

ON THE SOCIAL AND GENETIC COMPOSITION  
OF  
ROOK CORVUS FRUGILEGUS AND JACKDAW C. MONEDULA  
FLOCKS.

A thesis submitted for the degree of  
Doctor of Philosophy

Ian George Henderson  
Department of Zoology  
University of Leicester

1989

UMI Number: U018271

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI U018271

Published by ProQuest LLC 2015. Copyright in the Dissertation held by the Author.  
Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against  
unauthorized copying under Title 17, United States Code.



ProQuest LLC  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106-1346



X751537461

## ACKNOWLEDGEMENTS

This research was supported by a grant gratefully received from Science and Engineering Research Council.

The number of people deserved of thanks is enormous and includes most folks that I met over the last 3½ years. In a professional context I wish to thank Professor H.C Mcgreggor and all at the Department of Zoology, Leicester, and especially my supervisor Dr Paul Hart for being helpful and accommodating throughout my research. Frank Clark and Steve Ison deserve special mention for showing me the ropes and I am grateful to Mike Bruford and his patience in teaching me 'fingerprinting for a hobby' and likewise, to Elaine Cairnes'.

I am also grateful to Terry Burke, Ian Owens, Ian Hartley, Sean 'O' Malley and Olivier Hanotte for invaluable and much needed discussion, and the lone pipe of Des Thompson for his characteristic enthusiasm and encouragement. Dr John Bullock and John Beckett willingly provided statistical and computational assistance, and I thank Richard Waite for readily providing corvid information. Andy Village gave me a free demonstration of bird tagging and Jeff Kew's Wash Wader Ringing Group deserve special mention for three very frustrating cannon net sessions.

The farmers of Sludge Hall, Cold Newton Grange and Quenby Lodge deserve thanks for allowing me access to their land

and in this respect I am most grateful to the past (Mr and Mrs Bennion) and present (Mr and Mrs Martin) owners of Billesdon Coplow Lodge for tolerating my continued intrusion. And many thanks to the Leicester Ornithological Society corvid counters who willingly braved the rain on my behalf.

In a more domestic context, I must extend my thanks to the backup squad, including many fine right arms (and some of the legs weren't bad either).

Firstly, cheers Pete & Lian, Andy, Anne & Katy, and Speed. Cheers Colser, Eliot, Steph, John, Faz, Ian, Sean, Mike, Alistair, Hari and Janet. Thanks David for Kenya and thanks Andy and Andy for discussing big bangs, binary star systems (not to mention G5 main sequence dwarfs) and the merits of Jackie Daniels (famous inside right). My brothers and sisters deserve special mention för being good fun, as do all the family for their support.

### ENGLAND

SWEET changing Seasons! Winter cold and stern,  
Fair spring with budding leaf and opening flower,  
And Summer when the sun's creative power  
Brings leafy groves and glades of feathery fern,  
The glorious blossom of sweet scented May,  
The flowery hedgerows and the fragrant hay,  
And the wide landscape's many tinted sheen.  
Then Autumn's yellow woods and days serene;  
And when we've gathered in the harvest's treasure,  
The long nights bring us round the blazing hearth,  
The chosen haunt of every social pleasure.  
Land of green fields and flowers! Thou givest birth  
To the shifting scenes of beauty, which outshine  
Th' unvarying splendours of the Tropic's clime.

Alfred Russel Wallace 1878

For Mum and Dad

## CONTENTS

List of figures	i
List of tables	vi
List of plates	ix
List of appendices	x
<b>GENERAL INTRODUCTION</b>	<b>1</b>
<b>Theoretical background</b>	<b>1</b>
Improved foraging efficiency	2
Improved predator awareness	4
Dispersion	5
Genetic composition	7
Cause and consequence	8
<b>The study</b>	<b>9</b>
Study components	10
i) Interspecific association	11
ii) Intraspecific competitiveness	12
iii) Group kinship	13
<b>The species</b>	<b>16</b>
Evolutionary history	16
Behavioural properties	19
Species description	20
Rook literature précis	21
Jackdaw literature précis	27

<b>1 GENERAL METHODS AND MATERIALS</b>	<b>29</b>
1.1 The study site and habitat	29
1.1.1 The study area	29
1.1.2 The roost	29
1.1.3 The study site	32
1.2 Trapping, tagging and bleeding	34
1.2.1 Trap construction and use	34
1.2.2 Individual marking and recognition	36
1.2.3 The removal of blood samples	40
1.3 Nestbox construction and positioning	41
1.4 Data collection	43
1.4.1 Circuit recording	43
1.4.2 Focal bird sampling	45
1.4.2.1 Continuous sampling	49
1.4.3 Scan sampling	49
1.5 Recording methods	50
1.6 Statistical methods	50
 <b>2 DNA FINGERPRINTING - PROCEDURE</b>	 <b>53</b>
2.1 Introduction	53
2.2 Detailed procedure	55
2.2.1 DNA preparation	55
2.2.1.1 DNA extraction from red corpusles	55
2.2.1.2 DNA concentration and condition determination	57
2.2.1.3 Restriction digestion	58
2.2.2 Fingerprint preparation	61
2.2.2.1 Gel electrophoresis	61

2.2.2.2 Southern Blotting	61
2.2.3 Probing	66
2.2.3.1 Preparation	66
2.2.3.2 Pre hybridisation	68
2.2.3.3 Hybridisation	70
2.2.3.4 Nylon filters	71
2.3 Analysis	72
2.3.1 Scoring bands	72
2.3.2 Segregation analysis	73
2.3.3 Acquiring jackdaw families	78
 3 DIURNAL HABITS, HABITAT USE AND SEASONAL VARIATIONS	 79
3.1 Introduction	79
3.2 Dispersion and philopatry	79
3.2.1 Empirical data	79
3.2.2 From the literature	81
3.3 Population estimates	84
3.3.1 Observations	84
3.3.2 The Lincoln capture/mark/recapture index	85
3.3.2.1 Procedure	85
3.3.2.2 Assumptions	86
3.3.2.3 Justification	87
3.3.2.4 Conclusion	88
3.4 Winter diurnal activity	89
3.4.1 Procedure	89
3.4.2 Results	91
3.4.3 Resumé of daily activity	93
3.4.3.1 Assemblies	93



3.4.3.2 Foraging	94
3.4.3.3 Flock dynamics	95
3.5 Winter habitat use	98
3.5.1 Procedure	98
3.5.2 Results	99
3.6 Seasonal variations in flock size and composition	103
3.6.1 Flock size	103
3.6.2 Breeding season	105
3.6.3 Summer	109
3.6.4 Late summer and autumn	110
3.7 Functional flocks	110
3.7.2 Evidence for 'information centres'?	111
3.7.2.1 Rook foraging return times	111
3.8 Summary	114
 4 INVERTEBRATE PREY DISTRIBUTION AND ENERGY CONTENT	 115
4.1 Introduction	115
4.2 Soil invertebrate analysis	115
4.2.1 Sampling	115
4.2.2 Preparation and classification	117
4.2.3 Energy evaluation	121
4.2.4 Vertical distribution	123
4.2.5 The effects of temperature	126
4.2.6 The effects rainfall	127
4.3 Prey availability	127
4.3.1 Flock size	127
4.3.2 Rook age distribution	129
4.4 Summary	129

<b>5 INTERSPECIFIC ASSOCIATIONS</b>	<b>132</b>
5.1 Introduction	132
5.2 Frequency of association	133
5.3 Social attraction	135
5.3.1 Intra flock species distribution	135
5.3.1.1 Results	138
5.3.2 Index of interspecific mixing	141
5.4 Foraging niches	145
5.4.1 Niche overlap	147
5.4.1.1 Results	148
5.4.2 Competition free overlap	148
5.4.2.1 Results	149
5.4.3 Conclusion	150
5.5 Resource distribution	153
5.5.1 Soil analysis	153
5.5.2 Temperature	155
5.6 Interference	157
5.6.1 Published information	157
5.6.2 Empirical information	159
5.6.3 Conclusions	159
5.7 Vigilance	162
5.7.1 Overall flock vigilance	162
5.7.2 Intraspecific vigilance	164
5.7.3 Interspecific vigilance	164
5.7.3.1 Percent time spent vigilant	164
5.7.3.2 Flock proportions	164
5.7.3.3 Vigilance rates	166
5.7.3.4 Response times	166

5.7.4 Vigilance conclusion	167
5.7.5 Consequences	167
5.9 Experimental tests	168
5.10 Discussion	170
 <b>6 AGE RELATED FORAGING STRATEGIES</b>	 <b>173</b>
6.1 Introduction	173
6.2 Methods	175
6.2.1 Field identification	175
6.2.2 Procedure	177
6.2.3 Prey identification	179
6.2.4 Evaluation of errors	180
6.3. Results	182
6.3.1 Individual time budgets	182
6.3.2 Prey choice	185
6.3.3 Handling times	192
6.3.4 Prey intake rates (PIR)	192
6.3.5 Feeding success	194
6.3.6 Résumé	196
6.4 Energy assimilation and expenditure	196
6.4.1 Intake	196
6.4.2 Energy requirements	198
6.4.3 Net intake	199
6.4.4 Energy intake and flock size	202
6.5 Immatures dispersion	205
6.6 Discussion	205

<b>7 THE GENETIC AND SOCIAL STRUCTURE OF JACKDAW FLOCKS</b>	<b>210</b>
7.1 Introduction	210
7.2 Colonial relatedness	212
7.2.1 Procedure	212
7.2.2 Overall results	213
7.2.3 Sex differences	215
7.2.4 Conclusion	215
7.3 Intra colonial flock composition	215
7.3.1 General procedure	215
7.3.2 Intra flock co-occurrence	218
7.3.3 Overall results	218
7.3.4 Sex differences	218
7.3.5 Close co-foraging	221
7.3.5.1 Analysis	221
7.3.5.2 Close co-foragers	223
7.3.5.3 Female/female band sharing	226
7.3.5.4 Male/female relatedness	227
7.3.5.5 Male/male relatedness	228
7.4 Conclusions	228
7.5 Discussion	231
7.5.1 Hypothesis	234
<b>8 BREEDING BEHAVIOUR</b>	<b>236</b>
8.1 Introduction	236
8.2 Nestbox aquisition	236
8.2.1 Nestbox success	236
8.2.2 Nest site competition	237

8.3 Colony composition	239
8.3.1 Age structure	239
8.3.1.1 Identification	239
8.3.1.2 Breeding age	240
8.3.2 Occupation of traditional nest sites	241
8.3.3 Conclusions	241
8.4 Breeding success	241
8.5 Male foraging ability	245
8.5.1 Background	245
8.5.2 Hypothesis	246
8.5.3 Procedure	246
8.5.5 Results	247
8.6 Mate guarding	250
8.6.1 Background	250
8.6.2 Procedure	250
8.6.3 Results	251
8.7 General discussion	253
 9 SEXING JACKDAWS	 257
 9.1 Introduction	 257
9.2 Discriminating features	257
9.3 Biometrics	258
 10 SUMMARY	 262
 APPENDICIES	 272
 BIBLIOGRAPHY	 303

## LIST OF FIGURES

### GENERAL INTRODUCTION

A	The evolutionary divergent history of the Corvidae	18
B	The distrbution of rooks in Britain	22
C	The distribution of jackdaws in Britain	23

### CHAPTER 1

1.1	Location of the study area within Britain.	30
1.2	Map of the study area.	31
1.3	Trap design and dimensions.	34
1.4	The design and positioning of wing tags	37
1.5	Nestbox design.	42
1.6	Nestbox positioning.	44
1.7	The change in behavioural variance in relation to focal bird sample times.	46

### CHAPTER 2

2.1	Diagrammatic representation of minisatellite structure.	54
2.2	Human minisatellite probe 33:15.	54
2.3	Diagrammatic representation of the DNA fingerprinting procedure.	56
2.4	Process of Southern blotting.	64
2.5	Configuration of DNA sugar-phosphate polynucleotide.	65

2.6	Cloning and isolation of human minisatellite probe.	67
2.7	Diagrammatic representation of band linkage, allelism and homozygosity.	74

### CHAPTER 3

3.1	Percentage occurrence of tagged jackdaws in three regions of the study area.	80
3.2	Distribution of tag records about the study area.	83
3.3	Behavioural event categorisation for individual birds (§ 1.4.2) and for flocks.	90
3.4	The mean diurnal partitioning of time by mixed flocks of rooks and jackdaws.	92
3.5	Diurnal variation in size of mixed-species flocks of rooks and jackdaws.	96
3.6	Simultaneous short term variations in flock size following the initial post-dawn build up.	97
3.7	Utilisation of farmland by flocking corvids.	101
3.8	Seasonal variation in the use of arable land.	104
3.9	Seasonal changes in the utilisation of fields by rooks.	106
3.10	Seasonal variation in flock size and composition.	108
3.11	Groups size distribution of rooks departing from and returning to the rookery on foraging forays.	113

### CHAPTER 4

4.1	Diagrammatic representation of invertebrate soil sampling.	116
-----	--	-----

4.2	Berlese-Tullgren funnel extraction.	118
4.3	Variation in dry weight and unit energy content of earthworms, as a function of earthworm length.	122
4.4	The vertical distribution of invertebrate abundance and energy content within 5cm deep core samples.	124
4.5	The regression of invertebrate energy content and biomass on flock size.	128
4.6	Earthworm biomass with respect to adult and immature foraging positions.	130

## CHAPTER 5

5.1	Percentage of flocks comprising mixed species, and single species only.	134
5.2	Breakdown of single species flock sizes into flock size classes.	136
5.3	Regression of jackdaw numbers on rook numbers in mixed species flocks.	137
5.4	The percentage of rooks or jackdaws foraging and landing in the vicinity of conspecifics.	139
5.5	A diagrammatic representation of the probability of obtaining rook/jackdaw combinations in mixed flocks of faithful rook (RR) and jackdaw (JJ) pairs.	140
5.6	The winter diet of rooks and jackdaws.	146
5.7	Comparing the major winter food items of rooks and jackdaws.	152
5.8	Rook and jackdaws numbers as a function of biomass in the top 2cm of soil.	154
5.9	The variation of potential rook and jackdaw food	



resources in the top 2cm of the soil.	156
5.10 Intra and interspecific interference in and between rooks and jackdaws.	160
5.11 Comparison of three components of rook and jackdaws vigilance.	165

## CHAPTER 6

6.1 Facial characteristics of rooks in relation to age, and the wing feather sequence.	176
6.2 Comparing the facial characteristics of young rooks and carrion crows.	178
6.3 Regressions of % time spent feeding in adult and immature rooks.	184
6.4 a) encounter rate and b) the % time spent looking up in adult and immature rooks in three flock size classes.	187
6.5 a) Handling time and energy content, b) prey profitability and c) unit handling time per second as functions of earthworm length.	188
6.6 Comparing rook earthworm size selection with a) availability in the soil, and b) in relation to flock size.	191
6.7 The differences between adult and immature rooks in their prey a) handling times, and b) intake rates. c) illustrates the trade off between a) and b).	193
6.8 a) Gross energy intake, b) adult immature ratio and c) immature numbers in relation to flock size.	204

6.9	A diagrammatic representation of the costs/benefit pay-offs to adult and immature rooks as a function of flock size.	208
-----	--	-----

## CHAPTER 7

7.1	Dendrogram of most frequently and least frequently recorded co-foraging jackdaws.	220
7.2	Dendrogram representing the 15 most closely co-foraging jackdaws from 144 flocks.	222
7.3	Compostite summary graphs of band sharing levels.	229

## CHAPTER 8

8.1	Clutch, hatching and fledgling success of seven breeding males compared with male foraging return times.	249
8.2	Mean distance between the male and female jackdaws at three points before, during and after the females 'receptive' period.	252

## CHAPTER 9

9.1	The comparison of male and female jackdaws for five biometric parameters.	259
9.2	The discriminant analysis of male and female jackdaws on the basis of wing and tarsus length.	260

## LIST OF TABLES

### CHAPTER 2

- 2.1 Segregation analysis of single fragment paternal hypervariable loci in a family of jackdaws (male and 3 offspring). 77

### CHAPTER 3

- 3.1 The mean winter 24 hour partitioning of time by mixed flocks of rooks and jackdaws. 92
- 3.2 Agricultural land usage as a proportion of the study area and corvid flock usage within the same area, over a two year period. 100
- 3.3 The percentage distribution of group sizes among rooks departing from and returning to the rookery during foraging forays. 113

### CHAPTER 4

- 4.1 Unit energy values of earthworm size classes with full gut contents and emptied gut contents. 120
- 4.2. Spearman rank correlations ( $r_s$ ) between earthworm quantity and quality (energy) with respect to other miscellaneous invertebrates. 125

## CHAPTER 5

- 5.1 The nearest neighbours of both foraging and incoming rooks and jackdaws amongst mixed species flocks. 139
- 5.2 A summary of the progression through Busse's (1977) formula for calculating interspecific mixing within foraging flocks of rooks and jackdaws. 144
- 5.3 Overall flock vigilance in foraging rooks. 163

## CHAPTER 6

- 6.1 Error accumulated while attributing lengths of string to five length classes: simulating observer error in field prey length identification. 181
- 6.2 Spearman rank correlations ( $r_s$ ) relating the time spent on specific behavioural activities to flock size, in foraging rooks. 183
- 6.3 Regression coefficients (b) and t-test values (t) comparing the relationship between 'percent time spent feeding' and flock size in adult and immature rooks. 186
- 6.4 Earthworm soil abundance and selection by foraging rooks. 190
- 6.5 Handling times, feeding rates, success rates and the ratio of adult and immature rooks in relation to flock size. 195
- 6.6. Estimated winter 24 hour energetic\* intake and expenditure of free living adult and immature rooks

at 0°C (mean day length of 9.5 hrs).	201
6.7 The relative proportional gross energy intakes of adult and immature rooks in small medium and large flock sizes.	203

## CHAPTER 7

7.1 Mean (%) fingerprint band sharing a) in two populations of jackdaws and b) in flock foraging jackdaws.	216
7.2 Analysis of mean DNA fingerprint band sharing in closely affiliating, foraging jackdaws.	224

## CHAPTER 8

8.1 Jackdaw population breeding data for two seasons, 1987 and 1988.	242
8.2 Mean return rates and the corresponding clutch successes of seven breeding male jackdaws.	248

## LIST OF PLATES

### CHAPTER 1

1.1	Corvid roost, Billesdon Coplow.	33
1.2	Study site, the rookery at 'Tom Spinny'.	33

### CHAPTER 2

2.1	Concentration and condition analysis of a) genomic DNA and b) restriction digested DNA.	59
2.2	DNA fingerprint gel after 28 hours @60 volts.	62
2.3	Autoradiograph of isolated $^{32}\text{P}$ labelled probe following electrophoresis through a 0.6% agarose gel @100 volts for ~1½ hours.	69
2.4	DNA fingerprint of a male jackdaw and 3 offspring.	76

### CHAPTER 7

7.1	DNA fingerprints of, a) arbitrarily selected jackdaws from two separate colonies and b) co-flocking jackdaws from the Billesdon colony.	214
7.2	DNA fingerprint of close co-foraging jackdaws.	225

### CHAPTER 8

8.1	DNA fingerprint of a female and three offspring, the third offspring shares relatively few bands with the sibship.	255
-----	--	-----

## LIST OF APPENDICIES

### A (Chapter 1)

Tagging practicalities	272
i) Bird welfare	272
ii) Practicalities	273
iii) Selection for or against tags	273

### B (Chapter 2)

Table 1 The pairwise band sharing coefficients $x$ of one parent and three offspring.	274
--	-----

### C (Chapter 3)

Table 1 Daily activity.	275
Table 2 Early morning, and evening (pre roost) corvid assemblies.	276

### D (Chapter 4)

Table 1 Earthworm dry weights.	277
Table 2 Handling times (seconds).	278
Table 3 Invertebrate biomass (wet weight)/m <sup>2</sup> of from soil samples.	279
Table 4 Soil sampling data.	280

## **E (Chapter 5)**

Table 1 Winter foraging niche overlap of rooks (RK) and jackdaws (JD).	281
Table 2 Jackdaw time budget data.	282

## **F (Chapter 6)**

Table 1 Adult time budget data.	284
Table 2 Immature time budget data.	288

## **G (Chapter 7)**

Table 1 Band sharing data for Plate 7.1a.	291
Table 2 Tag record matrix of close co-foragers.	293
Table 3 Mean intra colony band sharing, plate 7.1b.	295
Table 4 Plate 2 close co-foragers.	296

## **H (Chapter 8)**

Table 1 Breeding success at Tom Spinny for two consecutive seasons.	297
Table 2 Male jackdaw return times to nestboxes when feeding incubating females (minutes).	298
Table 3 Male/female distance (at nestsite) in metres at 10 minute intervals.	299



## I (Chapter 9)

Table 1 Band sharing analysis for Plate 8.1.	300
Table 2 Tagged jackdaw biometrics	300

## GENERAL INTRODUCTION

Modern evolutionary theory accepts that natural selection (Darwin 1889) favours individuals that maximise their reproductive contribution to future generations. Thus, it has become established to express group behaviour in terms of the per capita costs and benefits that effect individual inclusive fitness (Hamilton 1964). Inclusive fitness encompasses the reproductive potential, not only of the individual under scrutiny but of all other individuals that are related to the first, relative to all individuals that are unrelated to the first (see Grafen 1984). In other words the reproductive potential includes all those individuals that share genotypic traits with the first. In consequence, flocking individuals may tolerate exploitation by conspecifics when the observer might expect otherwise, especially where conspecifics are close kin.

The decisions made by individuals are paramount to our continued understanding of grouping behaviour and social evolution. The objectives of this study were therefore to identify competitive heterogeneity (Barnard 1978; Caraco 1979; Rohwer and Ewald 1981) within flocks of rooks and jackdaws, from which the adaptive function of flock foraging may be explained in terms of subsequent individual decisions.

## Theoretical background

A great deal of attention has been attributed to the evolutionary function of flocking in birds (e.g.. Wynne-Edwards 1962; Crook 1965; Krebs et al 1972; Krebs 1974; Barnard 1980; Caraco and Pulliam 1980; Caraco 1981), for which the two major benefits are considered to be,

- i) improved foraging efficiency and/or
- ii) improved predator awareness and avoidance.

### *Improved foraging efficiency*

Patchy, transient food resources are located more efficiently by foraging groups than solitary individuals, because by chance, groups are more likely to locate ephemeral food reserves than single animals (Caraco 1979). Krebs et al (1972) and Krebs (1974) demonstrated that great tits *Parus major* and great blue herons *Ardea herodias* respectively, were able to improve their exploitation of unpredictable food reserves, when foraging in groups. However, foraging improvement relied upon the ability of individuals to receive and utilize information from conspecifics, and to subsequently be attracted to a discovered food patch ('local enhancement', Thorpe 1963). One extreme manifestation of local enhancement was the 'Information centre hypothesis' proposed by Ward (1965) and Ward and Zahavi (1973). The

Information centre hypothesis suggests that assemblies of animals, such as bird roosts and colonies, allow unsuccessful foragers to identify successful foragers so that the former may follow the latter to better foraging sites on future forays. The hypothesis is intuitively attractive, and there is evidence for its functional value (e.g. Krebs 1974, Andersson et al 1981, DeGroot 1980; McCracken and Bradbury 1981, Greene 1987). For a variety of reasons, the hypothesis is notoriously difficult to test (Bayer 1982; Elgar and Harvey 1987; Mock et al 1988). The inability to demonstrate that a previously unsuccessful individual gains a net advantage, as a result of following a successful animal, is perhaps the most difficult aspect to verify.

It is possible that successful foragers have little choice than to accept exploitation, as a delay in foraging may be costly to competitively successful foragers. They might also lose the protection of the flock that is normally afforded to them (see following section). Alternatively, previously unsuccessful foragers, would seem to have much less to lose by delaying their departure and biding their time.

Whatever the outcome, the information centre debate clearly demonstrates that in flocking systems costs are introduced, and that the discovery of a food patch by one individual may result in exploitation by other group members.

#### *Improved predator awareness*

That flocking can operate as an anti-predator strategy for avoiding or detecting predators, has been demonstrated on several occasions (e.g. Pulliam 1973; Powell 1974; Lazarus 1979). For example, woodpigeons *Columba palumbus* were clearly shown to respond more quickly to the attacks of goshawks *Accipiter gentilis* when foraging in larger groups (Kenward 1978). Meanwhile, Lazarus (1979) showed that larger flocks of quelea *Quelea quelea* responded more quickly than smaller flocks, both to the approach of a predator, and to an artificial alarm stimulus.

Such early detection of predators is now recognised as a consequence of increased overall flock vigilance with increased flock size, despite a simultaneous decrease in the per capita costs of vigilance (Hoogland 1979; Barnard 1980).

Hamilton (1971) proposed that many groups act as 'selfish herds', where individuals attempt to place as

many others between themselves and potential predators as is possible. Individuals vie for central positions within the groups, and as peripheral flock positions are more exposed to predators than central ones, vigilance rates vary accordingly (Jennings and Evans 1980). Not every individual secures advantages to the same degree, though each may try to maximise their energetic intake relative to the vigilant constraints placed upon them. The result is inevitably a trade off between the need to forage and the need for alertness.

### *Dispersion*

Cost /benefit compromises highlighted above, are familiar features of flock foraging (and indeed all biological systems) (Caraco 1979). The net benefits accrued by individuals affect the fitness and decisions of others, and ultimately the distribution of individuals within the habitat. Hence individual decisions are not independent of other participants, but continually vary relative to them.

That the subsequent decisions of foraging birds (according to the presence of others) could influence group composition and dispersion was illustrated theoretically by Fretwell (1972). Fretwell proposed that for two habitats of unequal quality (A= superior, B= inferior) individuals will continue to land and forage at A until, because of increased density and interference,

the quality of  $A = B$ , and the fitness of the next bird to land will be equal on whichever patch it chooses. Finally, one more individual appears and lands at B as the quality  $B > A$ . The net fitness of the individual at B is equal to each of those at A, while the fitness of the first bird to arrive at A declined to the mean level. As no individual could now improve its fitness by switching patch, the distribution assumed that of an ESS (Evolutionary Stable Strategy, Maynard-Smith 1974).

Fretwell's (op cit.) model was termed the 'ideal free distribution' because it assumed that individuals were free to choose between patches. Some studies have demonstrated that animals may distribute themselves according to the ideal free distribution (e.g., Harper 1982), although others have found discrepancies consistent with the idea that individuals must sample patches before decisions are made (Milinski 1984; Inman pers. comm.).

