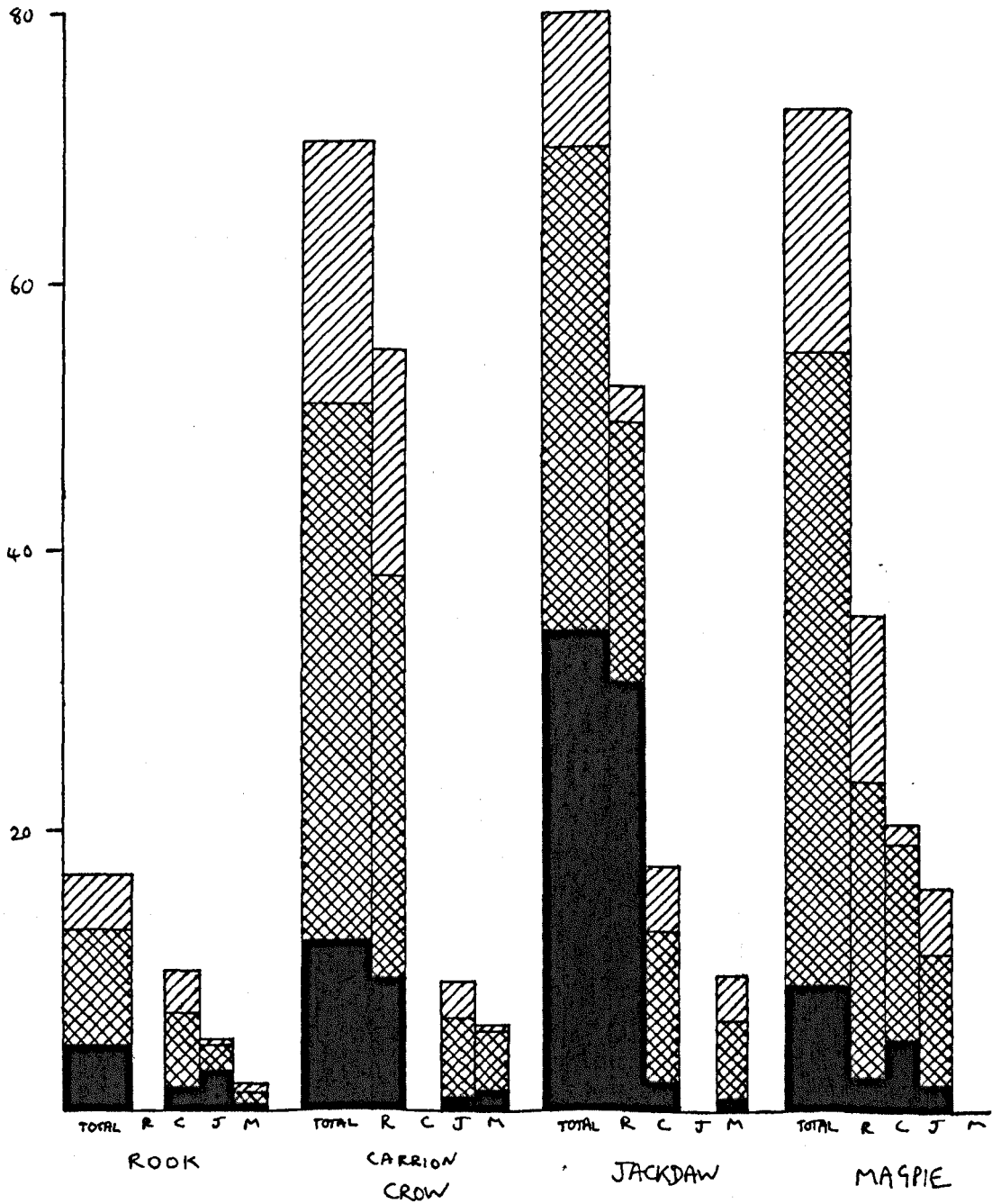ROOK   CARRION   *JACKDAW   MAGPIE
                  CROW

IMPACT OF EACH OF 3 OTHER SPECIES, AND THEIR TOTAL
IMPACT (SMALL LETTERS), ON EACH OF 4 CORVID SPECIES (LARGE LETTERS)

(b)

"ECOLOGICAL IMPACT" ($L = \alpha \times$ ABUNDANCE $\times$ MEAN PREY INTAKE RATE)

TOTAL R C J M — ROOK
TOTAL R C J M — CARRION CROW
TOTAL R C J M — JACKDAW
TOTAL R C J M — MAGPIE

IMPACT OF EACH OF 3 OTHER SPECIES, AND THEIR TOTAL IMPACT (SMALL LETTERS) ON EACH OF 4 CORVID SPECIES (LARGE LETTERS)

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. Morse 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 (Morse 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 com-

petition is of limited importance in this guild.

Various evidence has been presented to show how mag-

pies, 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.

Feare (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 (Feare 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

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 suggest-

ing 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 loca-

tions 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.

The data in Feare et al's (1974) study in Aber-
deenshire 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.

Hogstedt (1980b) showed that in the breeding season
magpies and jackdaws overlapped by only 0.54 in the taxo-
nomic 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 jackdaws 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 propor-
tion 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 inter-
specific aggression between carrion crows, rooks and jack-
daws 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 respec-
tively were able to feed on artificially provided dense
clumps of non-invertebrate food.

Higuchi (1979) reported that jungle crows (Corvus
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 occu-
pied 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 Bossema 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 sup-
ported 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.   Baeyens (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 organisa-

tion 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 sub-surface 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.