Certainly, some flocking costs are associated with intraspecific interference, as has been demonstrated in various wader species (charadriiformes). For example, Goss-Custard (1976) showed that disturbance of prey by foraging redshanks *Tringa totanus* significantly reduced the prey intake rates at high flock densities.

Oystercatchers *Haematopus ostralegus* too were subject to lower prey intake rates due to mutual interference (Vines 1980; Goss-Custard et al 1983a&b; Sutherland and Koene 1982), while in other wader species, prey depletion

and reduced prey intake rates were further costs of increased flock density (Goss-Custard 1985).

However, in only a few cases has it been demonstrated that intraspecific interference significantly alters the foraging distribution and composition of flocks (Ulfstrand 1979; Goss-custard and Durell 1981, 1983a). Thus it was of interest to know whether such interference was significant in promoting the dispersal of young.

#### Genetic composition

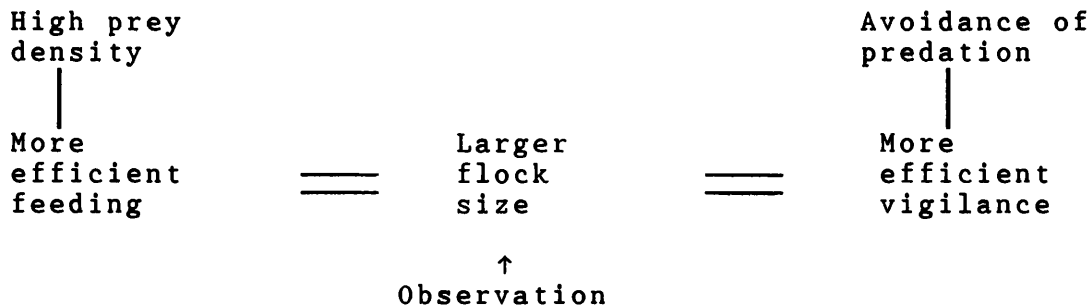
Many of the social ties and constraints that an individual bird must consider before joining a group, may not be immediately detectable. One such component, that has not received so much attention, is that of the genetic composition of flock groups. In contrast to the agonistic behaviour discussed above, kin selection may be important in retaining immature flock members, which because of their ties with parents and close kin, are afforded greater tolerance, and succumb to a lower than average rate of interference. In social systems where altruistic foraging behaviours are adaptively favoured, kinship can be expected to flourish and form a major part of the social matrix (Dawkins 1979). This is because altruistic strategies will invade a population of passive flock foragers, as in the long term, the former will benefit from the general flock strategy as well as from their own altruistic investment. Non altruists will subsequently accrue fewer benefits than altruists and



support less viable offspring than the latter. However, the question remains as to whether kinship and intra flock relatedness are an advantage in the first place?

### Cause and consequence

There are problems in trying resolve the causal and consequential mechanisms of behavioural systems because not all behavioural traits may have selective value (Gould and Lewontin 1976). Some traits may appear as a consequence of selection for more fundamental requirements. For example, foraging efficiency can increase in flocks as a result of either increased prey density or because of decreased per capita vigilance.



Both effects vary concurrently and result in similar consequential observations. That is, that larger flocks are selected for on both counts.

Thus, it is often difficult to ascertain the true evolutionary causes of the flock development because it happened at a time in the past. However, one can throw

some light on the matter by isolating the factors which still maintain flock form and function. The following questions therefore formed the basis of the thesis.

1) Did intra (or inter) specific competition exist in and between such highly social species as rooks and jackdaws and if so did it truly affect flock composition?

2) Was there a significant genetic component required for the maintenance of the flock structure.

### **The study**

In the first field season I experienced considerable difficulties in trapping a large enough sample of rooks to enable sufficient data to be collected, to formulate accurate foraging relationships, and more importantly to identify individual differences in competitive ability. A further problem was acquiring enough offspring to implement rigorous DNA fingerprinting segregation analysis (explained in section 2.6). During the approach to the spring of 1987, after having spent much of the winter trying to improve rook trapping results, I decided to switch emphasis towards jackdaws.

Jackdaws were advantageous in that their nests were often more accessible than those of rooks, while their semi-colonial nature would save time when searching for nests. However, having realised that the breeding rook

colony was host to many jackdaws I suspected that a nestbox scheme might also be feasible. This proved to be the case, and with the breeding colony established and a centre for activities, jackdaw trapping was completed with much greater success than before.

In consequence, I used one or the other of the species to investigate different principles in flocking behaviour. It was therefore necessary to look at the relationship between the two species in some detail and to formulate an opinion on the justification of extrapolating principals across from one species to the other. In the event, the inclusion of interspecific information proved invaluable by providing comparative explanations for flocking associations, without need or cause to revert to genetic or altruistic explanations.

### *Study components*

Prior to the main body of work general aspects of the study population are discussed, along with the techniques used to acquire more specific information. The investigation subsequently revolves around three basic components that analyse aspects of social behaviour across inter and intraspecific flock mechanisms. The study format is therefore arranged as follows:

- i) Background information.
- ii) Interspecific association.
- iii) Intraspecific competition.

iv) Intraspecific genetic composition.

1) Interspecific association

Despite their familiarity, at present there is no clear evidence indicating the precise ecological forces responsible for the maintenance of rook/ jackdaw aggregations. Tentative explanations have been suggested, that include the ability of jackdaws to dilute the harrying, agonistic attentions of carrion crows (Röell 1978; Waite 1984a). Territorial carrion crows *Corvus corone* L. did habitually disturb corvid flocks (Röell 1978; Waite 1984a; pers. obs.), perhaps because the latter represented a competitive cost on the territory. However, this subtle modification of the 'dilution affect' (Hamilton 1964) did not explain heterospecific, as opposed to monospecific, aggregations.

Other investigations of mixed species flocking have shown that increased vigilance is often afforded to one species by another (Barnard and Stephens 1983; Barnard and Thompson 1985; Henderson In press) and can play a significant role in the readjustment of the time budget, by providing more time for other activities.

As in single species flocks, a species may also be drawn to new feeding areas by heterospecifics (Krebs 1973; Barnard and Stephens 1983) or the disturbance of prey by one species might increase prey availability to a second (Morse 1978; Rubenstein et al 1977).

Alternatively costs may be associated with significant interspecific niche competition. To this effect Högstädt (1980) demonstrated that the presence of jackdaws significantly reduced reproductive success of local magpies *Pica pica*. However, despite some claims (Lockie 1956; Höglund 1986), significant levels of inter specific aggression have never been shown to exist between rooks and jackdaws. Furthermore, while niche dimensions have been investigated on the basis of micro-habitat requirements (Loman 1980; Waite 1984) and morphological similarities and differences (Olsson and Persson 1979), strict quantitative comparison of the diets of the two species has not yet been made. This fundamental aspect of their ecology was subsequently investigated in this study.

#### ii) Intraspecific competitiveness

Since jackdaw foraging behaviour closely resembled that of rooks, many original features of the investigation could be continued. However, jackdaws selected prey that was small and difficult to identify from field observations. Thus, while feeding rates were calculable, reliable estimates of energy intake would have been difficult to formulate.

For the sake of studying energy budgets, I continued instead, to monitor prey selection in rooks. But, rather than compare individually tagged birds, I decided to

exploit the easily identifiable differences in age to investigate age related decision rules. Since this work was implemented from the beginning of the study it seemed economical to continue to utilise already acquired data. As the success or failure experienced by immature animals may determine the future structure of the social group (Goss-Custards and Durell 1981) this point was also investigated.

The manner in which adults and immatures acquired food was assessed by estimating energetic accumulation and expenditure of both parties. Energy intake evaluations were based on techniques used by Barnard and Stephens (1983) and Barnard and Thompson (1985), by assessing prey size according to length relative to the birds bill. Such estimations were to some extent crude, but it is hoped that good comparative information was acquired.

### iii) Group kinship

One of the factors central to the theme of social behaviour and the evolutionary development of social communities is kin structure. Many of the apparent costs associated with group foraging (intraspecific competition and interference) might well be explained in terms of inclusive fitness so that successful foraging individuals tolerate exploitation by related subordinates. However previously, kinship has been difficult to study in field

situations because years of study were required to follow the fate of known offspring within the population. Even then, true parentage was not certain. Recently though, developments in DNA fingerprinting have meant that these problems can be solved.

The human minisatellite probes were originally developed (Jeffrey et al 1985a) to indentify multiple minisatellite loci (see Chapter 2) for tracing human parental lineages. Since then Burke and Bruford (1987) were able to demonstrate that these same human probes could also be used successfully to study relatedness in a variety of bird species. This success was then, supported by a demonstration of the applicability of the technique to investigate aspects of social behaviour in birds. Thus, Burke and Bruford (op. cit.) were able to show that from a family of house sparrows *Passer domesticus* (male, female and eleven offspring) one offspring deviated from the expected probability of band sharing on the paternal side. This enabled them to conclude that the putative male was not the biological father of that offspring and that the most likely explanation was that a second male had successfully copulated with the present female.

The power of DNA fingerprinting to disentangle the complexities of avian mating systems was further demonstrated in a study of the dunnock *Prunella modularis* (Burke et al 1989). The dunnock has a variable mating system comprising monogamous, polygynous and polyandrous combinations, depending upon habitat and resource quality

(Davies 1985). Burke et al (1989) were able to show that in polyandrous situations, of the two males present, the most dominant (alpha) sired a slightly greater proportion of offspring, than the subdominant male (beta). However, both males continued to feed offspring regardless of whether they were the biological father or not, so long as each male had copulated with the female. If for example, the  $\beta$  male failed to copulate with the female then he invested no further effort in the offspring. Male nestling investment was therefore judged according to female access and the chance that some nestlings were his. Females meanwhile had a higher reproductive success when two males fed the brood, and so, encouraged the  $\beta$  males to mate.

Hence the power of DNA fingerprinting to unravel complex kin relationships and add rigorous quantification of reproductive success to field studies could hardly be overstated.

Nevertheless, real limitations to the technique exist, and need to be appreciated (but see Chapter 2 for a more thorough account).

Though multilocus DNA fingerprinting is very powerful at identifying the parentage of closely related individuals (siblings and offspring) it does not have the power to discriminate between less closely related individuals such as cousins and half siblings. This is because, as the level of relatedness decreases, there is an increased likelihood that the fingerprint band



pattern could have occurred simply by chance mutation, because fewer matching minisatellite loci are involved. Thus the chance of misidentifying a closely related pair of individuals is less than one percent, whereas similar misidentification of half relatives is of the order of 50% (Brookfield pers. comm.).

However, DNA fingerprinting can be used to investigate relative interrelatedness of selected groups (such as within flocks). Thus, by random comparison of fingerprints one can establish mean population levels of relatedness, against which, selected groups within the population can be statistically compared for higher than average levels. Significance then relies on group sample size and the level variance of intra group 'relatedness'.

### **The species**

#### **Evolutionary history**

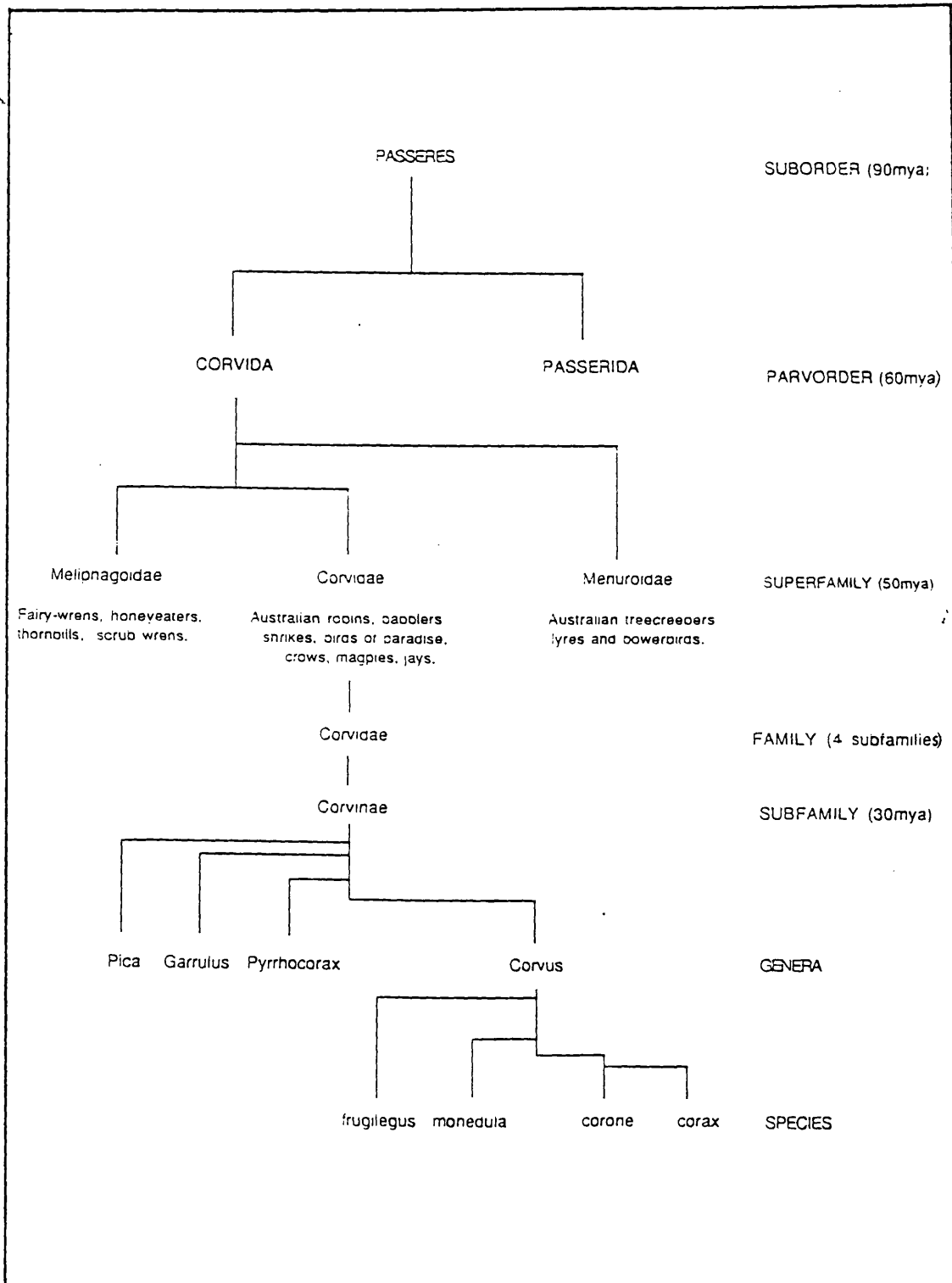
Recent DNA-DNA hybridisation studies (Sibley and Alquist 1986) suggest that the Corvida (a large group of families including flycatchers, warblers, and thrushes) had evolved some 55 million years ago (55 mya) in parallel with similar Afro-Eurasian passerine groups (Sibley and Alquist 1982; Sibley and Alquist 1986). Thus, like the marsupials and placental mammals, the Corvida produced convergent forms with Passerida. One group of the Corvida, the Corvini (magpies, jays, crows) are

thought to have subsequently invaded and radiated from Eurasia some 30 million years ago. The genus *Corvus* (true crows including rooks and jackdaws) then diverged from the ancestral Asian stock, and except for South America, spread to all parts of the world, including Australia.

It is plausible that the ancestors of the *Corvini* were arboreal species, as much of Eurasia and even regions as far north as Canada and Greenland were temperate and afforested 60-30 mya (Sibley and Alquist 1986). For those species that adapted to thrive in more open country (for example the plains and steppe regions of central Asia) despite eventual persecution by man, their success was guaranteed with the spread of agriculture and the consequential thinning of the forests.

Rooks would appear to epitomise the latter situation as their distribution in Britain at least, closely correlates to the activities of agriculture. Jackdaws too are well adapted to exploit the spoils of mans activities. However, their ability to nest on cliffs and ledges, and their being less dependent on earthworms and grain has allowed them to colonise areas more open and less inhabited than those utilised by rooks. Breeding rooks nevertheless, outnumber breeding jackdaws by approximately 2:1 in Britain (Lack 1986). This may be a consequence of the overall relative scarcity of nest sites for hole nesting species (see Chapter 8), but may also reflect pre-adaptation in the ability of rooks to successfully exploit the agricultural environment.

Figure A The evolutionary divergent history of the Corvidae (Goodwin 1976; Sibley and Alquist 1986)



## Behavioural properties

Both rooks and jackdaws were in many ways convenient species in which to study social behaviour. The following list lays out the properties applicable to both species that made them suitable for this behavioural study.

- i) Highly gregarious and social
- ii) Diurnally active species
- iii) Relatively large size
- iv) Conspicuous
- v) Sedentary
- vi) Reasonably predictable in their daily movements
- vii) Common in Britain
- viii) Used to human presence, therefore observer effect reduced.
- ix) Familiar species, with much background ecological and physiological information available.

Both species are, therefore, relatively easy to locate, observe and study in the wild.

## Species description

**Rook** *Corvus frugilegus*, Linnaeus 1758.

**Length:** 55cm    **Average weight:** f 420g m440g (this study).

**Description:** Nominate race *C.f.frugilegus* has glossy black plumage with metallic green/purple sheen. Face unfeathered and pale. Bill grey black, slender and pointed. Legs black. Immatures - see Chapter 6. East Asian race *C.f. dastinator* has a more feathered face.

**Moult:** Juvenile summer partial, the flight feathers are retained for one year. >1 yr summer complete moult beginning in April (Seel 1976).

**Habitat:** Lowland farmland comprising arable and pasture land use with sporadic concentrations of mature trees.

**Food:** Especially grain, earthworms and other invertebrates, particularly tipulid larvae.

**Breeding behaviour:** Nests usually in treetops, colonially in clumps of trees or small woods. Nest material comprises twigs, lined with dried grass, leaves and straw (Goodwin 1976). Male and female build.

**Clutch size** - Normally 3-5 eggs laid in from February to March occasionally April depending on latitude (Britain). Asynchronous incubation by the female only.

Incubation 16-18 days

Fledging 32-33 days

**Status:** Resident in the British Isles. Common; estimated British population ~ 1 million pairs, with possibly four million birds wintering in Britain and Ireland (Lack 1986).

**Distribution:** World distribution is restricted to Europe and Asia (including China) north to 63° latitude (56° Siberia), south to the Mediterranean (Goodwin 1976). Introduced to New Zealand. In Britain common and widespread below 300 meters, especially on mixed farmland (Lack 1986). Largely absent from the Highland and Floc regions of Scotland. The British population is resident with some local movements. Other continental populations are more migratory and many Scandinavian rooks appear in Britain during the winter.

#### *Literature précis*

Because of their long association with man and agriculture, much is known about the general breeding, feeding and diurnal activities of rooks (e.g. White 1789; Steward 1911; Burkitt 1935; Lockie 1956b; Holyoak 1968; Dunnet and Patterson 1968; Patterson et al 1971; Feare et al 1974; Coombs 1978; Waite 1981).

Rooks are a diurnal, colonial, tree nesting, and

**Figure B** The distribution of rooks in Britain (modified from Lack 1986)

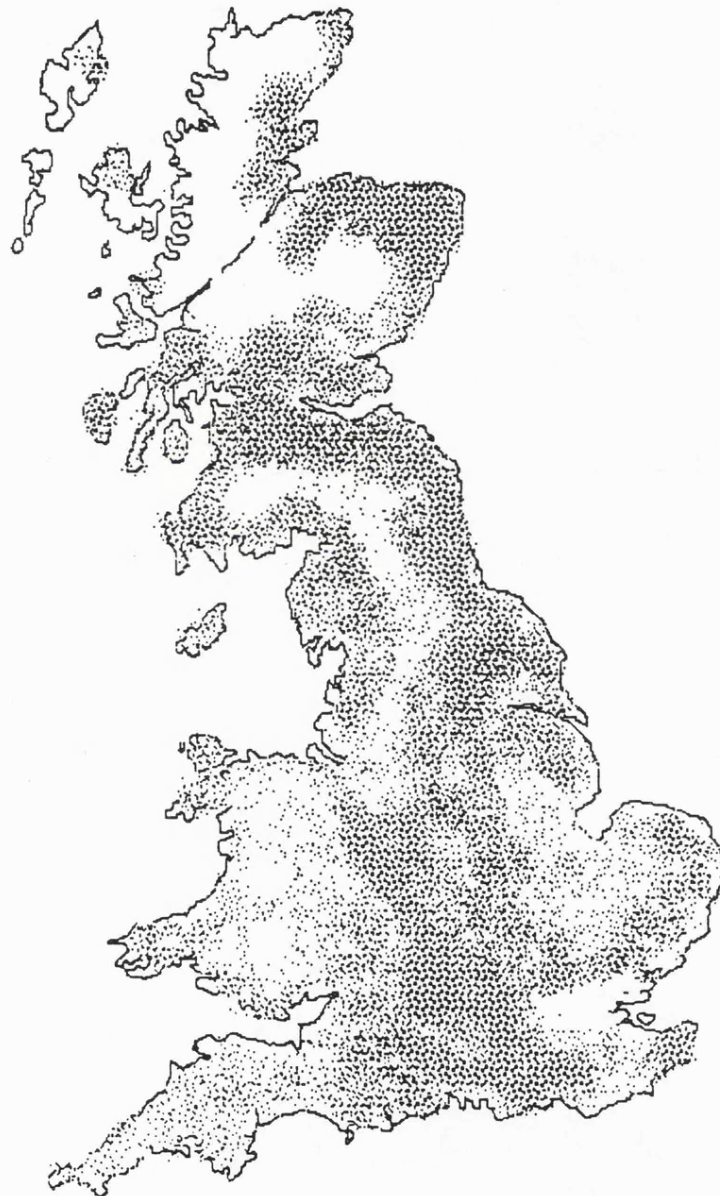
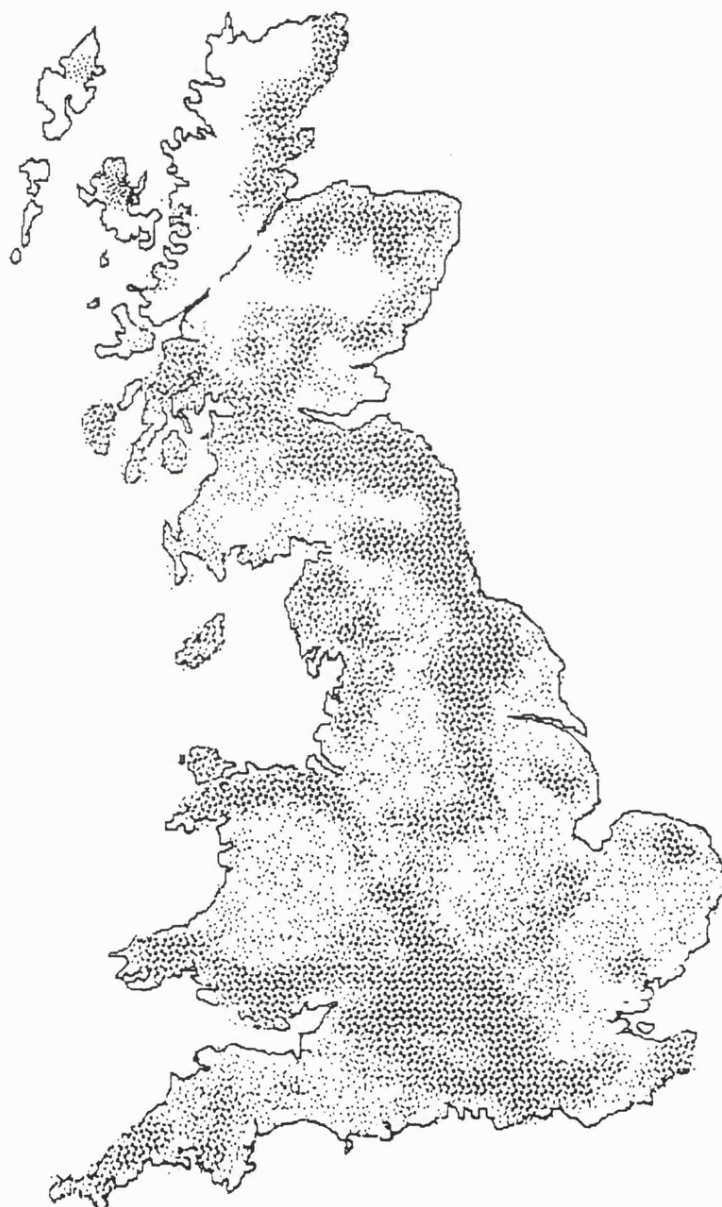


Figure C The distribution of jackdaws in Britain  
(modified from Lack 1986)





monogamous species (but see Green 1982; Røskaft 1983) , and largely sedentary in Britain (Busse 1969; Holyoak 1971). They form conspicuous winter roosts, usually in the presence of other corvids (particularly jackdaws), that have attracted the curiosity of man for at least two centuries (White 1789; Richardson et al 1979). The true functional significance of these colonies is still not properly understood.

A linear hierarchy is recognised in both roosting (Swingland 1977) and foraging situations (Feare et al 1974), with immatures and females being recognised as the subdominant factions. There is evidence however, that females are able to exceed their nominal rank by pairing with high ranking males (Swingland 1977).

Studies of food requirements have also been completed (Lockie 1955, 1956a; Holyoak 1968), in which two major food types dominated. They were earthworms (Lumbricidae) and grain. Coombs (1978) suggests that Lumbricids (and probably also Tipulids) were especially important for the welfare of nestlings, as grain failed to provide the necessary proteins. Hence, rooks breed early (usually in March), which it is thought times the hatching of nestlings to coincide with a highly accessible and numerous soil invertebrate crop (Coombs 1978). As the summer progresses into June drier soils prevents access to such prey (Patterson et al 1971; Feare et al 1974).

The reproductive cycle of rooks reflects the seasonal physiological changes of the gonads in both sexes (Marshall and Coombs 1957; Coombs 1978; Lincoln et al 1980). Reproductive cells begin to develop in February and reach a peak of activity in March. Gonad regression and inactivity is then characteristic of April and the following summer. Renewed gonad activity from August to October is again characterised by increased levels of sexual behaviour and nest building activities. Coombs (1978) supposes that shortening day length probably suppresses reproductive behaviour at this time (until spring), though apparently there are records of young having been hatched in November (Yarrell 1845). Second clutches are likely to be rare however, unless they replace clutches lost soon after they are laid.

**Jackdaw *Corvus monedula*, Linnaeus 1758.**

**Length:** 33cm. **Average weight:** m 254g, f 226 (this study).

**Description:** Nominate race *C.m. monedula* from Scandinavia; bluish/black body plumage, flight feathers greenish/black, secondary coverts with a purplish sheen. Silver/grey nape, legs and bill black, the latter short but pointed. The British race *C. monedula spermologus*, is darker especially on the body feathers. Three other races include;

*C.m. soemmeringi* - Eastern Europe and Asia

*C.m. iberensis* - Iberian peninsula

*C.m. cirtensis* - Algeria and Morocco

**Moult:** Juvenile summer partial (retains flight feathers).

> 1yr annual summer complete from mid to late May to mid to late June (Svensson 1985).

**Habitat:** Typically, grassland including upland (but not highland) areas where trees are sporadically distributed. Quick to exploit grain resources. Jackdaws also occur around the suburbs and parks of towns and cities and coastal cliffs.

**Food:** Broad diet, but especially, grain, weedseeds, and invertebrates including Coleopteradae, Tipulidae and Gastropodidae.

**Breeding behaviour:** Semi-colonial according to nest site availability and dispersion. Nest site in holes in trees, cliffs, chimney pots. Has also been reported to have nested in rabbit burrows on banks and hill sides (White 1789). Nest material very variable, but typically twigs and soil lined with dry grass, moss and hair. Built mostly by the female.

Clutch size - Up to 7, normally 4 eggs laid in April (Britain). Asynchronous incubation, by the female only.

Incubation - 16-18 days.

Fledging - 30-35 days

**Status:** Common, ~ 500,000 pairs in Britain, and perhaps 3 to 3½ million wintering birds in Britain and Ireland (Lack 1986).

**World distribution:** Europe and Asia east to Ussuriland, north to 66° latitude (60° Siberia), south to the Mediterranean, Morocco and Algeria. The British distribution is similar, though broader than that of rooks, with a more westerly bias (Fig. C).

**Movements:** Migrates on the continent from northerly to southerly climes in winter. Scandinavian birds move to the low countries, sometimes Britain. Birds in USSR move to southern Asia and the Mediterranean. British birds are rather more sedentary, with some partial migration south and west as far as Ireland (Busse 1969).

#### *Literature précis*

Linear hierarchies are recognised in jackdaws (Tamm 1977; Röell 1978; Lovari 1979) and like rooks there is a suggestion that females attain a higher rank when they pair with high ranking males (Röell 1978). Röell (1978) reports that both sexes are required for the defence of a nest site and that males cannot hold such a site on their own. Males consequently have little opportunity to successfully defend resources, therefore mate acquisition and pair bond stability should be a priorities for both sexes, prior to nest site acquisition.

There is no account of the physiological changes that might occur within a jackdaw, but clutches laid after May are rare, and one suspects that like rooks there is gonad regression during the summer period. One clutch a year may also account for the close pair bonds and high paternal investment observed. Extra pair interactions may also be prevalent (extra-pair copulations and female brood parasitism) as insurance policies against clutch failure. However, high male investment should pre-empt males from helping to raise potentially sired offspring in neighbouring broods.

A detailed account of many of the jackdaws behavioural activities was made by Lorenz (1952) who discussed the functional significance of postures, vocalisations and social interactions of captive birds. Lorenz (op. cit.) also noted a tendency for communal defence of colony members that were endangered or threatened at the nest by other aggressive jackdaws. Similarly, both wild and captive jackdaws have been observed chasing non resident jackdaws from breeding colonies (Lorenz 1931, 1932, 1952 and Zimmerman 1951, in Goodwin 1976). This latter point was also noted by Röell (1978) and was of special interest to this study, as such behaviour could have been interpreted as altruistic, if non resident birds were significantly less related to residents than residents individuals were to themselves. This point immediately ties in to the investigation of intra flock relatedness mentioned above.

## 1 GENERAL METHODS AND MATERIALS

### 1.1 The study site and habitat

#### 1.1.1 The study area

The study area lies 18 Km to the east of Leicester (Fig. 1.1a) and occupies approximately 8Km<sup>2</sup> of farmland between the villages of Billesdon, Hungarton and Tilton. The focal point of the study area is a substantial winter corvid roost at Billesdon Coplow. The land is typical of many areas of lowland Britain; consisting of undulating terrain and 'patchwork' type countryside. Seventy percent of the land is pasture upon which sheep, cattle and occasionally horses graze. Arable crops comprise largely of wheat and barley with occasional fields of potatoes, sugar-beet and fruit (strawberries).

Three rookeries exist within the study area: Ingarsby circa 80 pairs, Tom Spinny circa 69 pairs and Cold Newton 24 pairs (Fig. 1.1b). Only Tom Spinny, of Billesdon Coplow Lodge Farm, was studied intensively and this became the site of the jackdaw study population.

#### 1.1.2 The roost

Woodland covers approximately twenty percent of the study area and the largest tract of woodland, Billesdon Coplow/ Botany Bay (SK 710 550), is also the location of

Figure 1.1 Location of the study area. a) with in Britain, and b) within Leicestershire. The study area is encircled.



Figure 1.2 Map of the study area. Most observations were made within the area surrounding the main study rookery (numbered fields). Other regions within the study area are Cold Newton (lettered fields) and Ingarsby (undesignated fields to the west). The winter roost for corvids from all three regions was Billesdon Coplow wood.





a substantial corvid roost throughout the winter months. Billesdon Coplow is a prominent geographical feature within East Leicestershire rising to 210 meters (Fig 1.2; Plate 1a). The wood is oak *Quercus* spp. and beech *Fagus sylvatica* dominated but includes a number of other species such as sycamore *Acer pseudoplatanus* and larch *Larix decidua*. The adjacent Botany Bay also supports substantial quantities of ash *Fraxinus excelsior*. The roosting birds consisted largely of rooks and jackdaws but also included carrion crows *Corvus corone* and occasionally magpies *Pica pica*. The total population of birds peaked in the region of 600 individuals, the majority of which are rooks (circa 300) and jackdaws (circa 250).

### 1.1.3 The study site

The rookery, Tom Spinny (Fig. 1.2; Plate 1b), stands 500 meters to the north east of Billesdon Coplow and comprises 1.6 hectares of ash dominated woodland with some oak and sycamore interspersed. The late leafing of ash trees is an important feature of the wood which allows for clearer observational access throughout the greater part of the jackdaw breeding season and throughout all of the rook breeding season.

Plate 1a. Corvid roost, Billesdon Coplow.



Plate 1b Study site, the rookery at 'Tom Spinny'.



## 1.2 Trapping, tagging and bleeding

### 1.2.1 Trap construction and use

Three cage traps were built to specifications recommended by Patterson et al (1968). Each trap measured 2m x 2m by 1m high, with two ground funnels tapering in towards the centre (Fig. 1.3). The funnel entrances measured 300mm radius tapering to 100mm wide on the inside (60mm for jackdaws). 2.5mm chicken wire was used for the cage material.

A variety of baits were used, including rolled oats, maize, sunflower seeds and kitchen waste. White bread eventually proved to be the most successful, perhaps because of its visibility against a dark ground. Best results were achieved by baiting the traps at dusk, minimising disturbance and detection by other birds, and baiting them daily the following day. The use of baited traps was successful in capturing jackdaws, greatly improving the number of birds captured. The funnels tapered inwards towards the rear of the trap, preventing the movement of birds into the trap, and preventing the movement of birds out of the trap. Occasionally, though, jackdaws showed reluctance to enter the trap.

Following significant captures, traps were left open and baited for three or four days to allow for a recovery of confidence among the birds in the colony. Captured

Figure 1.3 Trap design and dimensions.

Two traps were situated in separate fields (fields 21 and 26, Fig 1.2) 200m and 300m respectively, away from the rookery and beneath regular flight paths to and from foraging sites. Both traps were used the whole year around but only intensively during the breeding season (March to July). The third trap was situated within the rookery itself though trapping only commenced after the majority of jackdaw chicks had hatched. This reduced the chance of desertion by captured adults following the disturbance and trauma of being trapped.

A variety of baits were used, including rolled oats, maize, sunflower seeds and kitchen waste. White bread eventually proved to be most successful, perhaps because of its visibility against a dark background. Best results were achieved by baiting the traps at dusk, thus minimising disturbance and detection by roosting birds, and revisiting them early the following morning to check for captured birds. Success in capturing jackdaws was greatly improved by narrowing the inner mouth of the funnels to 60mm rather than 100mm. Inner funnel wire flaps, preventing outward movement of birds were used occasionally, though many jackdaws showed a reluctance to push them open on entry.

Following significant captures, traps were left open and baited for three or four days to allow for a recovery of confidence among the birds in the colony. Captured birds were fitted with patagial wing tags (see below),

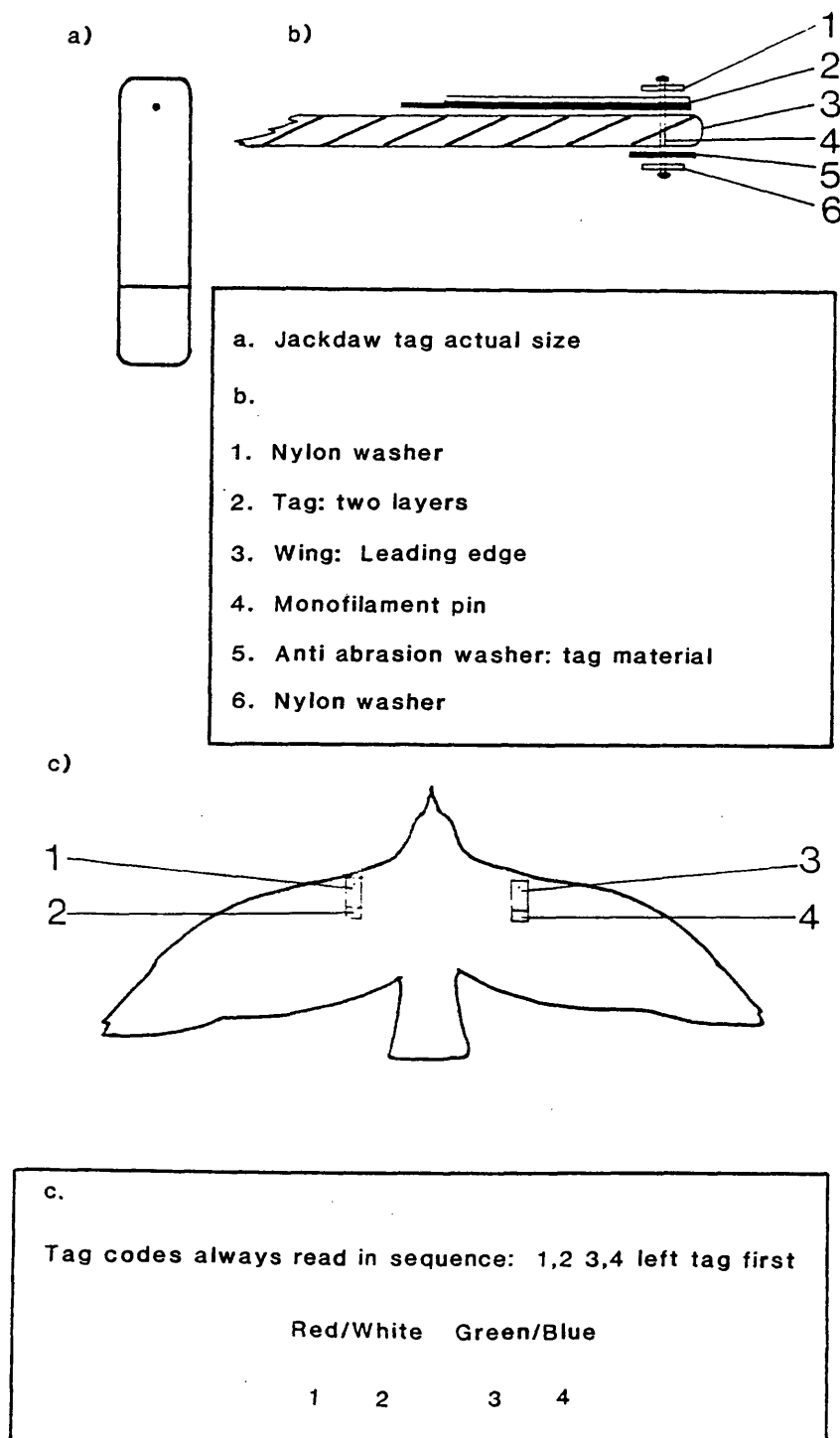
blood samples were taken (see below) and the following parameters recorded: weight, wing length (maximum chord; Svensson 1985), tarsus length and bill length and depth, using standard techniques as recommended by the British Trust for Ornithology (B.T.O. 1984).

### 1.2.2 Individual marking and recognition

Rooks and jackdaws were fitted with patagial wing tags (Figure 1.4) to enable individual identification of the birds in the field. Wing tags were preferable to coloured leg bands as the latter were easily obscured by other flock members, clumps of earth and long grass. Wing tags also had the advantage of being visible while the bird is in flight. Initially, it was intended that standard 'Darvic' plastic tags would be used on rooks, with coded letters and figures painted onto the surface (Anderson 1963, Patterson 1978). However, during field trials, this type of tag proved difficult to read, even with the aid of a telescope. Wind vibration, feathers, and scratched tags all added to the confusion. Consequently, colour coded tags were designed and used for future marking (Village, pers. comm.).

Colour coded tags were cut from strips of flexible, nylon tarpaulin. This material is tough, does not tear and the flexibility allows the bird to 'preen' the tag so as to lie with the contours of the feathers. Tags were made by gluing one coloured strip of material, on top of

Figure 1.4 The design and positioning of wing tags, with a) tag dimensions, b) cross section of wing tag attachment, and c) position of tags on the birds and the code sequence.



a second, so that only the last 1.5cm's of the lower strip was visible (Figure 1.4a). Feathers tended to obscure the top half of the tag so that only the lower half could be used for identification. Despite the glue, the two plastic strips would often separate with wear. The wing pin prevented complete separation but it was a good idea to melt the two halves together where the colours bordered each other.

Wing pins were manufactured from strong nylon monofilament (1mm diameter), cut (~13mm) and tapered at one end, and melted at the other end to form a butt. Nylon washers were placed over the wing pin both below the wing and on top of the wing and tag (Figure 1.4b). The tapered end of the pin was then melted over with a match to form a second butt. All of these materials were inert, non-corrosive plastics which helped prevent damage to the wing (Hart 1987; § Appendix A). Fitting the tags was not difficult with a little practice and could eventually be achieved by one person. Matches were generally more controllable than lighters and could be used to press down on the melted pin to form a butt. Birds were not burned! Each individual was placed with the head inside a bird bag and held down on ones lap, dorsal side up. Each wing was then slightly extended and the wing pin pushed through the patagium avoiding blood vessels. The protruding pin was trimmed down to within two or three millimeters of the top washer (using nail clippers) and melted with the underside of the flame,

which otherwise burned away from the bird. The procedure was carried out within the confines of a vehicle or building - away from the wind. If the melted butt only formed a thin flange, the latter would eventually break off and the tag then lost. It was important then to make sure that the pin stem was widened in transverse section. It was even possible to retain the tag by crushing the end of the wing pin with a pair of pliers. However, long term success is unlikely. The pros and cons of tagging are described at more length in Appendix A while the effects of tagging on breeding success are discussed in Chapter 8.

A field trial at a distance of 100 meters with 10x50 binoculars indicated that the following five colours were most easily separated from each other (25mm x 70mm strips): red, white, green, light blue, and yellow. Each tag consists of two colours and a tag was fitted to each wing (Fig. 1.4c), giving a possible 625 colour combinations. Because of the limited number of colours being used, the colour sequence had to include both wing tags to achieve the number of permutations required. Thus both wings needed to be visible in order to positively identify the bird. However, this was normally achieved within a typical sample period of 2 minutes.

Jackdaw pulli were not tagged until the flight feathers



were well developed, that was, until a predicted five to seven days prior to fledging. Pulli were fitted with coloured leg bands once the tarsus was thick enough, in case for one reason or another tagging was missed. Once tagged the colour bands were removed. Great care was taken when returning the fledglings to the nestboxes to prevent them 'exploding' out of the nest. Plugging the nestbox entrance with leaves worked well and these were later removed by the returning parent bird.

Tag codes are described in Fig. 1.4c. This tagging scheme was registered with the B.T.O., and licensed appropriately by the Nature Conservancy Council.

### 1.2.3 The removal of blood samples

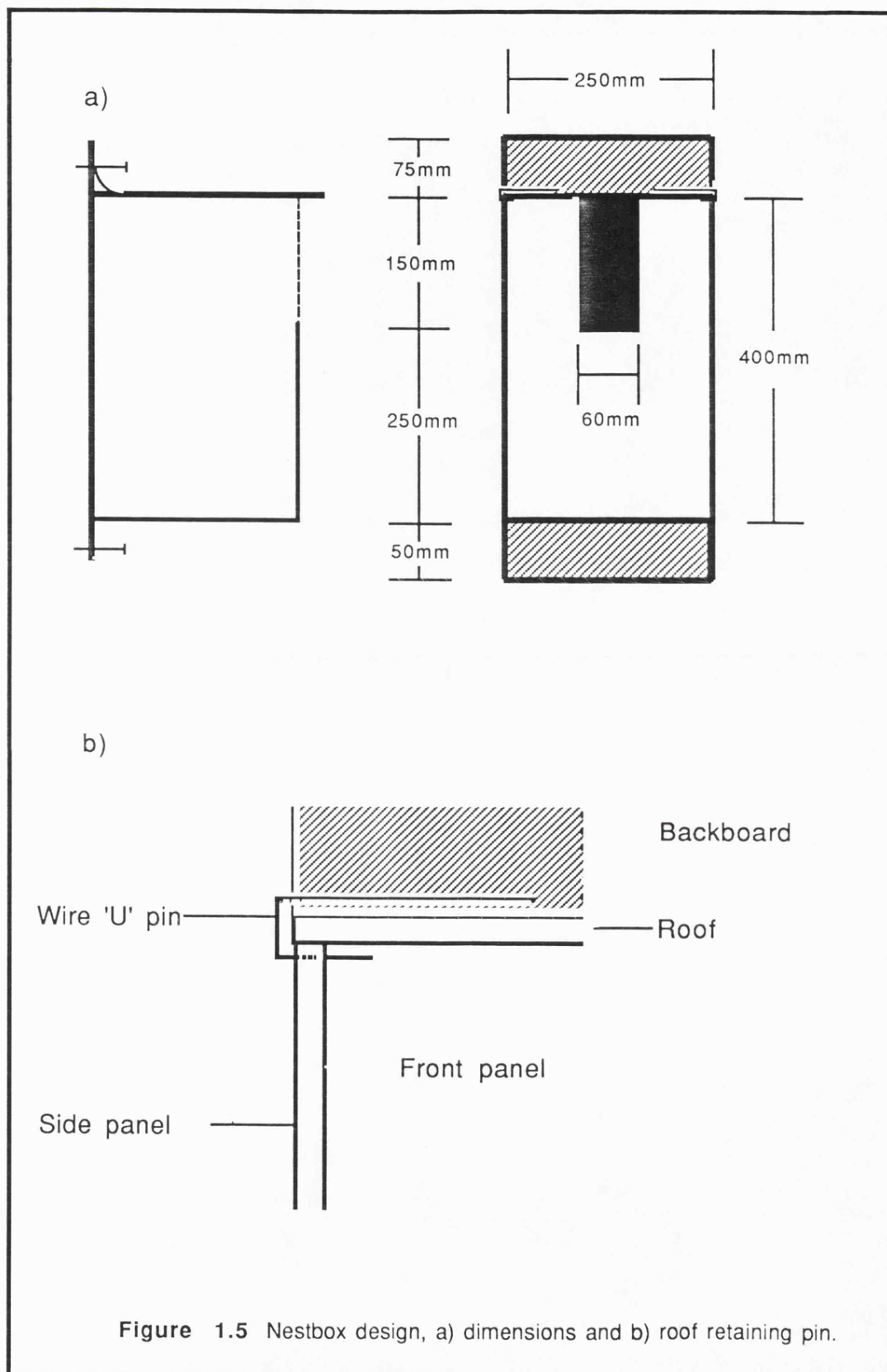
Blood was removed from adult birds, via a heparinised needle and syringe, from the brachial wing vein as it passes over the joint ('elbow') between the humerus and the radius/ulna (Burke pers. comm.). Blood samples normally ranged between 0.2ml and 0.5ml in volume. Birds were placed on their backs and their heads covered with a cloth. Under these conditions they normally lay still and quiet. Blood samples were preserved in 2ml eppendorfs containing buffer (1xSSC/EDTA pH 7.4, see Chapter 2) and stored at -70°C as soon as possible.

Blood samples were taken from jackdaw pulli by clipping the end of a claw while the bird was still naked and the claws soft. Eighty to 140µl of blood were collected in heparinised capillary tubes from the bead of blood

exuding from the toenail. The capillary and blood samples were then dropped into eppendorfs as before and again frozen. Pulli were returned to the nest once the bleeding had stopped. Toenail clipping also served as a method of identifying young in the nest until they could later be ringed. However, by the time the birds were ready to leave the nest, the clipped toenails were barely distinguishable from the rest (further details are given in Chapter 8).

### 1.3 Nestbox construction and positioning

Twenty nestboxes were built from 4mm exterior grade plywood to the following specifications: 400mm high x 250mm x 250mm (Fig. 1.5a). The backs of the boxes measured 550mm in height to allow for attachment to the trees. The nestbox openings measured 150mm high x 60mm wide, the bottom edge ideally being 200mm or more (250mm in fact) from the base (R.S.P.B pers. comm.). The opening was cut out from the top edge of the nestbox, which later facilitated access into the box. The roof was hinged at the back with strips of plastic or rubber and held down by two 'U' pins against the side panels (see Figure 1.5b). 4mm plywood is inexpensive, light and easy to work with but the lifespan of the box is limited (approximately three to four seasons). For long term studies, heavier more durable material should be used, or the wood treated with a non toxic preservative.



Nestboxes were attached to trees with two nails (one top and one bottom) and held firm with wire twisted tight around the trunk. Nestboxes were positioned between 3.5 to 4 metres high, facing north or north-west where possible (away from the prevailing wind and direct sun). Occasionally, because of soft ground or branches, boxes faced other directions. (Fig. 1.6). All of the nestboxes were erected during the second week in March 1987 (§ 8.1.1).

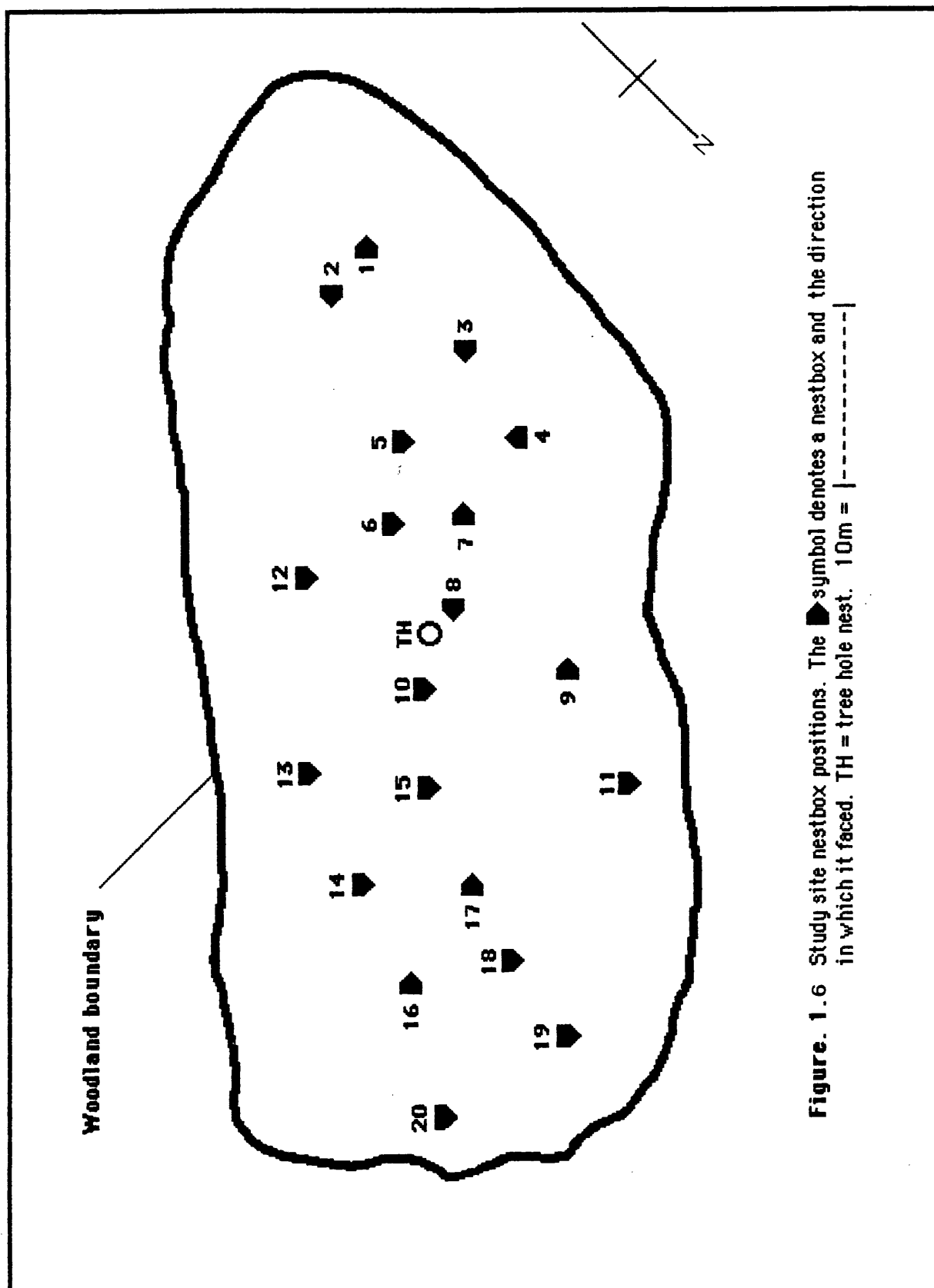
#### 1.4 Data collection

##### 1.4.1 Circuit recording

Approximately 90 % of the study area could be observed from a 10 kilometer circuit of roads (Fig. 1.2). Each circuit could be completed within 30 to 45 minutes provided that weather conditions were not too severe. All flocks or individual rooks and jackdaws, located on the circuit, were recorded along with the following criteria:

- a) Field identification number (Fig. 1.2), field type, temperature and estimated wind speed and direction.
- b) Presence of livestock, hay, straw, manure.
- c) Presence of other corvid species.

At least two circuits a week were completed, between 0900 and 1100 hours or 1430 and 1600 hours GMT. The



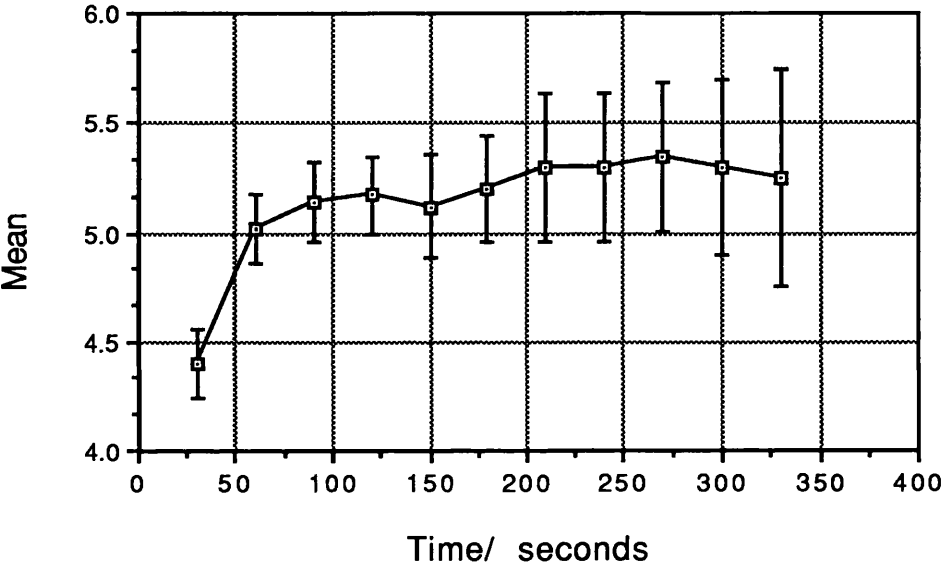
**Figure. 1.6** Study site nestbox positions. The [Solid black diamond] symbol denotes a nestbox and the direction in which it faced. TH = tree hole nest. 10m = [Dashed line]

circuit could be extended to include the surrounding countryside in the absence of rooks or jackdaws within the study area. Circuit records provided information on habitat use and field preferences of the local rook and jackdaw population, and levels of inter-specific association.

#### 1.4.2 Focal bird sampling

Focal sampling was the main technique employed in the collection of behavioural data (Lehner 1979). Focal birds were selected arbitrarily from within foraging flocks and all of their movements and actions recorded over a given period of time (discussed below). In order that concurrent variables, such as flock size, density and weather conditions did not change dramatically during the sample period, sample time were kept reasonably short. However, short sample times were subject to greater fluctuations in variance across behavioural sequences and consistency of data was obtained by recording over longer sample times. To test whether sample times were representative of a bird's full behavioural repertoire 276 focal samples were separated initially into 30 second blocks and the number of distinct behavioural activities occurring within that time recorded and plotted (Fig. 1.7). Note, that the recurrent frequency of each behavioural event was ignored, each one being scored only once on the first appearance.

**Figure 1.7** The change in behavioural variation in relation to focal bird sample times. Error bars = tx SE.



The procedure was repeated for time intervals of 60, 120, 150, 180, 210, 240, 270, 300 and 310 seconds. Behavioural variation began to plateau around sample times of 90 seconds (Fig. 1.7). Samples times of less than 90 seconds were therefore discarded. In practice this question tended to be of hypothetical interest, as corvid flocks were exceptionally fluid in their movements. This often prevented the inclusion of long sample periods and as a result periods in excess of four minutes were uncommon. The total mean sample time equalled 137.32 seconds (SE= 17.04, N= 263).

Behavioural activities were categorised as follows:

- 1) Pecking - probing or hammering the ground.
- 2) Feeding (FE) - mandibulations terminating with the bird throwing back the head and swallowing. (The proportion of time spent in contact with prey).
- 3) Walking - walking whilst not obviously searching, scanning or avoiding other birds.
- 4) Searching - head down looking for prey. May coincide with 'Walking' in which case search took precedence.
- 5) Looking up - a clear movement involving lifting the head and scanning of the area. Again took precedence over



'Walking' if the two coincided.

6) Sitting - inactivity or preening, but not scanning.

7) Flying - often terminates the time budget, cause identified where possible.

I also recorded:

i) Encounter rate (ENC) - aggressive interference or avoidance behaviour per minute of the time sample.

ii) Prey intake rate (PIR) - actual rate of prey capture per minute of the time sample.

Two criteria were used to estimate flock density. Flock density overall, was taken as the mean of the nearest neighbour distances between all the birds in a flock. The distance between birds was estimated in terms of birds lengths (1,2,3,4,5,10,15,20,30,40, or 50..etc.). The Nearest Neighbour Distance (NND) of focal birds was also recorded, again by estimating the distance in bird lengths, of the nearest individual to the birds under observation. Both of these estimates of density were recorded at the beginning and end of each focal sampling period, and the mean in each case used in the final analysis.

#### 1.4.2.1 Continuous sampling

Continuous sampling was used to investigate the behaviour of a number of individuals simultaneously - in otherwords focal groups. The technique was basically similar to focal bird sampling except that more than one individual was under observation and sample times often continued over a period of hours rather than minutes. A typical example of this method's application, was the recording of the sequence of events occurring at one or more nestbox (§ Chapter 8).

#### 1.4.3 Scan sampling

When employing this method of sampling (Lehner 1979), each flock was scanned in as short a time period as was possible and every individual's behaviour or position recorded. The objective was to try to capture an 'instantaneous' image of the flock, portraying the specific mode of behaviour of each individual bird. One could then assess the proportion of individuals involved in any one particular behaviour at any one time. The technique was used most frequently to compare the relative proportions of rooks and jackdaws engaged in vigilant activities in relation to flock size and composition (§ 5.6). Either the behaviour or the position of the birds were recorded on separate sampling occasions. This minimised the quantity of information that needed to be collected within each sample, thereby

allowing the technique to be carried out more efficiently. The behavioural categories used, were described in 1.4.2 above.

### **1.5 Recording methods**

Most events and samples were recorded initially on cassette tapes and later transferred onto record sheets or a computer data base. An exception was circuit data, where speed was not necessarily required and record sheets could be used immediately. Focal sampling information was played back and typed into a computerised event recorder (BBC 'Basic' time budget programme). The programme calculated either the time allocation, or occurrence rates of the behavioural events designated above (§ 1.4.2). Observations were subsequently stored as individual time budgets and later tested for correlative relationships with the other variables as and when required. Video recordings were used to investigate the simultaneous response of individuals within a flock to the approach of a predator (§ 5.7.3.4). Video tapes were also used on occasions to identify the nearest neighbours of birds foraging or joining flocks (§ 5.3).

### **1.6 Statistical methods**

Much of the analysis involved the use of non parametric tests of correlation because the data were not normally distributed. There were cases where, within a series of

non parametric tests, parametric tests could have been performed, but for the sake of continuity were not selected. When more sophisticated techniques were required suitable data transformations were completed. This was true of the SPSS<sup>X</sup> partial regression programmes. Parametric statistical analysis of percentages or proportions always follow the suitable transformation of data (that is: arcsin transformation =  $\sin^{-1}\sqrt{\%/100}$ ). The procedures for t, z and F tests are described in Fowler and Cohen (BTO guide) and Bishop (1983). For non parametric statistics see Siegel (1956).

The resultant standard errors of the products (X) of multiplied components (A) were calculated according to the formula (Norton pers. comm.):

For,

$$A_1 \cdot A_2 \cdot A_3 = X$$

$$\left(\frac{SE_X}{X}\right)^2 = \left(\frac{SE_1}{A_1}\right)^2 + \left(\frac{SE_2}{A_2}\right)^2 + \left(\frac{SE_3}{A_3}\right)^2 \quad (1.1)$$

The resultant standard errors ( $\Delta SE$ ) of N = 2 cumulative means (and standard errors 1 & 2) were calculated

according to the formula (Norton pers. comm.):

$$x(SE_1) + x(SE_2) = \frac{\Sigma x}{N}$$

$$SE^2_1 + SE^2_2 = \frac{\Delta SE^2}{N} \quad (1.2)$$

---

## 2 DNA FINGERPRINTING - PROCEDURE

### 2.1 Introduction

First developed by Jeffreys et al (1985a) DNA fingerprinting provided biologists with an individually specific genetic marker, which through its heritability allowed workers to trace parentage and relatedness in human populations.

It was recognised that certain regions of the human genome were highly variable in nature, due to short sequences of DNA being variably repeated at high frequency within those areas (e.g. Wyman & White 1980; Bell et al 1982). These short sequences, comprising tandem repeats of only a few tens of base pairs, were termed 'minisatellites' (Jeffreys et al 1985a) and substantial minisatellite length polymorphisms were responsible for the so called 'hypervariable' regions of the genome previously detected (Jeffreys et al 1985b).

Hypervariable regions can be isolated by fragmenting the DNA with restriction enzymes that recognise specific target base pair sequences not present within the minisatellites (Fig. 2.1). Thus fragments of DNA, comprising variable minisatellite repeats, can be separated according to length (charge to mass ratio), by gel electrophoresis. Essentially, in humans, the number of repeats of all minisatellite sequences throughout the genome is individually specific. Consequently the array

Figure 2.1 Diagrammatic representation of minisatellite structure.

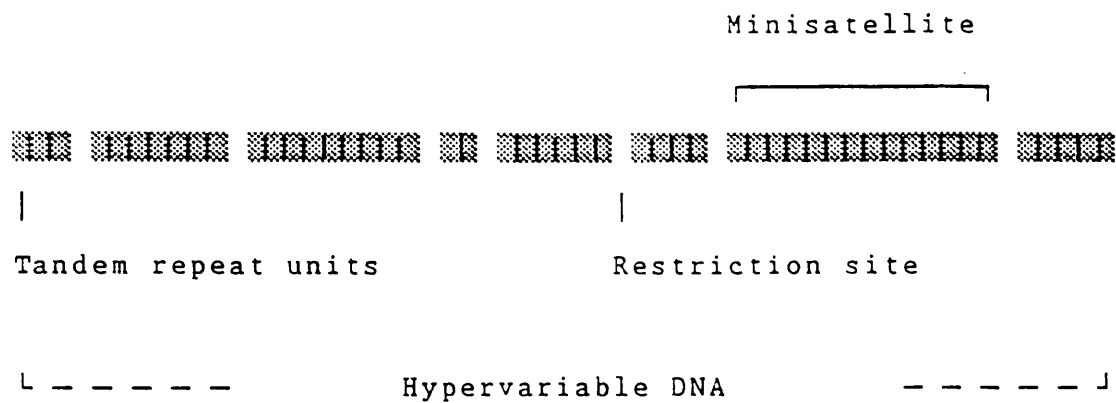


Figure 2.2 Human minisatellite probe 33:15, comprising 29 repeats of a 16 base pair sequence (Jeffreys et al 1985a) showing regions (in bold) compatible with the minisatellite core.

Minisatellite core sequence: GGAGGTGGGCAGGA G

Probe sequence (33:15): AGAGGTGGGCAGGTGG x29

of fragment bands separated by gel electrophoresis provided an individually specific genetic marker (the 'fingerprint').

All minisatellites contain repeats of a common core base-pair sequences. The core sequences can be cloned and used as probes to detect other hypervariable regions of the genome (Jeffreys et al 1985a). By radioactively labelling the probes with  $^{32}\text{P}$  isotope, and exposing the labelled fingerprint onto X-ray film, the DNA fingerprint could then be visualised.

More recently, the probes originally developed to hybridise with human minisatellites, were shown to detect similar hypervariable regions of the genome in some birds (Burke & Bruford 1987), and some other mammals (Jeffreys & Morton 1987). I used one such probe (termed 33:15 consisting of 29 repeats of a 16 base-pair variant of the human minisatellite core sequence (Fig. 2.2)) for my investigations of relatedness in jackdaws.

## **2.2 Detailed procedure**

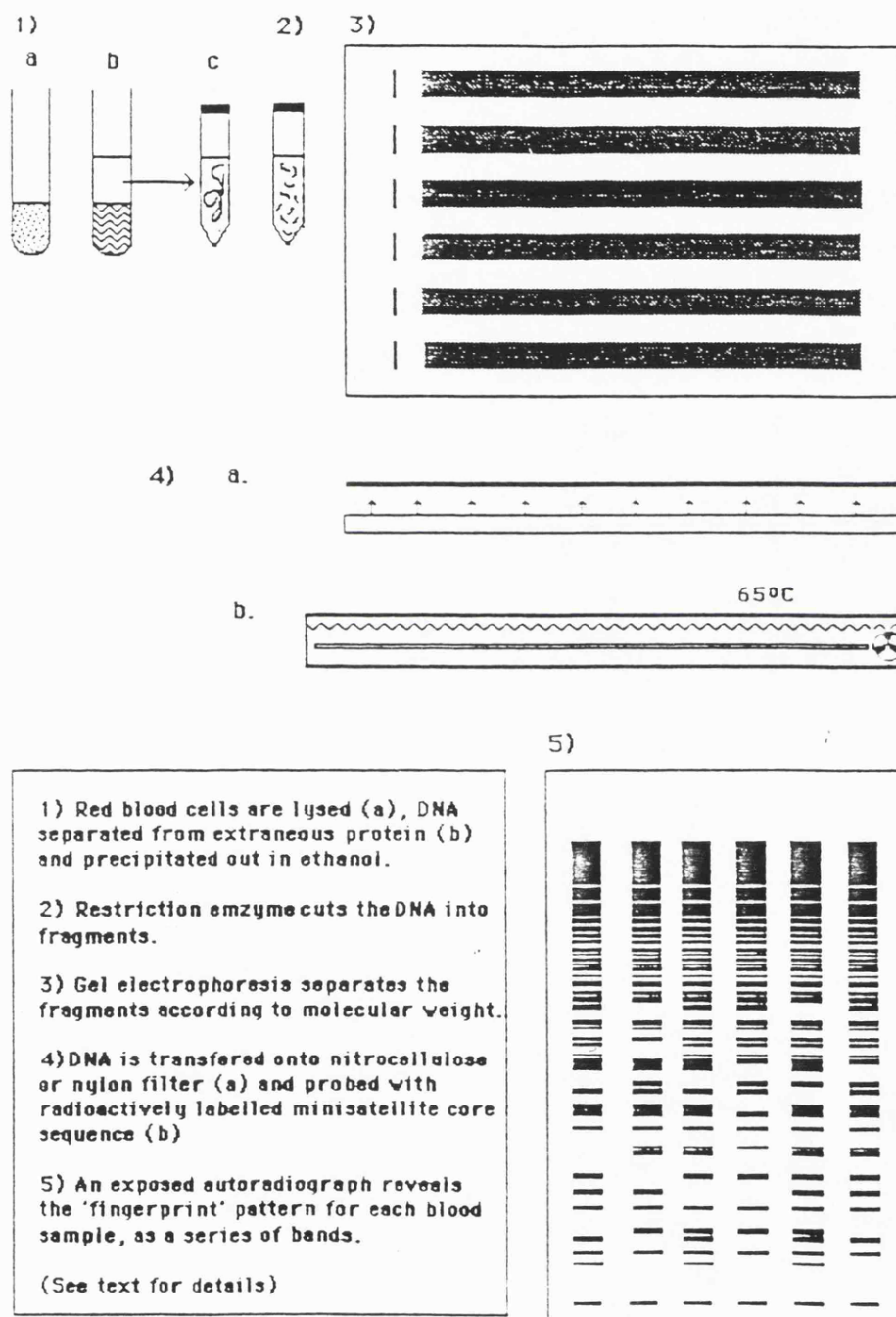
### **2.2.1 DNA preparation**

#### **2.2.1.1 DNA extraction from red corpuscles**

The blood samples were thawed at room temperature and 100  $\mu\text{l}$  suspended in 2ml of 1x TNE (0.1M Tris-HCl pH 8.0



Figure 2.3 Diagrammatical representation of the DNA fingerprinting procedure



0.1 M NaCl, 1mM EDTA) before being incubated with 2.5 units ml<sup>-1</sup> proteinase K (Sigma) and 80 µl 25% (that is 0.5% SDS (sodium dodecyl sulphate) at 37°C for eight hours (or 50°C for 2 hrs). Thus the cells were lysed and the protein digested. Occasionally DNA was extracted from muscle tissue by macerating the tissue in a drop of liquid nitrogen and then proteasing as before.

DNA was separated from extraneous protein by two phenol/chloroform (100g phenol, 0.1g 8 hydroxyquinoline, 100ml CHCl<sub>3</sub>, 4ml isoamyl alcohol) and one chloroform/iso-amyl alcohol (24:1) extraction, the supernatant (containing DNA) having being pipetted off at each stage.

The DNA was then precipitated with 2x volume ethanol, pelleted by centrifugation at 3000 rpm (12300g's) and washed in 70% ethanol to remove residual salts. The ethanol was removed and the DNA pellet air dried.

#### **2.2.1.2 DNA concentration and condition determination**

The DNA pellet was re-dissolved in 1 ml 51 Tris/EDTA (10mM Tris, 1mM EDTA, pH 7.5) and 2 µl of each sample was made up to 15 µl with 1x Tris borate/EDTA (TBE) pH 8.3 loading buffer and electrophoresed at 100 volts for one hour through a 0.7% ("Seakem") agarose gel (Maniatis et al 1981) in 1xTBE (130mM Tris, 75mM Boric acid, 2.5mM EDTA) running buffer.

The DNA was visualised by staining with ethidium bromide (added to the gel solution at a concentration of

0.5 µg/ml) and viewed under ultra-violet light. Ethidium bromide binds to DNA, is fluorescent under UV light and thereby provides a visual estimate of the condition and quantity of DNA present. Degraded DNA comprises low molecular weight fragments, and a diffuse fluorescent band will travel ahead of the expected position given the number of volt-hours supplied (Plate 2.1a). Quality DNA of high molecular weight formed tight compact bands and therefore appeared on the gel as such. The intensity with which the bands fluoresced, provided a measure of the concentration of DNA present in the sample when compared with simultaneously run λDNA concentration standards (see Plate 2.1). The gel was photographed under UV light (Polaroid 545 Land camera, Polaroid 52 film, 3 secs.). From the concentration gel one was able to assess the volume of sample required to yield 5µg of DNA for restriction digestion.

#### 2.2.1.3 Restriction digestion

Typically, 5 µg samples of DNA were subjected to digestion by 15 units of Alu 1 restriction endonuclease in the presence of buffers 'BRL Reac 1' (supplied) and 'Spermidine trichloride' at 37°C overnight. Alu 1 recognises specific A G C T 4 base-pair recognition sites (not present within the minisatellite fragments), thereby cutting the DNA very frequently, as required for a suitably informative fingerprint pattern.

Plate 2.1 Concentration and condition analysis of a) genomic DNA and b) restriction digested DNA. In both cases samples were electrophoresed through a 0.7% agarose gel, at 100 volts for one hour (see text).



The digested DNA was recovered from solution via one phenol extraction (in 1.5 ml eppendorfs), and precipitated in 2x volume ethanol/4µl 5 M (that is, 100mM) NaCl solution at -70°C (that is, two dry ice /ethanol baths for 5 minutes and centrifuged at 3000rpm (12300g's) of 5 minutes in between). The precipitated DNA was washed in 70% ethanol, centrifuged for 5 minutes, the supernatant poured off and the remaining pellet of DNA air dried for two hours.

The dried DNA was allowed to dissolve in 25 µl of 1x TBE loading buffer at 50°C for ten minutes. Two µl (ideally 0.4 µg) of each sample was then added to 13 µl of 1x TBE and run on a second 0.7% agarose gel for one hour at 100 volts. The condition of the fragmented DNA was monitored from a photograph of the gel (Plate 2.1b). A tight band indicated fragmentation of the high molecular weight RFLP's and degradation of the DNA. Otherwise broad evenly spread tracks indicate clean, well digested DNA (Plate 2.1b). There was no absolute test of concentration though previously run test fingerprints had indicated adequate concentration of DNA on the basis of a sample track intensity such as track 4 Plate 2.1b (Bruford pers. comm.). However, for an evenly resolved autoradiograph, even loading of the fingerprint gel was of more importance than the absolute a concentration values. Thus, brighter bands indicating higher concentrations of DNA required that less volume be loaded. Less bright bands indicated that more original

genomic DNA needed to be digested and added to the already digested sample to bring the concentration up to the desired amount.

## **2.2.2 Fingerprint preparation**

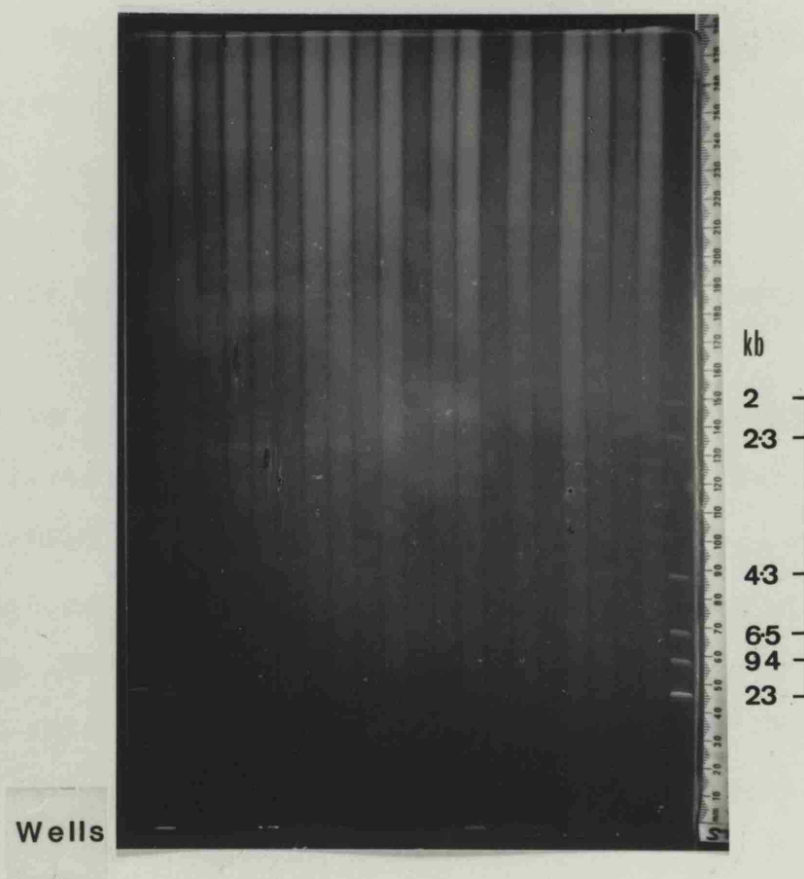
### **2.2.2.1 Gel electrophoresis**

In order that minisatellite bands should be sufficiently well separated and adequately resolved, the DNA samples were run through a 30 x 20cm 1% agarose gel in 1x TBE electrolite, including 0.5 µg/ml ethidium bromide. Lambda DNA markers (Plate 2.2), of known base-pair (bp) length, ran parallel with the samples and served to calibrate the fingerprint pattern. Electrophoresis was arrested after the 2 kilo base-pair (kb) λ marker had travelled approximately 27.0 cm. In jackdaws resolution of fingerprint bands is poor in fragments of less than 2 kb in length. Informative fragmented DNA, occurs in bands between 10 and 2 kb in length (see below Plate 2.4).

### **2.2.2.2 Southern Blotting**

The DNA needed to be transferred onto a medium convenient and stable enough to withstand the rigors of hybridisation and to allow the probe access to the minisatellite DNA. Thus, the gel DNA is transferred first onto a Sartorius 0.45 µm pore size nitrocellulose (or

Plate 2.2 DNA fingerprint gel after 28 hours @60 volts.

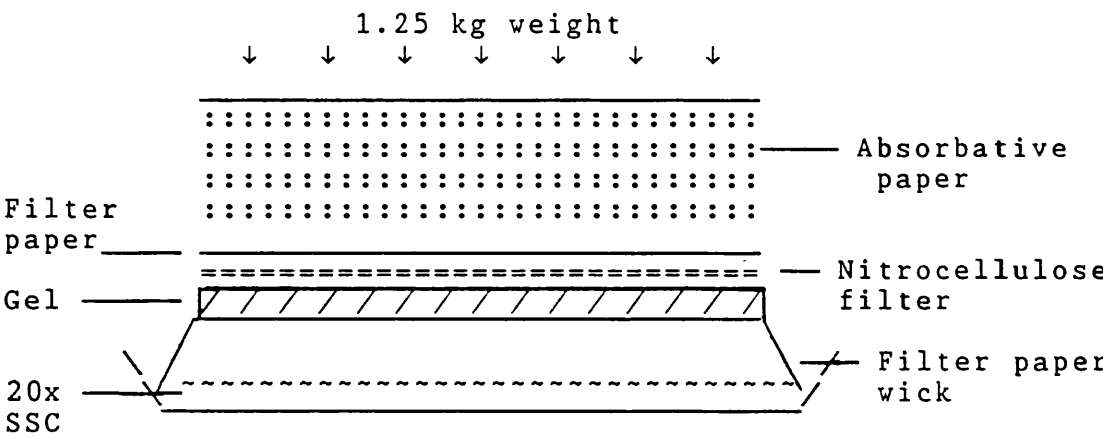


nylon 'Amersham Hyband') filter by process of Southern Blotting (Southern 1975, Jeffreys et al 1986). The filter was placed on top of the gel which lies in contact with 2x SSC solution via a Whatman 3MM chromatography filterpaper wick (Fig.2.4). Pressure applied to the filter (1.25 kg weights on top of paper towels) caused solution to be drawn up, through the gel and through the filter. The DNA attaches to the filter in precisely the same pattern as was distributed across the agarose gel. The DNA was then fixed to the nitrocellulose filter by baking the filter at 80°C for 2 hours (nylon filters were irradiated with a powerful UV source for 15 seconds).

Prior to Southern blotting the agarose gel was subject to two important treatments. The gel was first washed (2 x 7.5 mins) in 0.25M HCl. This process, termed acid depurination, served to hydrolyse the purine bases (adenine and guanine) which because of their size and configuration would otherwise prevent the DNA to pass through the gel matrix (Fig. 2.5). Secondly, the gel was washed (2 x 15 mins.) in 0.5M NaOH, 1.0M NaCl. This process denatured the DNA, into single strands, to allow access for the probes during hybridisation. The gel was then neutralised in 1M Tris-HCl pH 7.4, 3M NaCl for 15 minutes to remove traces of alkali which would otherwise have damaged the nitrocellulose filter.



Figure 2.4 Process of Southern blotting. See text for details.



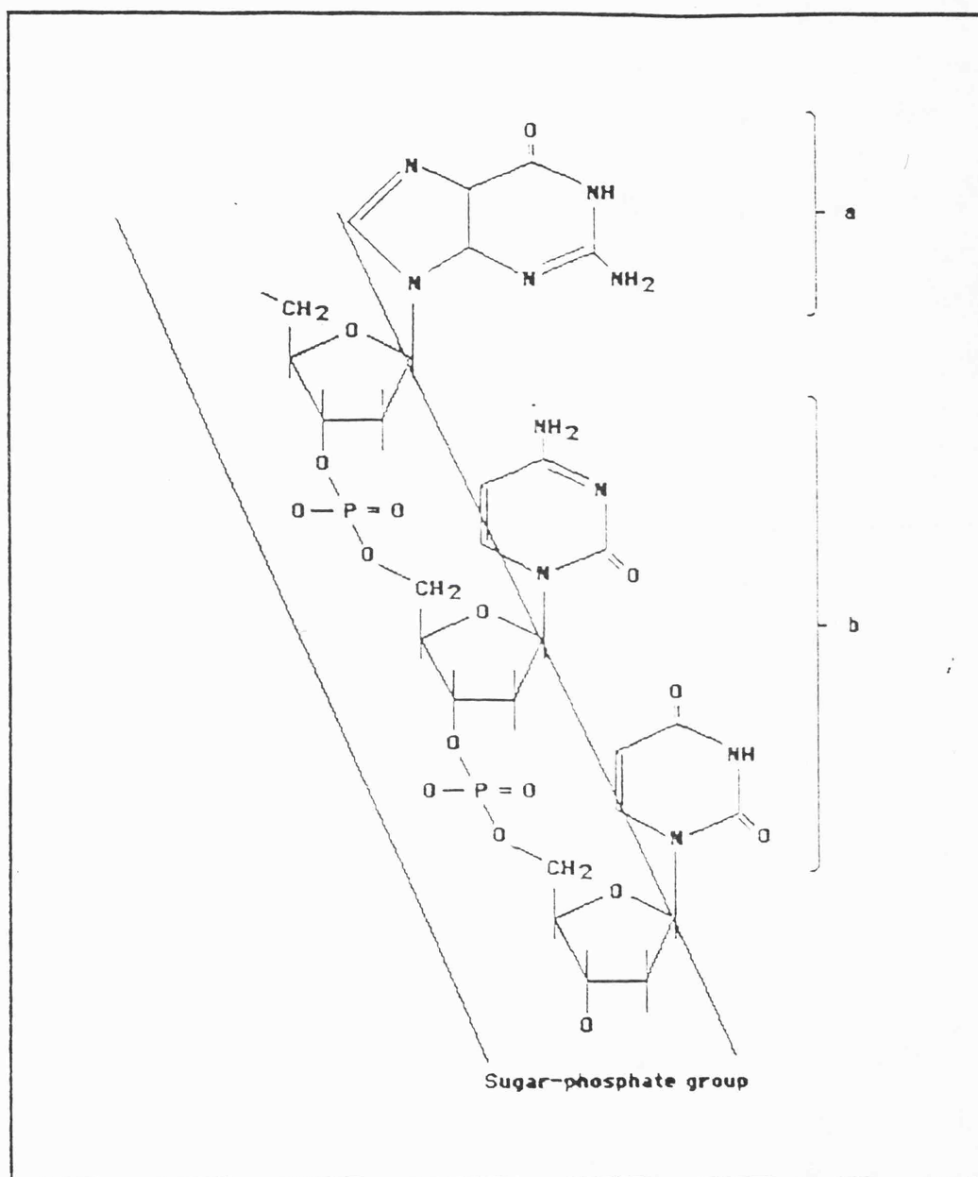


Figure 2.5. Showing the configuration of the purine ('a' adenine and guanine) and pyrimidine ('b' cytosine and thiamine) bases protruding from the 5' - 3' sugar-phosphate polynucleotide backbone of DNA. (Modified from Benjamin and Lewin, 1983.)

## 2.2.3 Probing

### 2.2.3.1 Probe preparation

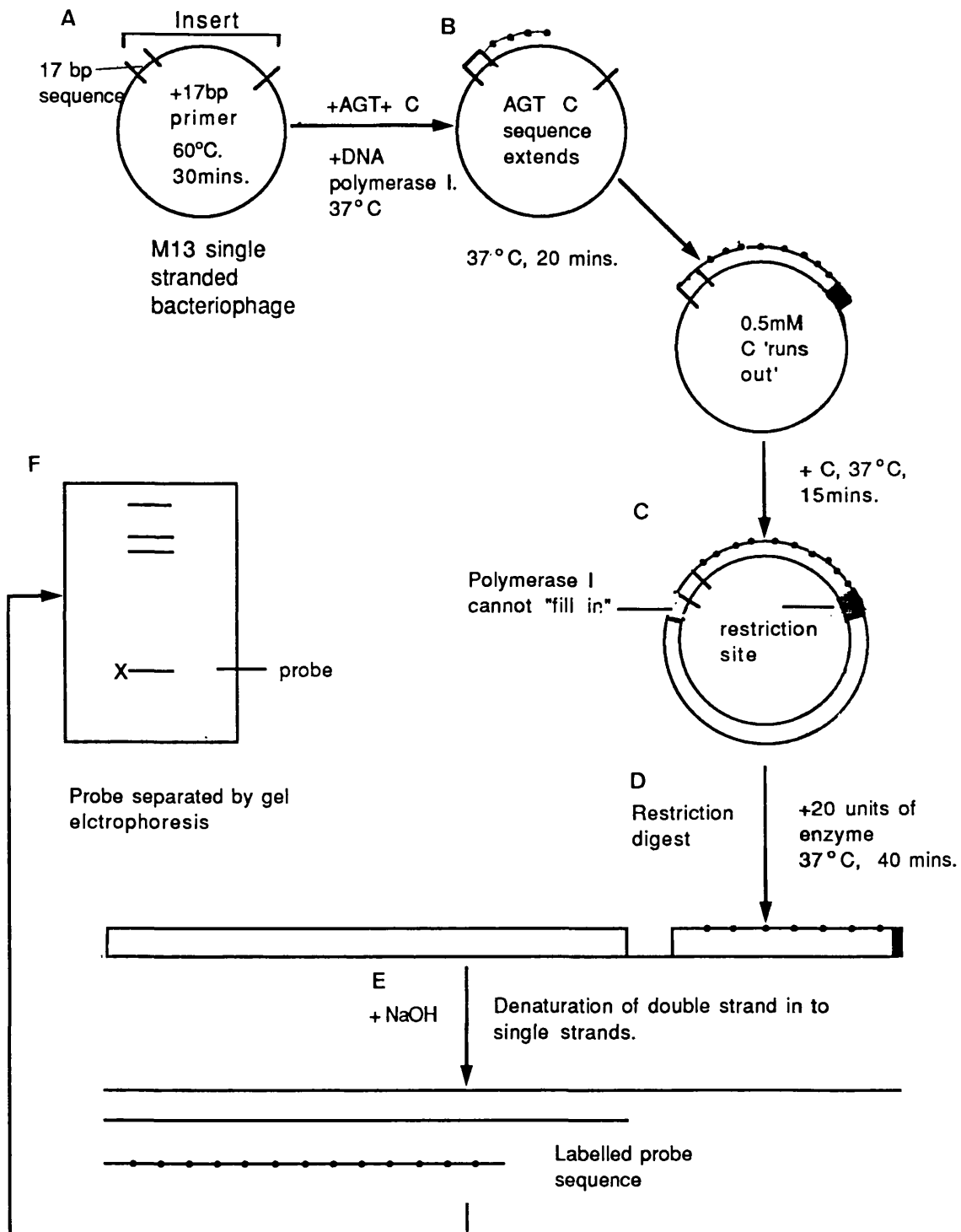
The probe is prepared from single stranded human minisatellite (33:15) M13 bacteriophage recombinants by primer extension (Jeffreys et al 1985a), radioactively labelled and isolated according to the following procedure (Fig 2.6):

i) 10 $\mu$ l DNA (M13), 2 $\mu$ l TM (buffer), 6 $\mu$ l 17 primer, 3.3 $\mu$ l H<sub>2</sub>O was incubated at 60°C for 30 minutes. The primer recognises a specific 17 base-pair sequence in the M13 genome, hybridises strongly providing a site from which probe sequence replication can begin (Fig 2.6A).

ii) The radioactive probing sequence is spun down and added: 20 $\mu$ l AGT, 12 $\mu$ l TE, 5 $\mu$ l dCT<sup>32</sup>P, 1.5 $\mu$ l 10.5 (units) DNA polymerase I (Klenow fragment): 37°C for 20 mins. The probe bases extend from the primer sequence to replicate with the M13 insert sequence. Labelled cytosine is included at this stage (Fig. 2.6B).

iii) Add 5 $\mu$ l dCTP 37°C for 15 mins. Only replication of the insert sequence is required, the rest of the M13 genome is filled in with unlabelled cytosine, though polymerase I cannot complete the link with the primer sequence and leaves a gap (Fig 2.6C).

**Figure 2.6.** Cloning and isolation of human minisatellite probe sequence by primer extension with M13 bacteriophage



iv) Add 6µl Spermidine, 3µl Bam H1 enzyme, 6µl React 3 buffer: 37°C for 40 mins. The restriction enzyme fragments the double stranded replicate at a specific site (Fig 2.6D).

v) Add 11µl NaOH, 30µl agarose beads: load onto an agarose gel (50 ml 1x TB ph 8.3, 0.6g fine agarose ('Sigma sea plaque'), 45 µl ethidium bromide (10mg/ml H<sub>2</sub>O). NaOH denatures the double stranded sequences to create three single stranded sequences one of which, the shortest, includes the probe sequence (Fig 2.6E). The probe sequence is then isolated from the rest of the DNA by gel electrophoresis (Fig 2.6F).

The gel runs for 6cm or ~ 1½ hours at 100 volts in order to separate out the probe DNA from extraneous material (Plate 2.3). The position of the radioactive probe sequence is identified by exposing the gel onto Kodak X-Omat film for five minutes. The probe region of the gel ('X' Plate 2.3) was then cut out as a thin ('1 mm) sliver of agarose, and stored at -20°C until required for hybridisation (see below).

#### 2.2.3.2 Pre hybridisation

In order to prevent the radioactive probe hybridising randomly with all areas of the filter, the filters must undergo pre-hybridisation treatment so that blocking agents (e.g. Denhart's solution) occupy areas of the

Plate 2.3 Autoradiograph of isolated  $^{32}\text{P}$  labelled probe following electrophoresis through a 0.6% agarose gel@100 volts for ~1½ hours.



fingerprints were therefore soaked in 2x SSC for five to ten minutes, placed in flat hybridising chambers and subjected to four pre-hybridising solutions prior to addition of the radioactive probe.

(i) 20 ml 1x-SSC  
(ii) 20 ml 1x-D  
(iii) 20 ml CPE  
(iv) 0.1% SDS, 30 minutes.

(v) 40 ml CPE  
0.005% SDS, 30 minutes.

3.3.3 Hybridisation  
The radioactive probe was added to the filter (4x), (after the filter was washed for 2 minutes in this solution).

The filter was finally washed in the following sequence of solutions to remove background radiation from non-hybridised regions:

(i) 2x-SSC, 0.1% SDS 30 minutes at 65°C  
(ii) 1xSSC, 0.1% SDS 30 minutes, 65°C and repeated three times.

filter where hybridisation would be weak, that is, where there are no minisatellite fragments.

The nitrocellulose fingerprint filters were therefore soaked in 2x SSC for five to ten minutes, placed in flat hybridising chambers and subjected to four pre-hybridising solutions prior to addition of the radioactive probe. The four solutions were:

- i) 20 ml 1x SSC at 65°C for 10 minutes.
- ii) 20 ml 1x Denhardt's at 65°C for 30 minutes.
- iii) 20 ml CFHM, 1x Denhardt's, 1x SSC, 520 µl 25% (that is, 0.1%) SDS, made up to 130ml with H<sub>2</sub>O at 65°C for 30 minutes.
- iv) 40 ml CFHM + PEG (6%) (5.4g polyethylene glycol 6000 'BDH' dissolved) at 65°C for 30 minutes.

#### 2.2.3.3 Hybridisation

The radioactive probe was added to the 20 ml CFHM + PEG (6%), (after the former had been boiled in 1ml distilled water for 2 mins., to remove agarose) and the filter bathed in this solution, at 65°C, overnight.

The filter was finally washed in the following sequence of solutions to remove background radiation from non hybridised regions:

- i) 2x SSC, 0.1% SDS 30 minutes at 65°C
- ii) 1xSSC, 0.1% SDS 30 minutes, 65°C and repeated three

or four more times as necessary to reduce the background count down to normal levels.

Filters were air dried on Whatman filter paper and exposed onto Kodak X-Omat or Amersham MP film with either one or two Cawo intensifying screens. Exposure time varied according to the radioactive intensity of the filters but was typically 3.5 to 4 days, at a radioactive intensity of 25 - 30 counts per minute, at  $-70^{\circ}\text{C}$ . The film was developed (Kodak X-ray developer, 4 minutes), fixed (10 minutes) and washed under cold running water (20 minutes).

#### 2.2.3.4 Nylon filters

There were some modifications to the hybridisation and pre-hybridisation procedures when nylon filters were used. Pre-hybridisation took place over 6 hours with the filter being agitated in a  $0.5\text{ M Na}_2\text{HPO}_4$ ,  $1\text{mM EDTA}$ ,  $7\%$  SDS,  $1\%$  bovine serum albumin solution (blocking agent). The filters were hybridised in the same solution with the probe added as above, for 10-12 hours. Post hybridisation washes of nylon filters were as follows:

i)  $0.5\text{ M Na}_2\text{HPO}_4$ ,  $1\text{mM EDTA}$ ,  $1\%$  SDS for 15 minutes at  $65^{\circ}\text{C}$ .

ii) Two washes in  $2\times\text{SSC}$ ,  $1\text{mM EDTA}$ ,  $0.2\%$  SDS for 20 minutes at  $65^{\circ}\text{C}$ .

iii) Three washes in  $1\times\text{SSC}$ ,  $1\text{mM EDTA}$ ,  $0.2\%$  SDS for 20 minutes at  $65^{\circ}\text{C}$ .



## 2.3 Analysis

### 2.3.1 Scoring bands

The probability of band sharing ( $x$ ) between two individual fingerprints was scored according to the formula (Burke pers. comm. and Burke and Bruford 1987, Table 1):

$$x = \frac{1}{2} \left( \frac{n}{b_1} + \frac{n}{b_2} \right) \quad (2.1)$$

where  $n$  equals the number of bands shared between two individuals and  $b$  equals the number of resolvable bands for individuals 1 and 2 respectively. Values of average band sharing (Chapter 7) were calculated from the means of pairwise  $x$  coefficients for the each group of individuals under investigation.

There existed a degree of subjectivity in the scoring of fingerprint patterns, exacerbated by fluctuations in the surface of the filters. However, by measuring the band migration relative to lambda markers, analysis was completed. Band intensity was also problematic. Common co-migrating bands may vary as much as two times in intensity, because an intense band may originate in an individual, from parents both having had an allele of similar mobility. Thus, if co-migrant bands differed in intensity by a factor greater than two, they were not

considered shared, unless track band intensity was consistently low due to an uneven loading of DNA ('U' Fig. 2.7).

### 2.3.2 Segregation analysis

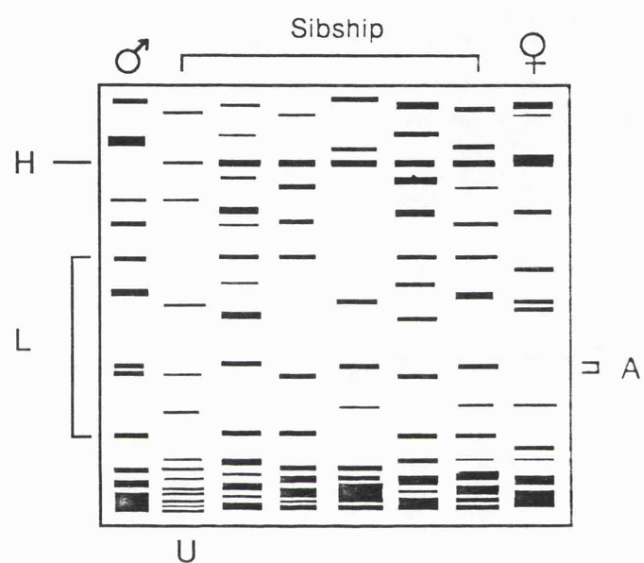
Segregation analysis establishes the probability of independent, recombinant paternal or maternal fingerprint bands becoming distributed throughout the sibship according to the binomial distribution (Burke & Bruford 1987). Observed band transmission should match expected transmission, that bands are inherited (and therefore segregate) in true Mendelian fashion (i.e. 50% to offspring).

Closely linked bands show no recombination but cosegregate at meiosis and thus appear simultaneously in the fingerprint pattern of relatives (Fig. 2.7'L'). Linked loci effectively reduce the band permutations available for analysis.

Allelic bands (two fragments from the same locus representing separate alleles) always segregate at meiosis and therefore show no co-inheritance (Fig. 2.7'A'). As allelic bands are not independent of each other they should be scored as just one site in the band sharing analysis.

Homozygous loci should be eliminated from fingerprint analysis as the probability of band transmission is twice that of heterozygous bands. Band transmission would approach 100% between parents and offspring rather than

**Figure 2.7** Hypothetical DNA fingerprint sibship showing non independent linked (L), allelic (A) and homozygotic (H) bands. U is an underloaded track.



the expected 50%. Homozygous fragments are identified as common co-migrant bands of the parents and all offspring (Fig. 2.7'H').

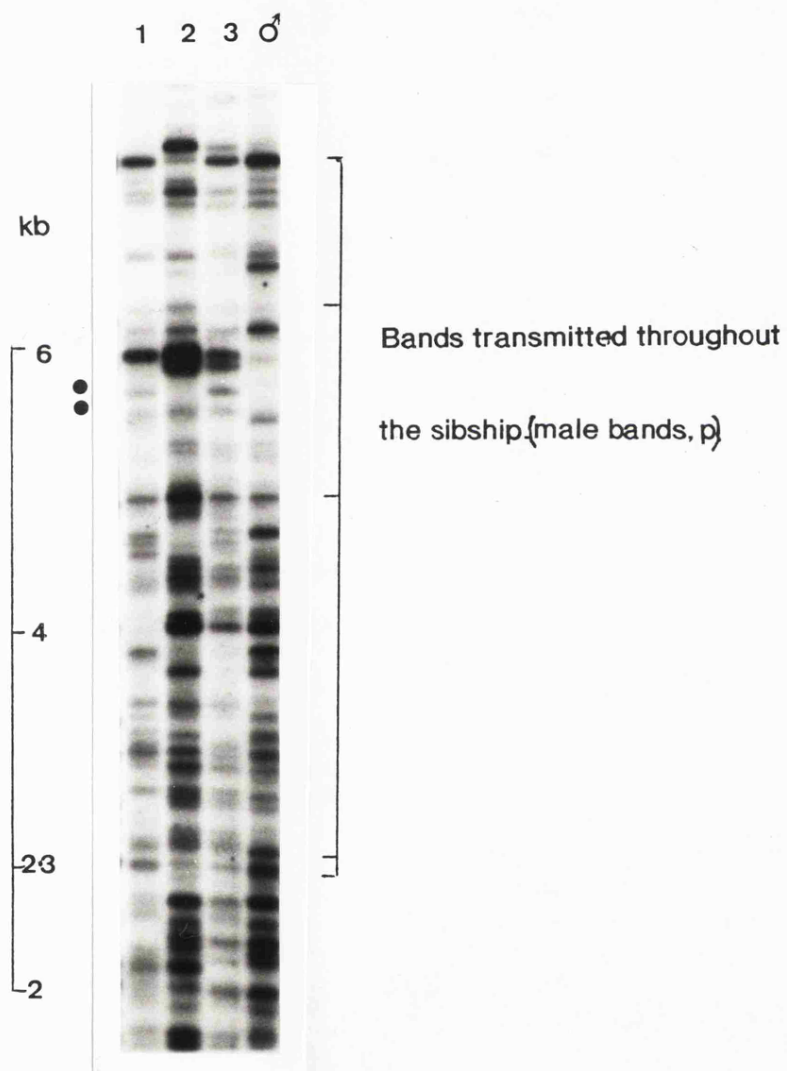
One can quantify linkage, allelism and homozygosity by analysing band sharing between parents and known offspring (Bruford pers. comm.). In large sibships, the the chance of mis-identifying closely linked loci is small, because the probability of band co-segregation (at two loci) occurring in, for example, one parent and 12 offspring, by chance equals  $(p^{1/2})^2 = 0.00024^2 = 5.96 \times 10^{-8} = 5.96 \times 10^{-6}\%$  (where  $p=0.5$ ). In this situation co-segregating loci can be assumed to be linked with some confidence. Alternatively, from one parent and three offspring the chance of two loci co-segregating into all three offspring, is much greater, and equals  $(p^3)^2 = 1.56\%$ .

I was unable to acquire a suitable sibship for rigorous segregation analysis. Thus, with a maximum of only three offspring and one parent it was not possible to quantify true rates of linkage. Fingerprint analysis was then continued assuming linkage, allelism and homozygosity occurred only at low frequency in jackdaws.

Even so the segregation analysis of one male jackdaw and three offspring (Plate 2.4) still demonstrated that bands were shared within the sibship, according to the expectations of the binomial distribution (Sokal & Rolf 1980). Thus, the majority of loci were independently dispersed throughout the genome, (Table 2.1). The

Plate 2.5 DNA fingerprint of a jackdaw family comprising the father and three offspring.

(● example of female bands. q)



**Table 2.1** Segregation analysis of single fragment paternal hypervariable loci in a family of jackdaws (male and 3 offspring).

Transmission to no. of offspring (r)	$f(p=0.5)$ $(q=0.5)$	fex	obs	$\chi^2$
0	0.125	4.75	5	0.25
1	0.375	14.25	15	0.75
2	0.375	14.24	11	3.25
3	0.125	4.75	4	0.75
Totals		38		5.00
Means		9.5	8.75	
Transmission frequency $\pm$ SE	0.577 $\pm$ 0.083			

Segregation was consistent with the expected binomial distribution for transmission frequencies of 50% ( $p = 0.5$ ,  $q = 0.5$ ;  $p^3 + 3p^2q + 3pq^2 + q^3 = 1$ ).  $\chi^2$  test for goodness-of-fit,  $P \ll 0.05$ ,  $df=3$ . U test for concordance (Elliott 1977)  $U = 1.68$ ,  $SE = 50$ , thereby (as  $U \ll SE$ ) also agreeing with the binomial expectation.

percentage of paternal bands transmitted to three offspring was approximately 13% ( $p^2$ ). That five bands co-segregated (6.6% pairs) in all three offspring, implies  $6.6 - 1.56 = 5.04\%$  of alleles were linked, that is four in 38. A much greater sibship was required for the quantification of allelism and homozygosity.

### 2.3.3 Acquiring jackdaw families

As jackdaw nestling mortality was high (Chapter 8) it was necessary to bleed nestlings when young in case they died, or extract DNA from the muscle tissue of dead nestlings, before the DNA had degraded (~24 hours). In the former case I could only initially extract small volumes of blood from the nestlings and hence acquire correspondingly small yields of DNA. The second case required the checking of all nestboxes every day, thereby sustaining an undesirable rate of disturbance. Over the two breeding seasons of 1987 and 1988 I managed to acquire six offspring from one female (GWYW) though DNA was degraded in two cases (from muscle biopsies) and the yield of DNA in the blood of a third nestling was too small for sufficient analysis.

### **3. DIURNAL HABITS, HABITAT USE AND SEASONAL VARIATIONS**

#### **3.1 Introduction**

This chapter collates some general aspects, of the daily habits and movements of the corvid flocks within the study area, relevant to the more specific points of investigation.

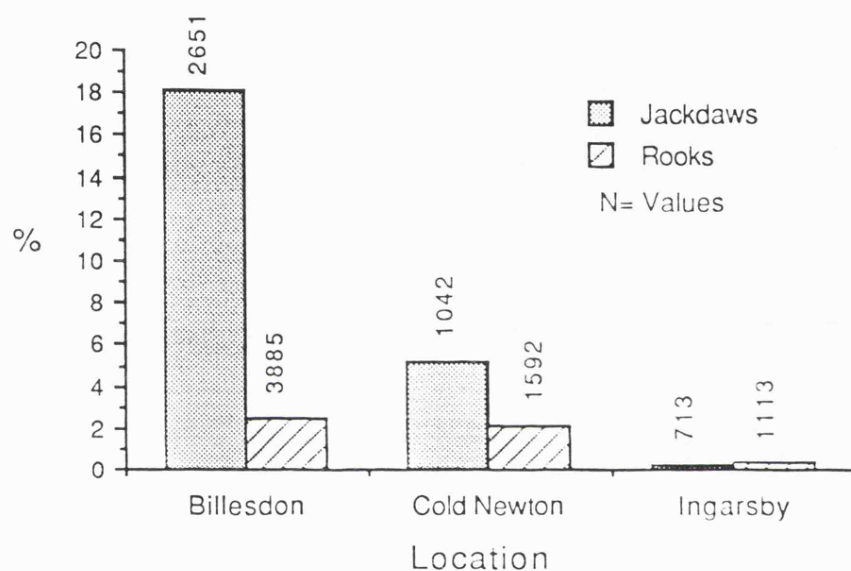
#### **3.2 Dispersion and philopatry**

##### **3.2.1 Empirical data**

Both jackdaws and rooks contained themselves within limited regions of the study area for the majority of the winter (see also Coombs 1961; Patterson et al 1971; Röell 1978). Records of tagged jackdaws at Ingarsby were rare (0.3%) (Fig 3.1) despite close proximity to the Billesdon Coplow rookery (1Km respectively Fig 1.2). Eighteen percent of the jackdaws recorded in the Billesdon region were tagged, and this was similar to the population ratio of non-tagged : tagged individuals. Tagged jackdaws and rooks were recorded at Cold Newton relatively frequently (five and two percent respectively), implying that excursions that far afield were reasonably common. With only six percent of the winter population of rooks tagged, quantitative conclusions were not justified. However, tagged rooks were recorded on only four occasions (from 1113 individuals) at Ingarsby.



**Figure 3.1** Percentage of tagged to untagged rooks and jackdaws in three regions of the study area. All birds were tagged in the Billesdon area, and the proportion encountered there on routine transects remained high.



Thus, birds trapped at the study site, Tom Spinny, generally foraged over an area north and east of the roost (or perhaps centered around the study site rookery). Ingarsby jackdaws roosted at Billesdon Coplow and I recorded eight occasions when jackdaws and rooks left at dawn in the direction of Ingarsby, while a second group of birds established pre-foraging assemblies around the Billesdon Coplow area.

Tagged birds were trapped between April and June of each year and therefore represented the breeding population. Winter flocks of rooks, and possibly jackdaws too, may have been swollen by Scandinavian migrants in winter (Busse 1969; Holyoak 1971), and these migrant birds may wander extensively. However, each major rookery formed the focus for a core of philopatric rooks and jackdaws, that ranged from that point, occasionally overlapping with neighbouring birds, and amalgamating in cold weather. Otherwise each colony utilised a well acquainted region. Jackdaws closely reflected the movements of rooks throughout the winter period (see Chapter 5).

### 3.2.2 From the literature

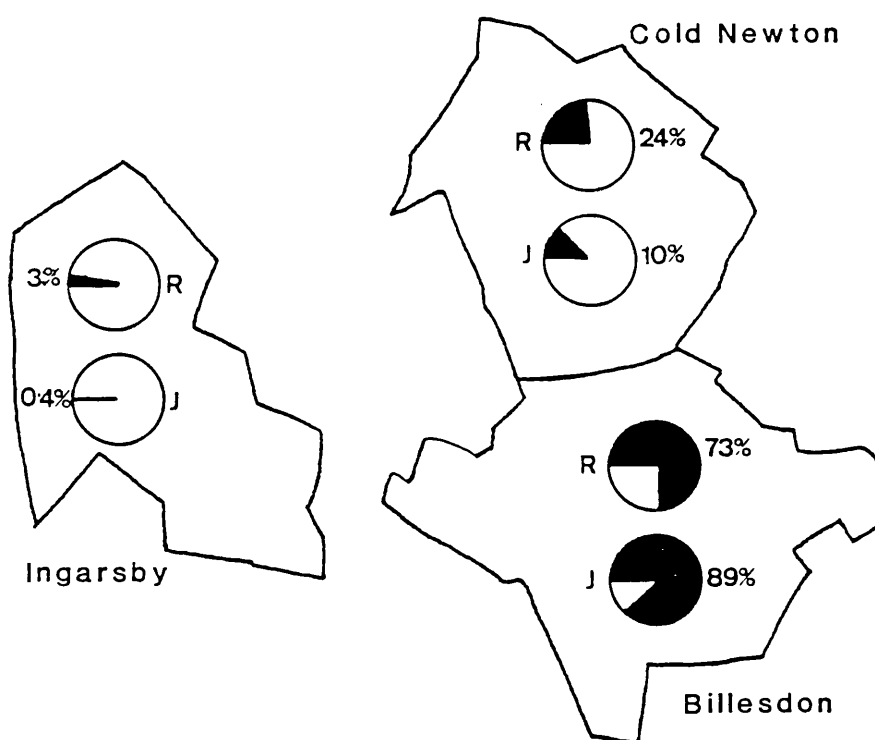
The movements of rooks and jackdaws in winter varies considerably from location to location. McKilligan (1980) discusses at length the winter exodus of rooks and jackdaws from the upper Deeside valley, in contrast to

the winter increase in rooks numbers into the Ythan valley (Dunnet & Patterson 1968; Leitch 1972). Movements appear not to have been correlated with weather but rather with the availability of food, particularly on stubble fields. Across Britain, daily winter movements vary extensively, from up to 45km in Deeside (McKilligan op. cit.) to 1-2km on my study area.

In contrast to the Scottish Highlands, the mosaic of habitats characterised by many lowland areas of England, seems feasibly, to explain the greater dispersion, smaller concentrations, and shorter daily distances travelled by rooks and jackdaws in Leicestershire (see also Staffordshire, Waite 1981). Rooks in Lowland England relied less heavily on grain than their Scottish counterparts (Waite 1981; this study, below). Thus, because grain, earthworms and breeding sites (the latter were scarce in Aberdeenshire, Patterson et al 1971), were more evenly distributed in England, rook distribution reflected the dispersion of these resources. Even so, Scottish rooks were still reported to form core groups, associated with the rookeries from which they originated (Patterson et al 1971).

Phillipson (1933) interpreted the dispersion of foraging winter rook flocks in terms of feeding territories. However, I have seen no evidence of territorial aggression between flocks or groups of individuals.

Figure 3.2 The distribution of tag records about the study area.



In Leicestershire, both rooks and jackdaws were capable of wider movements, as not all tagged birds were accounted for on each circuit transect. By chance I came across one tagged adult jackdaw (GWYW) feeding some 30 miles away in Northamptonshire. The latter individual turned up on the study area at a later date. Nevertheless, for most of the time rooks and jackdaws showed a high degree of site philopatry and affinity towards a particular rookery (Fig 3.2).

### **3.3 Population estimates**

#### **3.3.1 Observations**

The population of rooks and jackdaws within the study area was estimated in the region of 250-300 rooks and 200-250 jackdaws. Evidence for these figures came from four sources.

1) On routine circuit transects (§ 1.4.1) flocks of up to 500 birds (rooks and jackdaws) were rarely encountered, and six flocks of over four hundred birds ( $X=406.8$  rooks and jackdaws only) were recorded in two years. Not all birds in the study area would have been present in these flocks (there was continuous influx and outflux) but they probably reflected a major proportion of the population. Rooks normally out-numbered jackdaws slightly (§ 5.2).

2) A synchronised multi-observer, winter census of the study area, in very poor (wet) weather, revealed 260

rooks but only 180 jackdaws.

3) The number of nests from the three rookeries in the study area totalled approximately 170. Not all nests were occupied (~ 85% occupancy at Tom Spinny), and an estimate of 140 breeding pairs would not have been unreasonable.

4) Jackdaw trapping results provided a population estimate, via application of a capture/mark/recapture technique (Lincoln 1930).

### **3.3.2 The Lincoln capture/mark/recapture index**

#### **3.3.2.1 Procedure**

Forty five adult jackdaws were tagged in 1987. From five trapping sessions, at the same site one year later, there was nine re-traps in a total of 49 birds. The Lincoln method (op. cit.) estimates the size of a population from the equation:

$$P = \frac{a \times R}{r} \quad (3.1)$$

where  $a$  = the number of birds originally marked,  $R$  = the total number of birds trapped in the second year and  $r$  = the number of marked birds re-trapped in the second year. The variance ( $s^2$ ) and confidence limits are calculated from the equations:

$$s^2 = \frac{a^2 R(R - r)}{r^3} \quad (3.2)$$

$$\text{confidence limits} = t \cdot \sqrt{\frac{s^2}{n}} \quad (3.3)$$

These formulae gave a population estimate of  $245 \pm 91.7$  (95% confidence limits). However, the Lincoln mark/recapture method asks for certain conditions to be satisfied if the test is applied.

### 3.3.2.2 Assumptions

Between birds being originally marked and subsequently recaptured:

- i) marking should not affect the animals.
- ii) the marks must last for as long as the study.
- iii) marked animals must be completely mixed in the population before re-sampling.
- iv) the likelihood of capturing an animal must be the same throughout the population.
- v) there must be no immigration or emigration.
- vi) births and deaths can be determined or are not important throughout the period of investigation.

### 3.3.2.3 Justification

By and large the first three conditions were satisfied (see Chapter 8 and Appendix A). There were no obvious adverse effects from tagging, and tags remained intact for at least as long as the study. There was also enough time over the course of one year for tagged birds to be completely dispersed in the population. I had no reason to suppose that traps were in any way selective towards particular groups of jackdaws, for example, those of a certain age or those tagged or untagged. Therefore, condition iv) was apparently satisfied. Condition v) was probably not satisfied and I had then to assume that immigration over the course of one year was not substantial. Jackdaws do undertake internal movements within Britain, though adults are more sedentary than immatures (Busse 1969) and there is evidence that much of the movement is reciprocated (Lack 1987). Violation of this last condition would have led to an overestimate of the population size if, at the extreme, non tagged immigrants 'swamped' tagged residents. However, in my study area the number of originally tagged jackdaws remained high from one year to the next.

For condition vi) I assumed that births replaced untagged deaths. Trapping commenced during the breeding season, thereby eliminating individuals of less than one year old and prone to higher rates of mortality (~45%, Röell 1978). Röell's annual mortality estimates for Dutch adult jackdaws averaged only 20%. Of the original



birds tagged on my study area, 75% were present the following year (§ Chapter 7) inferring that tagged adult 'mortality' rate was also in the region of 20% (allowing for some lost tags and dispersal). Thus tagged birds were surviving and remaining in the area and there was no reason to suppose that deaths were higher amongst tagged individuals than other members of the population.

#### 3.3.2.4 Conclusion

In conclusion, immigration of untagged individuals, mortality amongst tagged birds and loss of tags, possibly resulted in a population overestimation. Thus a study site (Tom Spinny) population of 200 jackdaws was probably realistic. Approximately 40 pairs bred in Billesdon Coplow/Tom Spinny area implying that a large surplus of non-breeding adults and sub-adult birds must have been present. I do not know to what extent the latter group of jackdaws were drawn from other regions of the study area. However, to the present population total we must add other breeding pairs within the study area that would not have been included in the sampling programme. Other than artificial colonies like the study site, jackdaw nests were common but more dispersed than rooks (pers. obs.). I would put an upper limit of 350 individuals on the total study area population, though I have never recorded this number of birds during the winter months, and I feel a population of 250 is more likely.

### 3.4 Winter diurnal activity

#### 3.4.1 Procedure

Twenty-four hour, flock time budgets were compiled from 6 full and 38 half day observations (equivalent to 25 days) between October and February 1986/87 and 1987/88. For the purpose of calculating daily activity, half days were coupled into morning and afternoon combinations. I preferred this method to the alternative of extrapolating from half a day to a whole day, as morning and afternoon behaviour was not necessarily similar.

During each observational period a corvid flock was followed continuously, either from the point of leaving the roost, or in the case of afternoon observations, from the point of location to the point of returning to roost. During each observation period the time allocated by flocks to the following behavioural categories was noted (See Fig. 3.3):

- 1) Foraging - including Walking, active Searching and Feeding behaviour.
- 2) Flying - including flights to and from the roost, between foraging sites and when temporarily disturbed.
- 3) Resting/preening - including pre and post foraging behaviour and periods of inactivity at foraging sites.

**Figure 3.3 Behavioural event categorisation for individual birds (§ 1.4.2) and for flocks (see immediate above).**

Focal sampling categories							Flock categories	
%	ST	WK	PK	LU	FE	SE	ENC	} FORAGING FLYING RESTING ROOSTING
Abbreviations (see 1.4.2):								
ST = Sitting								
WK = Walking								
PK = Pecking								
LU = Looking up								
FE = Feeding								
ENC= Encounter								

4) Roosting - period between birds settling at the roost and leaving the following morning.

The first birds to initiate any one of these activities were timed to the beginning of the next activity, and so on, providing the majority (>50%) of flock members followed suit. The duration of each behavioural event was recorded to the nearest minute. However, difficulties in following flocks over the countryside, probably limited the accuracy of some records to within 5 minutes either side of the observed value. Hence, activities of very short duration may have been under represented should they have occurred out of sight. The flight times of flock disturbances were also recorded to the nearest minute but discounted if less than half of the birds were involved.

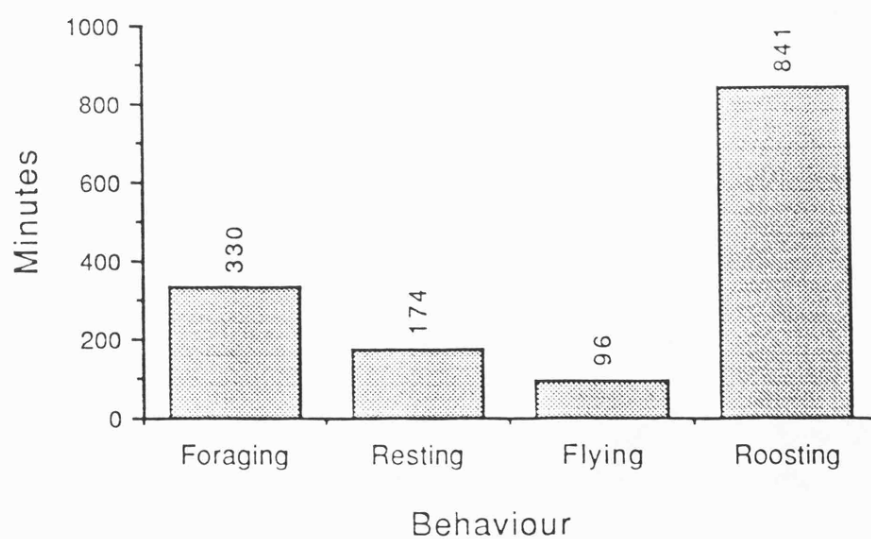
#### 3.4.2 Results

The daily allocation of time is summarised in Table 3.1 and Fig. 3.4. Mean daily foraging time occupied 330 (22.9%) minutes of the day ( mean day length = 570 minutes). Feare et al (1974) calculated rather lower values from N.E Scotland, that appeared to reflect the shorter day lengths of higher latitudes (480 minutes). There may also be habitat specific variations in foraging time. However my estimate stood in good agreement with that of Purchas (1980), who calculated a mean foraging time of 342 minutes/24 hrs during four winter months in

**Table 3.1** The mean winter 24 hour partitioning of time by mixed flocks of rooks and jackdaws. Standard errors follow in parenthesis, N= 26 days.

Behavioural category	Mean duration	
	minutes (SE)	hours
Foraging	330 (10.6)	5.5
Resting/preening	174 (10.8)	2.9
Flying	96 ( 4.6)	1.6
Roosting	841 ( 5.3)	14.0

**Figure 3.4** The mean diurnal partitioning of time by mixed flocks of rooks and jackdaws.



New Zealand (mean day length = 552 mins.). My mean estimates for the other events, roosting, loafing and flying similarly lie in good agreement with those of Purchas (op. cit.), and are relevant, to Chapter 6.

### 3.4.3 Resumé of daily activity

#### 3.4.3.1 Assemblies

At dawn, carrion crows *Corvus corone* were the first corvids to depart from the roost, often calling well before first light. Both rooks and jackdaws departed from the roost at dawn (see also Coombs 1978), after thirty minutes or so of vocalisations and wheeling around over the roost. The departure was sudden and very direct as both species flew together, apparently towards a predetermined destination. The activity of the flock varied according to climatic conditions. In very cold weather birds began to forage immediately, normally on stock feed or amongst straw. More commonly though, the flock would land and remain silent for some fifteen to thirty (mean = 20.17 mins., N= 21) minutes before individuals began to feed or moving away towards other sites. Gradually all members of the flock, of both species, followed these actions.

The purpose of this behaviour was not clear. Though the site of assembly was usually a field or the trees

edging a field, the location was not necessarily an immediate foraging site (on 12 out of 21 occasions foraging commenced elsewhere  $\chi^2 = 0.43$ , N.S, df= 1, where  $H_0$ = 50% of occasions). Birds also gathered before going to roost (see also Coombs 1978), at a location that was rarely the present foraging site (19 out of 20 occasions birds fed elsewhere  $\chi^2 = 16.2$ ,  $P < 0.01$ , df= 1,  $H_0$ = 50%). Towards the end of March and again towards the end of September the rookery was chosen most consistently as the place of assembly. It was possible that during these early morning assemblies, rooks and jackdaws were waiting for improved light conditions, as both species rely extensively on the visual location of prey (per obs.), and passerine visual resolution deteriorates markedly in low light conditions (Sillman 1972). However on cold days, when delays in foraging might have been expensive, the assemblies were subsequently dispensed with, perhaps because food (animal feeds) was invariably predictably placed and demanded little in the way of visual acuity for its detection.

#### **3.4.3.2 Foraging**

Foraging was generally most intensive during the morning (Feare et al 1974; Macdonald & Whelan 1987), and was usually followed by variable periods of resting, loafing and preening, from late morning through to mid afternoon. Except on very mild days, the late afternoon was again a period of intensive feeding, and remained so

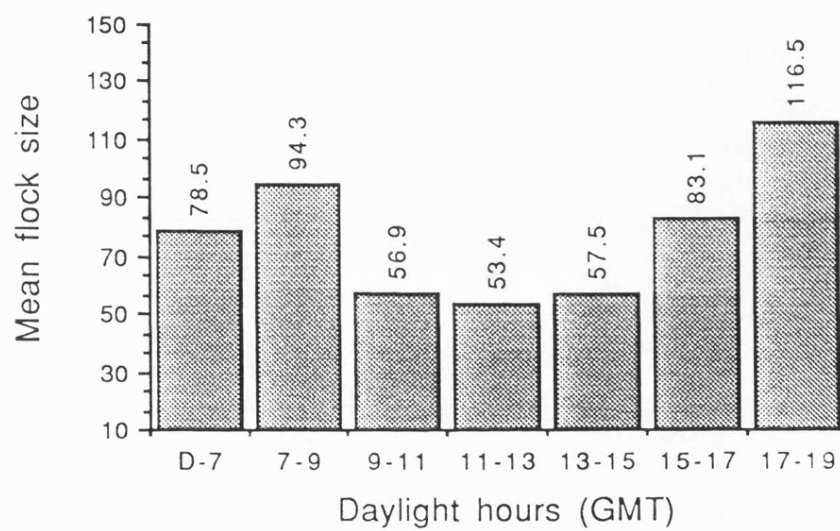
until birds began to gather at pre-roost assemblies. These patterns of activity were attributable to both rooks and jackdaws, though during periods of less intensive foraging the two species were often encountered in smaller, monospecific groups. As a result, flock sizes tended to be smaller during the middle of the day (Fig. 3.5).

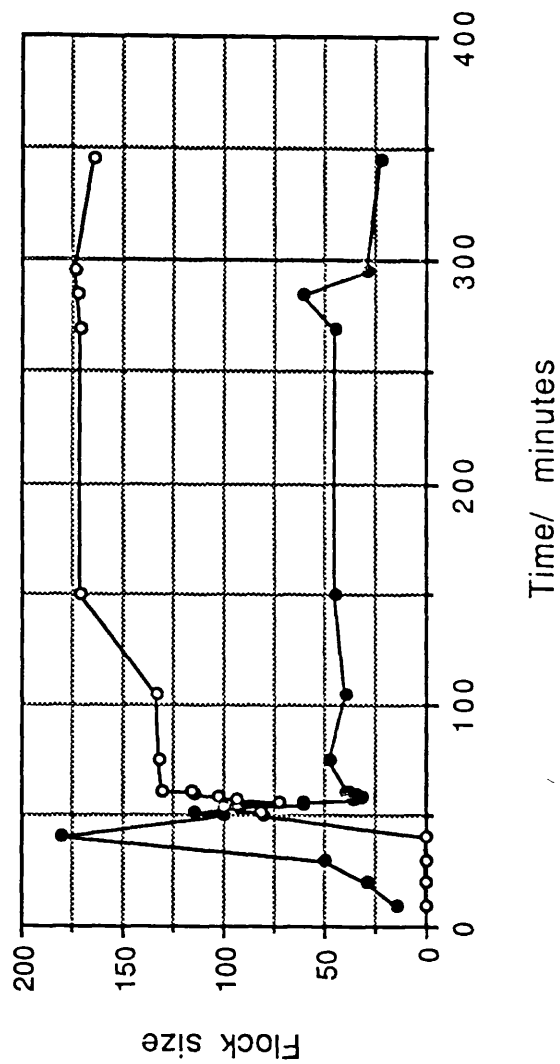
#### 3.4.3.3 Flock dynamics

From large dawn flocks the initial build up of birds normally receded to a steady flow of arrivals and departures, the balance of which dictated whether or not the flock remained at that size or established an equilibrium elsewhere (Fig. 3.6). These equilibrium flocks were similar to those described by Barnard and Thompson (1985) for flocks of lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria*. They formed equilibria as a consequence of continuous input and output of birds, on sites which had reached carrying capacity. The movement within equilibrium flocks was often unsettled and unsynchronised and the continuous influx and outflux of birds suggested that there was constant assessment of the profitability of the foraging location. This assessment was probably based on trade offs (Barnard 1980) between factors such as prey density, depletion and, quality (Chapter 4) and/or intra flock aggression (Chapter 5)(Patterson 1970).



**Figure 3.5** Diurnal variation in flock size of mixed-species flocks of rooks and jackdaws (see 3.6.1).





**Figure 3.6** Simultaneous short term variations in flock size following the initial post-dawn build up on field 17. Note both flocks reach an equilibrium state when undisturbed.

There was generally no obvious explanation for the characteristic and frequent eruptions of flocks into the air (Coombs 1978, provides an account of similar behaviour at rookeries). Large flocks normally resettled after these disruptions but small flocks tended to disperse (see also Barnard and Thompson 1975). Very cold weather always concentrated corvids in the vicinity of recent farm stock supplies. Typically, on such occasions, flocks would be large, and show little variation in either size or composition throughout the day.

### **3.5 Winter habitat use**

#### **3.5.1 Procedure**

All individual jackdaws and rooks encountered on routine circuit transects (§ 1.4.1.) were recorded together with field type. Only foraging flocks (as opposed to resting/loafing assemblies) were considered, and the size and respective composition of each was recorded, along with ambient air temperature. Field type was categorised as follows:

- 1). Pasture with and without livestock.
- 2). Arable: all cultivated land.
- 3). Fields of supplied hay, straw or animal feeds.
- 4). Manure: any field recently (within 7 days) spread with manure.

The estimated proportion of the study area covered by each of these categories was calculated from 1:10,560 scale (6 inches (150mm) to the mile) Ordnance Survey maps. The results are presented in Table 3.2. Appropriate Chi squared values compare habitat availability with rook/jackdaw usage. Assuming complete indifference for any particular habitat, the expected value for habitat usage should approach the environmental availability of each habitat. Hence the figures in row one of Table 3.2 were used as expected values. I had some difficulty in deriving precise measurements of area cover for some habitats. Thus fields in a temporary condition, as when covered with manure, were scored according to the maximum estimated area encountered, on any single observation day during the first two years of the study.

### 3.5.2 Results

Corvid flocks were most commonly associated with farm stock and pasture, but only in proportion to the occurrence of this habitat in the study area (Fig. 3.7). The proportion of time that corvid flocks allocate to foraging on pasture varies across the country according to proportional availability. In northeast Scotland permanent pasture is a rare commodity and Feare et al 1974 found that pasture was utilised by only 36% of rooks. Alternatively, Waite (1984b) observed 80% of rooks foraging on pasture in Staffordshire, which he

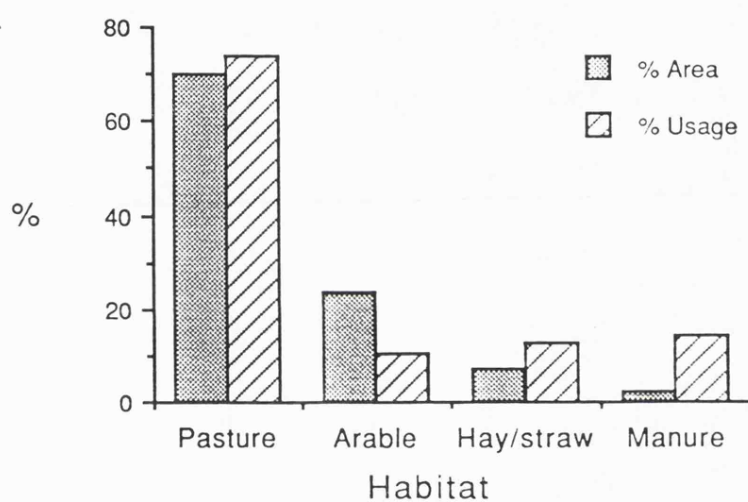
**Table 3.2** Agricultural land usage as a proportion of the study area (% area) and corvid flock usage (% usage) within the same area, over a two year period. N = 272 flocks.

	Habitat			
	Pasture	Arable	Hay/straw	Manure
% area	70.3	23.6	7.1max	2.3max
% usage	74.0	10.6	12.9	14.3
(N)	204	29	35	39

Sum  $\chi^2 = 218$ , df = 3,  $P < 0.001$ .

\* Max., indicates the maximum percentage of study area that fell into these categories over two years.

**Figure 3.7** Utilisation of farmland by flocking rooks and jackdaws.



describes as the most abundant and most utilised crop. My data also demonstrate proportional usage of pasture and suggest that rooks, at least, were not constrained by this habitat alone. In fact rooks and jackdaws were quick to exploit more readily available food types, as and when the opportunity arose, or when climatic conditions prevented otherwise. Consequently, farm activities played an important role in distribution of corvid flocks (see Patterson et al 1971; Fear et al 1974; McKilligan 1980). Manure, by containing substantial quantities of grain (one transect of twenty 25cm<sup>2</sup> quadrats revealed 75.4 grains of wheat and/or barley per m<sup>2</sup>), provided a ready source of food and its application would virtually guarantee the eventual presence of corvids. On 36 out of 39 occasions, rooks or jackdaws foraged on manure within 24 hours of the manure being spread. If the chance of a rook or jackdaw landing on a manure spread field was directly proportional to the area covered by manure, then one would expect to record their presence on that habitat on 2.3% of occasions. Thus  $\chi^2 = 1406$ ,  $P < 0.0001$ ). Hay and straw also provided quantities of grain, weed-seeds and invertebrates, though I did not quantify their true abundance.

Suprisingly, there was no significant difference between the usage of pasture fields with and without farm stock. However since the majority of pasture fields contained stock at some period, I had difficulty a) in deriving meaningful percentage values for area devoid of

stock and b) establishing whether 'empty' fields were made so recently, or had been so for some time. It was also significant that manure was normally spread on fields devoid of stock, and the effect of manure in attracting corvids has already been discussed. Manure was not immediately visible on a field after some two weeks of decomposition, though leached products may still have had a significant, attractive effect on the soil invertebrates (Wallock 1970 (pp 59-60), Edwards and Lofty 1977). A manured field could therefore remain attractive to corvids for some time after spreading, whether farm stock was present or not.

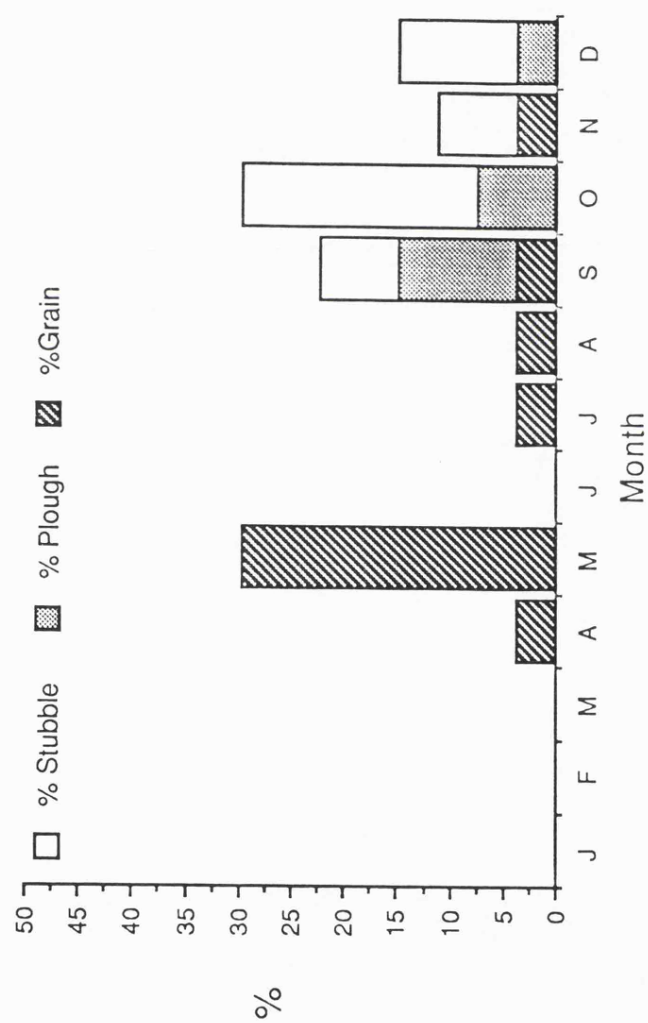
Extensive use of arable land was restricted to late summer and autumn and not normally exploited during the winter months by corvids, except when freshly ploughed (see also Waite 1984b). During the late summer and autumn, arable land was an important source of food, as ripe grain crops and newly sown fields were often intensely exploited (Fig. 3.8).

### **3.6 Seasonal variations in flock size and composition**

#### **3.6.1 Flock size**

I calculated mean flock sizes for each month of the year for two full years. The distribution of flock sizes tended to be heavily skewed towards the smaller groups, with singles and pairs always outnumbering large flocks.





**Figure 3.8** Seasonal variation in the use of arable land by corvid flocks.

Mean values were therefore likely to be underestimations of the flock sizes comprising the largest proportions of individual birds (see also Patterson et al 1971).

Seasons were catergorised in the following way:

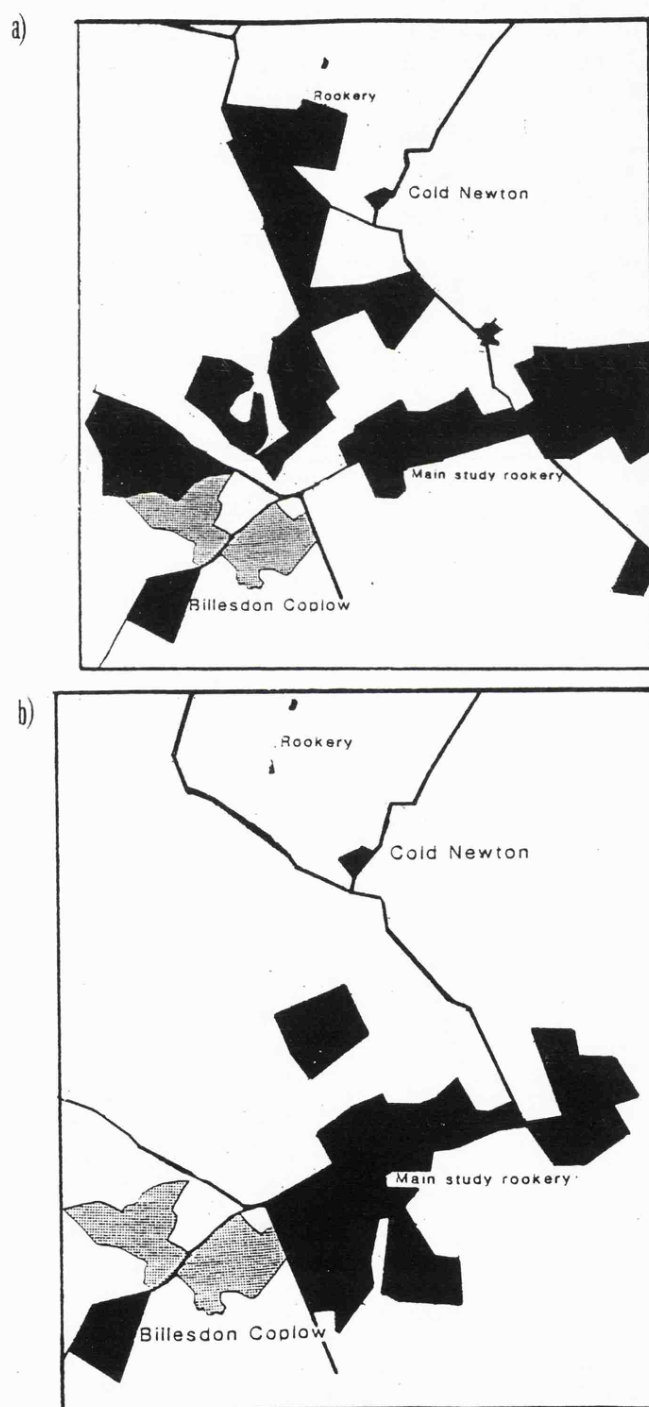
- i) Breeding season - March to May inclusive.
- ii) Summer, June and July
- iii) Late summer/autumn, August to October inclusive.
- iv) Winter, November to February inclusive.

### 3.6.2 Breeding season.

From the mid-March until late-July, most individuals, including many jackdaws, with little interest in the rookery as a nesting site, roosted in the rookery. Some of the latter returned to the winter roost throughout the spring and summer though they reassembled at the rookery each morning. The foraging range at this time was generally contracted to within an area nearer the rookery (see also Macdonald and Whelan 1986)(Fig. 3.9a & b) and I could find no evidence in support of Patterson et al (1971), who found that foraging range expanded at this time of year.

Flock sizes were significantly smaller than the annual mean (74.5) during the spring or early summer ( $\chi^2 = 11.01$ ,  $P < 0.001$ ,  $df = 2$ ) though not during the winter ( $\chi^2 = 1.14$ , N.S,  $df = 3$ ) (Fig. 3.10). Smaller breeding season flock sizes were attributable to the following factors:

Figure 3.9 Change in the distribution of fields utilised by rooks (black regions), from a) winter (November - February) to b) the breeding season (April - May). Birds concentrated their feeding efforts nearer to the rookery (main study site) in the latter period.



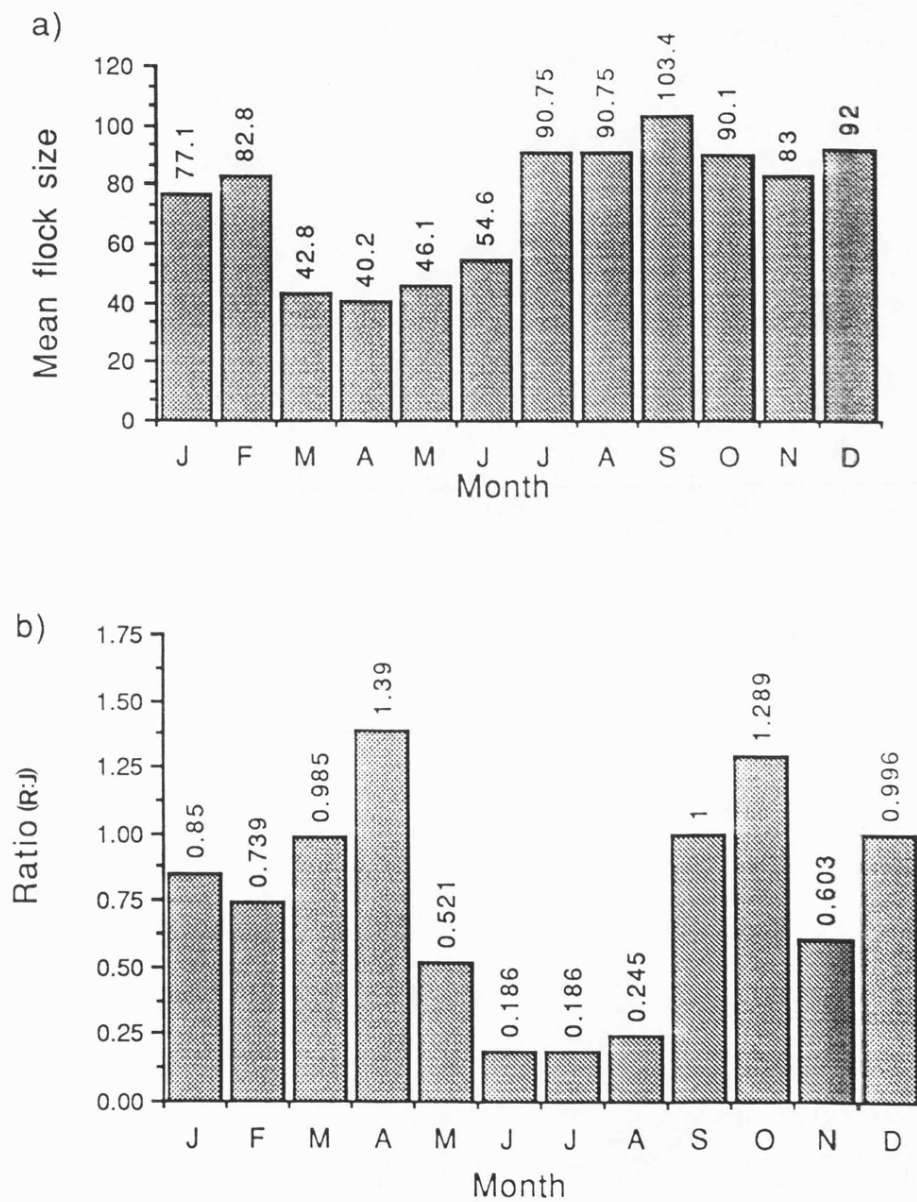
1) The dispersal of breeding birds to species specific breeding sites caused the winter concentration of corvids to disassemble. Thus from April to June inclusive, flocks comprised mainly non-breeding immatures and some locally breeding individuals.

2) Incubating females of both rooks and jackdaws were absent during April and May respectively (pers. obs., Coombs 1978, Røskaft 1981), lowering flock size, but not composition. The ratio of rooks to jackdaws remained high during April.

3) The respective breeding seasons of rooks and jackdaws did not coincide, thus affecting both flock size and composition from May to June (Fig. 3.10b).

4) The prey of jackdaws chicks (dung flies *Scatophaga* spp. pers obs., coleopteran imagines, Holyoak 1968) belonged to the more widely distributed surface invertebrate taxa than those of rooks chicks (Lumbricids and Tipulids e.g. Holyoak 1968). Dung flies in my study area at least, were both a predictable and renewable resource, in that their removal simply allowed immediate recolonisation of the dung pats (pers. obs.). I observed dung flies being carried by adults to chicks, and also on eight occasions (seven different nestboxes) in the gape of chicks upon handling them. Widely and regularly dispersed food is often responsible for reduced clumping in foraging groups (Crook 1965; Cody 1971; Murton et al 1971). Thus the higher ratio of rooks to jackdaws during the May/August period may have been a function of respective food distribution, with Lumbricids remaining

Figure 3.10 Seasonal variation in a) flocks size and b) composition.



more aggregated than arthropods.

5) Jackdaw broods (and to a lesser extent rook broods) hatch asynchronously (Gibbons 1987, pers. obs., see Appendix H ) both between and within broods, thereby preventing neighbouring adults from synchronising their foraging efforts.

### 3.6.3 Summer

Rook flocks were smaller and more dispersed during May, June and early July (Mean=39.8, SE= 6.3)(Patterson et al 1971, Macdonald and Whelan 1986) often forming family groups, though large aggregations of both rooks and jackdaws regularly assembled on freshly cut hay (Mean total flock size on hay was 119.6, SE= 28.8; Mean number of rooks = 65.4, SE= 16.0). Patterson et al (1971) and Feare et al (1974) considered this time of year to be the most difficult for rooks, as earthworms though widespread, were invariably inaccessible below dry surface soils. From the few birds I succeed in tagging (22), adult survival, at least, was good over the summer, while Richardson et al (1979) also recorded good adult annual survival/return rates of 79.2%. Juvenile mortality was nevertheless, high at this time (Stewart 1911; Burkitt 1935; Giban 1947; Holyoak 1971)

Adult jackdaws fared well over the summer with as 75% of tagged birds were recorded over the following winter (1987/88), as discussed in 3.3 above, possibly as a result of arthropods being both widespread and abundant.

#### 3.6.4 Late summer and autumn

From August through to October very large mixed species flocks were again particularly prevalent, initially on areas of cut hay, though later on fields of ripening grain or stubble. (Mean flock size = 94.5). Flocks were swelled by the presence of juvenile birds, rooks, jackdaws and carrion crows, all feeding on the same temporarily abundant resources.

#### 3.7 Functional flocks

Wide fluctuations in the size and composition of corvid flocks (of both species) were associated with both daily and seasonal changes and appeared to reflect food and breeding constraints (Patterson et al 1971; Feare et al 1974; McKilligan 1980; Waite 1981). However, one cannot infer from diurnal variations (Fig. 3.5) in flock size that predator constraints were not operative (Macdonald and Whelan 1986) as the cost/benefit pay-offs of activities other than foraging were not known. It may be that corvids when loafing, preening and flying are less vulnerable to predation than when feeding, and thus warrant only nominal measures of 'flock' safety (that is, to form smaller flocks). Hence, remaining birds continue to forage at greater risk.

The respective reproductive constraints of each species was of temporary importance in reducing flock size during the breeding season, though food at this time of year was

also more accessible and less conducive to the formation of large flocks (Krebs et al 1972). However, individuals free from reproductive constraints (especially immature jackdaws) continued to associate closely with the rookery at this time. The ecological aspects of food, predation and interspecific association receive further attention in Chapter 5 while intraspecific social constraints are investigated in Chapters 6 and 7.

### **3.7.2 Evidence for 'information centres'?**

The information centre hypothesis championed by Ward and Zahavi (1973) (but see Ward 1965; Zahavi 1971) essentially proposed that animal assemblies could be used by unsuccessful foragers to identify and follow previously successful individuals on subsequent foraging forays. Could this phenomenon be a significant function of corvid communities?

#### **3.7.2.1 Rook foraging return times**

The typical daily activity of a rookery was characterised by small numbers of rooks constantly leaving and returning to and from the rookery to feed either chicks or incubating parents. Notably, there was a tendency for departing individuals to be accompanied by conspecifics, while returning birds did so singly or alternatively in large groups that were indicative of some local disturbance elsewhere. I then spent some



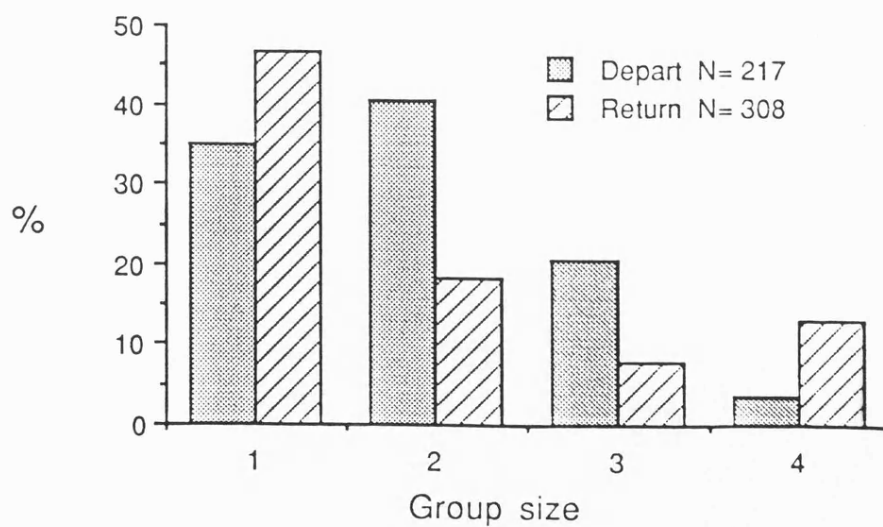
time quantifying the group sizes of rook departures and returns, by measuring the occurrence frequency of five group size classes, during five 10 minute sampling periods spread over two consecutive days (Table 3.3). Rooks were feeding pulli at this time.

The most striking feature of the data was the discrepancy between the percentage of birds leaving and returning in groups of two or three, in contrast to the 46% of individuals returning alone. One can draw two basic conclusions from this information. On the one hand, as foraging birds accumulate enough food, depending upon the demands of the offspring, they return as necessary back to the rookery, regardless of the whether other birds are ready to return or not. Would birds 'normally' return singly if it were not for their breeding responsibilities? Alternatively, the data may imply a preferential tendency for birds to follow or accompany others to but not back from foraging sites, consistent with the information centre hypothesis. The preponderance of departing groups of two birds, may also have reflected the likelihood that paired birds were foraging together. Thus from these data alone it would be unwise to infer too much, as it was difficult to predict an expected distribution of group sizes. Corvid colonies nevertheless, provide a promising capacity for further investigations of the information centre hypothesis, as many of the ecological criteria required for the implementation of an information centre are contained within the social framework of corvid

**Table 3.3** The percentage distribution of group sizes among rooks departing from and returning to the rookery during foraging forays.

Group size	1	2	3	4	>5	
Return	46.8	18.2	7.8	13.0	14.3	N= 308
Depart	35.0	40.6	20.7	3.7	0	N= 217

**Figure 3.11** Demonstrating the difference in groups size distribution of rooks departing from and and returning to the rookery during foraging forays.



coloniality (see Introduction and Chapter 7).

### 3.8 Summary

1) Both rooks and jackdaws were largely sedentary, restricting their movements to ~2km circumference.

2) Movements and breeding dispersion were consistent with a heterogeneous "patchwork" type habitat.

3) Population of the study area estimated at:

300-360 rooks

250-300 jackdaws

4) Annual mortality in jackdaws was ~20%. No estimate for rooks.

5) Mean active winter day (9.5 hours) for both species, included 5.5 hour foraging.

6) 70% of annual foraging was confined to pasture, though there was significant selection for farm 'provisions', especially spread manure and cut hay. Arable stocks were infrequently but intensively exploited.

7) Diurnal flock size reflected feeding commitments.

8) Breeding commitments and probably summer prey distribution lowered flock size and species composition respectively.

## 4 INVERTEBRATE PREY DISTRIBUTION AND ENERGY CONTENT

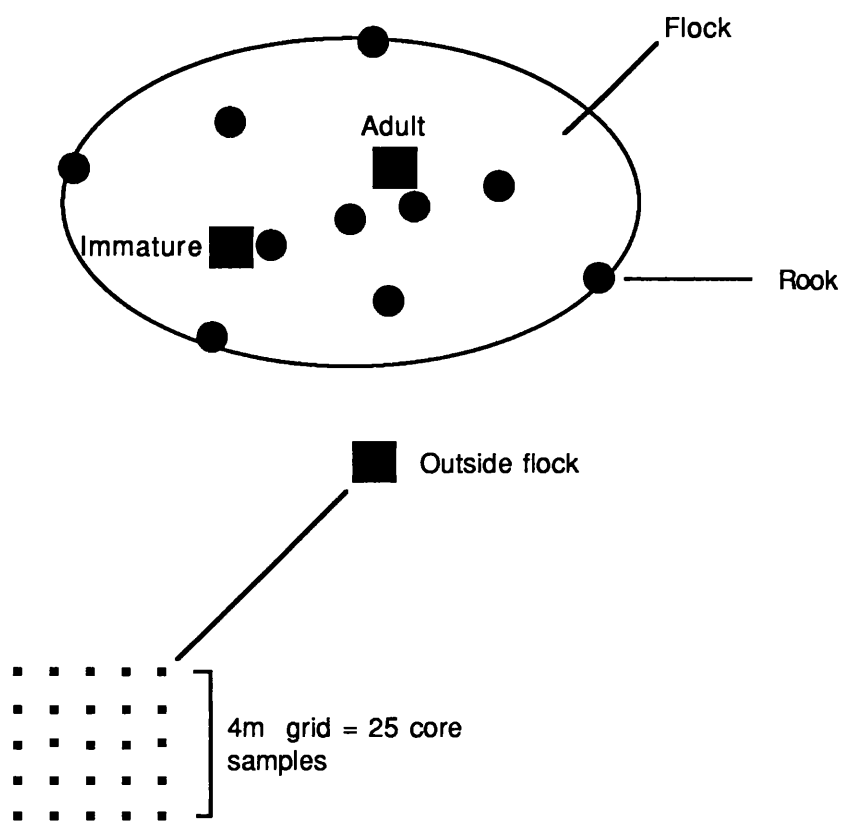
### 4.1 Introduction

As the Lumbricidae feature extensively in the diet of rooks their size and profile allowed some quantification of prey choice and energy intake (Barnard and Thompson 1985), from which one could investigate variations in the foraging successes of individual birds (Chapter 6). In this Chapter I investigate the local distribution of earthworms and their energy content within the immediate environment of corvid flocks, and compared the relative distribution of other soil invertebrates that featured in the diet of rooks and jackdaws.

### 4.2 Soil invertebrate analysis

#### 4.2.1 Sampling

Twenty five core samples (7.5cm x 4cm deep) were taken from 4m<sup>2</sup> grids from areas of pasture where immediately prior to sampling, flocks (N=19) of rooks and jackdaws had been observed feeding (§ 3.4.1). The intention was to establish the relationship between flock size and prey availability. Where possible, two grids were sampled from within each flock (as close as possible to areas being utilised by adults and immature birds respectively) and one beyond the flock 'edge' (always sited midway between the position of the nearest bird and the field perimeter) (Fig. 4.1). Locating the position of

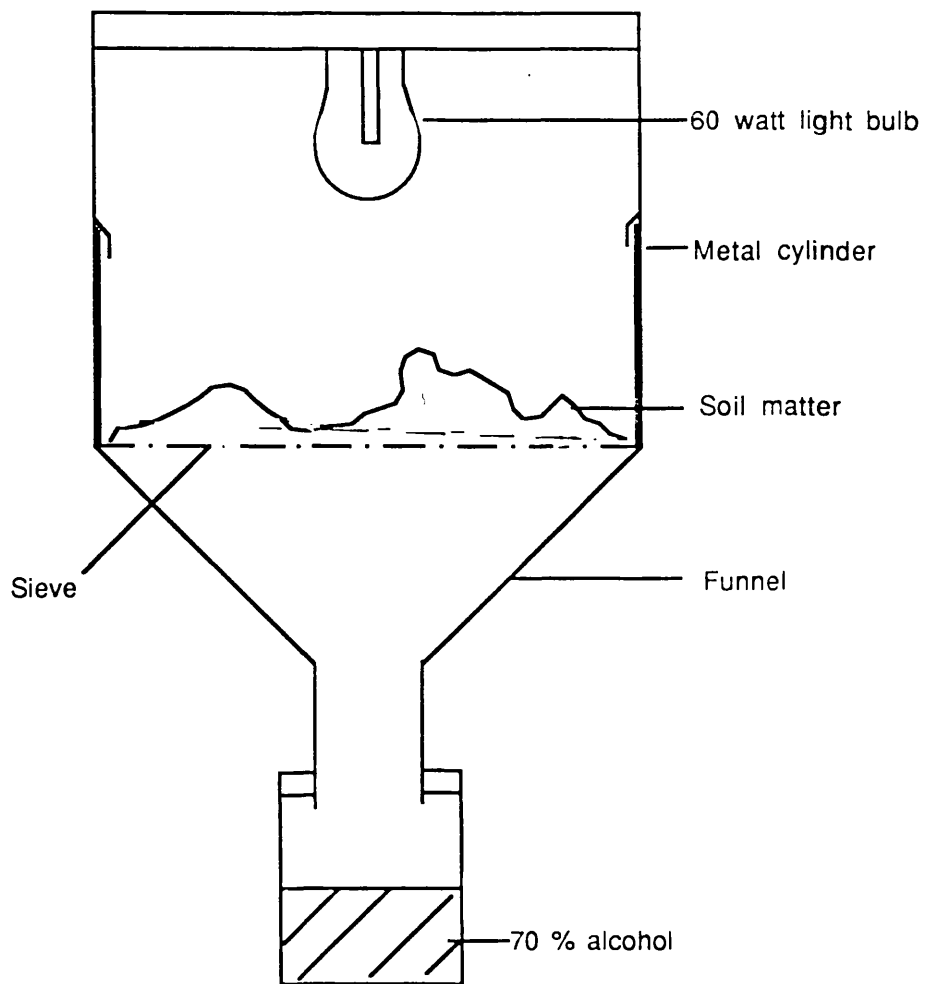


**Figure 4.1** Hypothetical flock diagram illustrating typical positions of three 4m invertebrate sampling grids taken from each flock (two inside the flock and one outside).

specific birds was difficult, and I needed to rely on landmarks such as fence posts and vegetation, as well as the distance between myself and the 'target' birds (measure with a camera lens) in order to locate as precise a sampling position as possible. I always concentrated on the position of the representative immature bird, and placed a marker there before removing samples from an adult position. Adult positions, because they were more numerous, did not require such critical placing as the positions of the immature birds, and this was also true of the positioning of the third grid beyond the flock perimeter. With immature foraging positions, I erred towards the direction from which the bird was last observed moving, thereby increasing my chances of sampling ground covered by that individual.

#### 4.2.2 Preparation and classification

Soil core samples were initially hand sorted in lateral transverse sections of 1 cm deep so that I could formulate a relationship between soil depth and invertebrate abundance. Hand sorting removed the majority of animals, especially the large ones, but small animals that I had overlooked were removed by Berlese-Tullgren funnel extraction (Southwood 1978) over the course of a seven day period. Earthworm specimens were sorted according to contracted length, prior to preservation in 70% alcohol. Unit length energy values were obtained



**Figure 4.2** Design of the Berlese-Tullgren extraction funnel for collecting animals from soil. The animals move away from the heat of the bulb.

using standard bomb calorimetry techniques (Southwood 1978) after the relationship between dry weight and earthworm length had been established. Dry weights were determined by first, air drying the samples at 60°C, until the weight had stabilized. The samples were then vacuum dried at 60°C until the weight had stabilized once more (Clark pers. comm.). Pre-preserved length classes were categorised as follows: <10mm, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, >90mm. Three pellets from each earthworm size class were prepared for bomb calorimetry. Other invertebrates were simply classified as miscellaneous, but belonged to the following taxa: Coleopteridae (larvae and imagines particularly of staphilinidae, scarabidae and curculionidae), Tipulidae (larvae and imagines), Scathophagidae, Arenidae, Gastropodidae plus unidentified diptera larvae. These miscellaneous invertebrates were air/vacuum dried and weighed.

Though the field identification of actual corvid prey items was rarely achieved to species, for the sake of completion I tested earthworm species for interspecific (Gerard 1964) discrepancies in the unit energy content. I also prepared a second series of earthworm size classes for bomb calorimetry, as before, but this time with the gut contents removed (pushed out), thereby testing the significance of the gut composition on the final energy value.

Dry weight and energy content values for the earthworm



**Table 4.1a** Unit energy values of earthworm size classes with full gut contents and emptied gut contents. Mean dry weights and energy content per size class are also given.

Size class (mm)	Mean energy content Joules/mg		Mean weight/ grammes	Joules per length(mm)	N
	a(full)	b(empty)			
<10-20	22.61	22.28	0.013	293.9	57
21-30	23.60	21.74	0.039	920.4	57
31-40	22.40	23.03	0.065	1456.1	99
41-50	22.34	22.14	0.061	1362.7	39
51-60	23.95	21.53	0.110	2634.5	27
61-70	23.11	20.79	0.222	5210.4	12
71-80	23.47	25.24	0.401	9411.5	7
>90	23.38	25.10	0.682	15945.2	9
Mean(SE)	23.21(.32)	22.39(.54)			

**b.** Mean energy values (Joules/mg) of lumped size classes (SE).

	10-40mm	41-90mm
Full gut	22.87 (0.36)	23.22 (1.34)
Empty gut	22.29 (0.21)	22.52 (0.37)

treatments above are presented in Table 4.1.

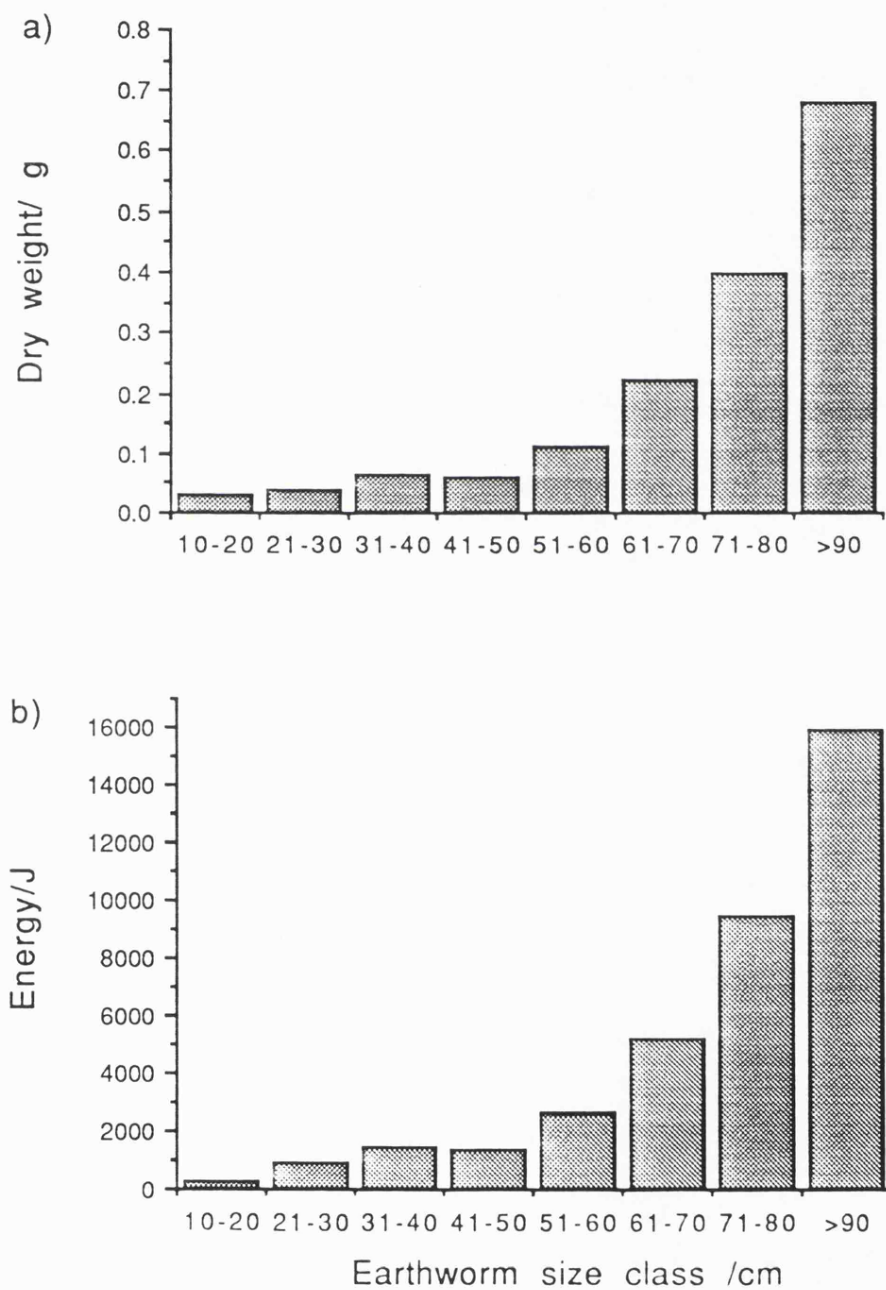
#### 4.2.3 Energy evaluation

Longer earthworms weighed proportionally more, per unit length, than shorter individuals (Fig. 4.3a). Dry weight, multiplied by the unit energy content of the earthworms, resulted in column five in Table 4.1. Again the energy content of the larger earthworm size classes increased disproportionately (Fig. 4.3b).

The mean unit calorific content of earthworms in larger, and smaller categories varied only slightly, (Table 4.1, columns 2 & 3) with a greater margin of difference (though still not significant) across the 'full gut' category and indicative of a disproportionate increase in internal volume of the larger earthworms.

I was unable to detect significant interspecific differences in the energy content of earthworms species, nor were there significant differences between earthworms with full and empty guts (Table 4.1b). Bolton and Phillipson (1976) showed that slight interspecific discrepancies were apparent according to the mode of existence of the earthworms under scrutiny and due to the organic composition of their gut contents. For example 'epigées' - defined as those which feed on leaf litter - were more likely, because of the lower organic content of their diet, to yield lower quantities of unit energy than

**Figure 4.3** The variation in a) dry weight and b) energy content of earthworms, as a function of earthworm length.

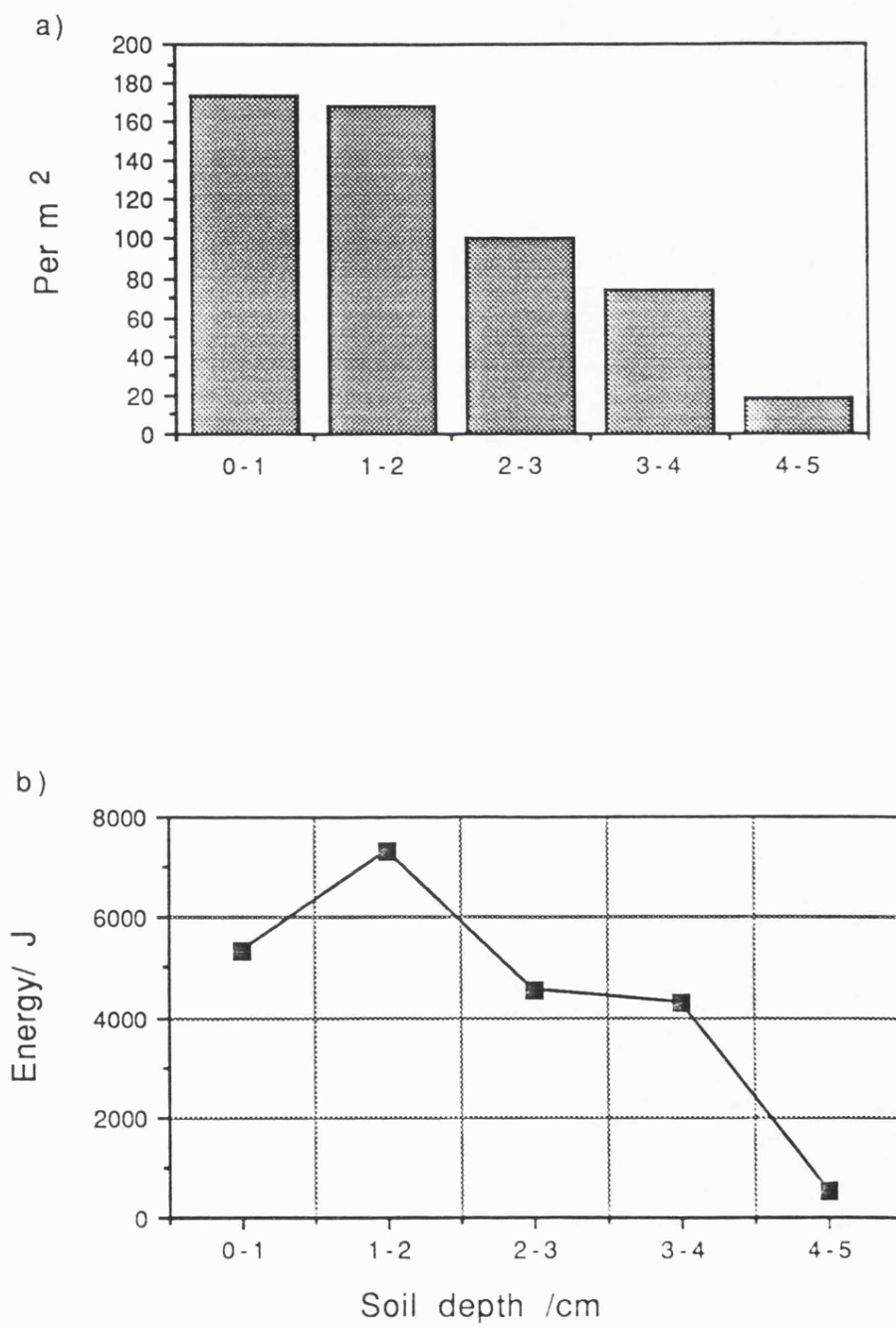


'endogées' - defined as those that feed directly on organic material available near the soil surface. The commonest species sampled in my study were *Allolobophora chlorotica* (Savigny) and *A. caliginosa* (Savigny), which are both endogeas, and *Lumbricus castaneus* (Savigny) which is an epigee. Bolton and Philipson (op. cit.) explain that in clay soils, a relatively low subsurface organic content causes the differences between endogées and epigées to be less marked. All earthworm specimens sampled in my study originated from areas of open pasture, consisting predominantly of clay soils. With slight errors of up to 3.5% of the mean ('full gut' unit energy value per species), during bomb calorimetry any small interspecific discrepancies were likely to have been obscured.

#### 4.2.4 Vertical distribution

Typically the overall abundance, dry weight and available energy of soil organisms increased towards the soil surface (Fig. 4.4a, see also Wallock 1970). Thus the greatest concentration of both prey items and potential energy, lay in this upper region. Depths from the surface down to 2cm were of greatest interest as these were potentially accessible to both rooks and jackdaws. However, subsurface invertebrate energy content (top 2cms) also varied consistently with the invertebrate energy content of deeper levels (Spearman's  $r_s = 0.7298$ ,  $P=0.005$ ; Fig 4.4b).

**Figure 4.4** The vertical distribution of invertebrate abundance (a) and energy content (b) within 5cm deep core samples.



**Table 4.2.** Spearman rank correlations ( $r_s$ ) between earthworm quantity and quality (energy) with respect to other miscellaneous invertebrates.  $N=19$ .

Earthworm parameter	Other invertebrates Parameter			
	Dry weight		abundance	
	$r_s$	$P$	$r_s$	$P$
<b>Top 2cms of sample:</b>				
Dry weight	0.578	0.005	0.467	0.022
Abundance	0.364	0.063	0.434	0.032
Energy content	0.426	0.035	0.447	0.027
<b>Total sample (5cms):</b>				
Energy content	0.578	0.005	0.508	0.013

Hence overall patch quality could be assessed from either surface or subsurface cues.

The abundance, biomass and energy content of earthworms sampled from all levels of the soil varied significantly and positively with other invertebrate stocks (Table 4.2). Thirty-three percent ( $r_s^2$ ) of the variance in earthworm abundance was explained by variation in other invertebrates. Therefore the presence or absence of one (either earthworms or miscellaneous invertebrates) could have predicted the presence or absence of the other. This substantial and important level of co-occurrence between the relative staple diets of rooks and jackdaws (Lockie 1956b; Holyoak 1968) provides great latitude for interspecific social attraction (§ Chapter 5).

#### 4.2.5 The effects of temperature

Only the total energy content of the 5cm core samples correlated significantly with temperature (Spearman's  $r_s = -0.427$ ,  $P < 0.34$ ,  $N = 19$ ). No other parameters, such as abundance and biomass, were affected significantly, though for the 19 sampled flocks the air temperature was (deliberately) never extreme, varying only between 6°C and 12.5°C (mean = 9.05, SE = 0.49) and therefore unlikely to have caused severe changes in the distribution of soil invertebrates. The negative correlation possibly reflected the migration of earthworms away from the soil surface when conditions were drying (Green 1980).

#### 4.2.6 The effects of rainfall

I did not measure rainfall on the 19 invertebrate sampling occasions as I deliberately tried to sample on uniform days when conditions were not extreme (to minimise confounding climatic variables). Consequently, I was never sure, in advance, of knowing the days on which I would be sampling. However I did acquire rainfall data from a local source (Appendix D), though it did not vary significantly enough to account for variations in invertebrate distribution (Spearman's  $r_s = 0.103$ , NS).

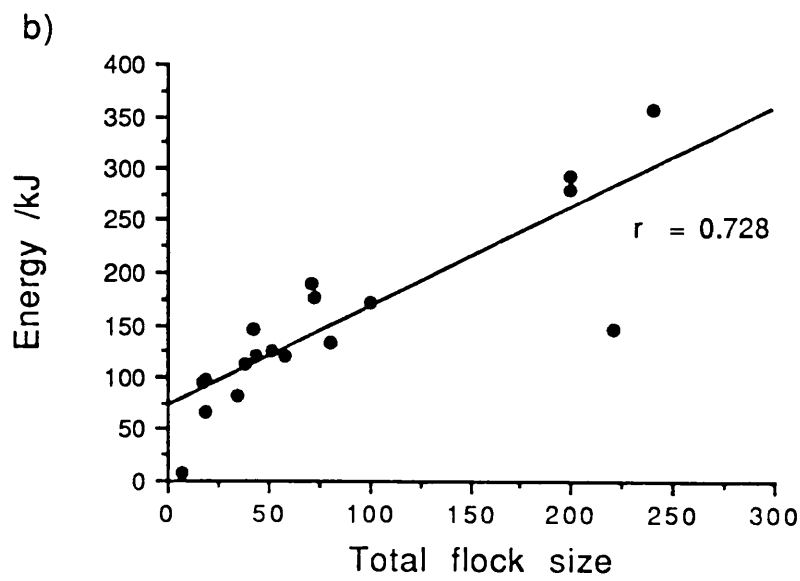
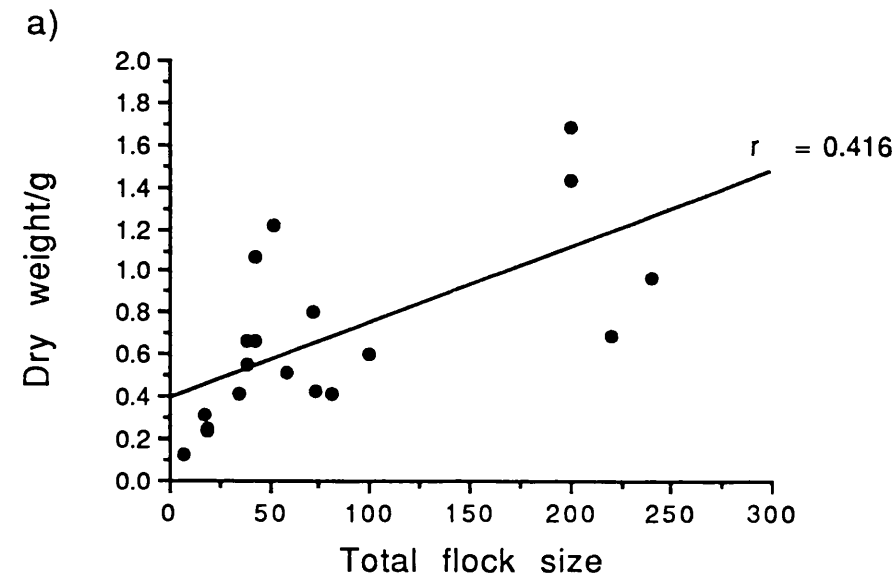
#### 4.3 Prey availability

##### 4.3.1 Flock size

Fluctuations in the energy content of soil invertebrates accounted for 53% ( $r_s^2$ ) of the variation in mixed species flock size (Fig 4.5a;  $r^2 = 0.728$ ,  $P = 0.000$ ,  $N = 19$ ). Biomass was less strongly correlated  $r^2 = 0.416$ ,  $P < 0.01$ ; Fig. 4.5b). The correlation coefficient between flock size and energy content was strengthened (1.5% and 1.7% for rooks and jackdaws respectively) when the effects of temperature were controlled for (see partial regression analysis, Sokal and Rolf 1969), implying that a small proportion of the variation in flock size, previously explained by the 'energy content of available prey', was instead attributable to variations in ambient



**Figure 4.5** The regressions of a) invertebrate biomass and b) energy content on flock size.



temperature.

Invertebrate abundance and flock size were poorly correlated, providing some indirect evidence that selection for prey quality was operative. In Chapter 6 this point is treated more thoroughly.

#### 4.3.2 Rook age distribution

There was no significant differences in the mean biomass ( $/m^2$ ) of invertebrates, sampled with respect to the positions of foraging (§ 4.2.1) adult and immature rooks ( $X_a = 44.2$ ,  $SE = 2.64$ ;  $X_i = 41.1$ ,  $SE = 4.61$ ;  $t = 0.75$   $df = 11$ , N.S.). However, the variance was marginally greater in immatures and perhaps indicative of a greater degree of inconsistency over their choice of foraging position. Adults were found on areas of pasture marginally but not significantly higher in invertebrate biomass compared to those areas not being utilised ( $X_{nu} = 33.86$ ,  $SE = 2.22$ ,  $t = 2.03$ ,  $df = 11$ ,  $P < 0.05$ ) (Fig 4.6).

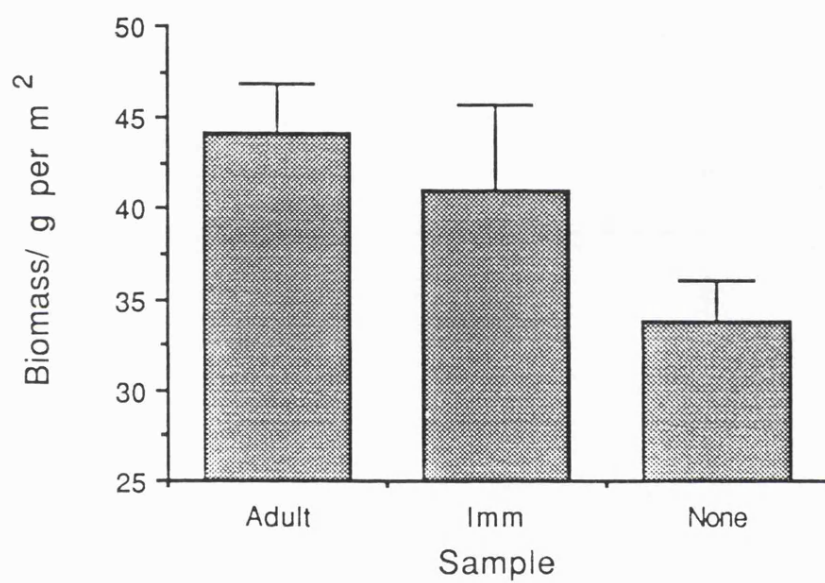
#### 4.4 Summary

1) Larger earthworms contained proportionally more energy than smaller individuals

2) Abundance, biomass and available energy of soil organisms increased towards the soil surface.

3) Subsurface energy varied consistently with energy at deeper levels.

**Figure 4.6** Earthworm biomass with respect to adult and immature foraging positions (Error bars = tx SE).



4) Abundance, biomass and energy content of earthworms varied consistently with other invertebrate stocks.

5) Total flock size was correlated with invertebrate energy content and biomass.

6) Adult and immature rooks fed on areas of similar soil invertebrate biomass.

## 5 INTERSPECIFIC ASSOCIATIONS

### 5.1 Introduction

Röell (1978) and Waite (1984a) postulated that dilution of interference from carrion crows *C. corone* L. may have been one possible benefit of rook/jackdaw mixed-species associations. Thus, flocks of rooks and jackdaws may deplete the resources of a carrion crows territory, for which the latter responds aggressively (pers. obs.). However, this manifestation of the 'dilution effect' (Hamilton 1971), while possibly of some significance, failed to explain the necessity, specifically, for mixed species flocks.

The major costs of mixed species flocking include those familiar to single species flocks, that is, competition for food and agonistic behaviour (Caraco 1979; Barnard & Thompson 1985). Possible benefits include social facilitation (Krebs et al 1972) and predator detection (Lazarus 1979; Barnard 1980), or protection (Hamilton 1971). In heterogeneous habitats, clumped food resources often occur together, with the food of one predator species existing by that of a second. Foraging guilds may therefore comprise species with distinct foraging niches (Perrins 1979) that spatially and temporarily co-occur. Alternatively, species with greatly dissimilar food requirements may still associate but benefit in a different manner. An example is the improved per capita vigilance afforded by the treecreeper *Certhia familiaris*

L. when associating with Parids, (Henderson In press). Otherwise, species with broad dietary requirements may share features which allow them to exploit the successes of each other (Krebs et al 1972).

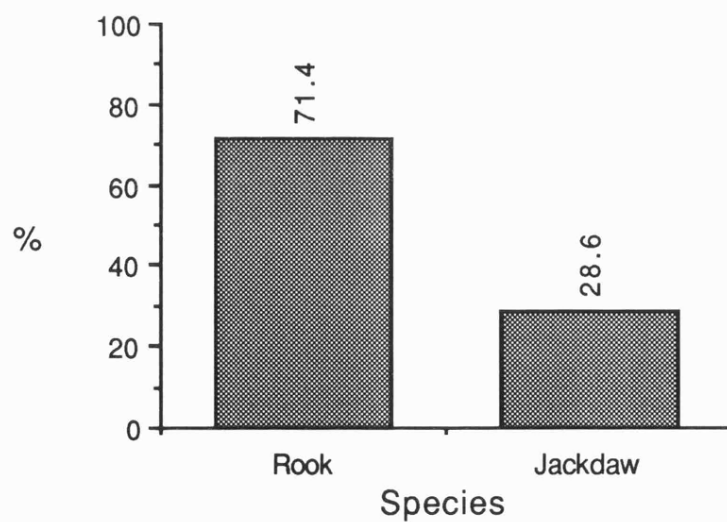
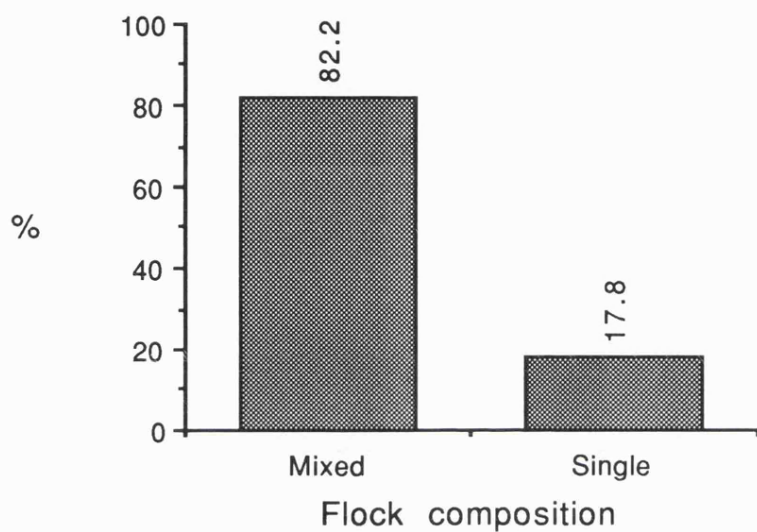
The basic concept of cost/benefit analysis has not been completed in rooks and jackdaws and this chapter investigates the frequency of association between the two species, relating this to their respective foraging niches. Questions are approached concerning the development of mixed-species flocking, and the factors responsible for the maintenance of interspecific aggregations, preempting those which challenge the necessity of kinship in flocking birds.

## 5.2 Frequency of association

I measured the degree of affiliation between rooks and jackdaws, from routine circuit transects (§1.4.1), over a period of two years (from the 12/12/85 to 14/12/87). Thus 276 foraging flocks comprised 227 mixed species and 49 single species flocks ( $\chi^2 = 114.8$ ,  $P < 0.01$ ,  $df=1$ , where  $H_0$  expects 50% mixed flocks by chance) (Fig. 5.1a). Mixed species flocks were therefore markedly predominant, implying an active rather than coincidental or passive relationship.

The 49 single species flocks comprised 35 rook and 14 jackdaw flocks ( $\chi^2 = 9.0$ ,  $P < 0.01$ ,  $df= 1$ ,  $H_0 = 50\%$  of flocks) (Fig. 5.1b), though of the two species, jackdaws, because of their more general choice of habitat (Coombs

**Figure 5.1** a) the percentage of flocks comprising mixed or single species, and b) the percentage of single species flocks comprising either rooks or jackdaws.



1978), were those most likely to have been overlooked. One single species jackdaw flock comprised 105 members but all other single species flocks comprised fewer than 50 members (Fig. 5.2). No large ( $>50$ ,  $N=38$ ) flocks of rooks were devoid of jackdaws. A positive correlation existed between rook and jackdaw numbers in mixed species flocks (Pearson correlation  $r^2=0.654$ ,  $N=136$ ,  $P<0.01$ ; Fig. 5.3), suggestive of continued, positive payoffs for both species.

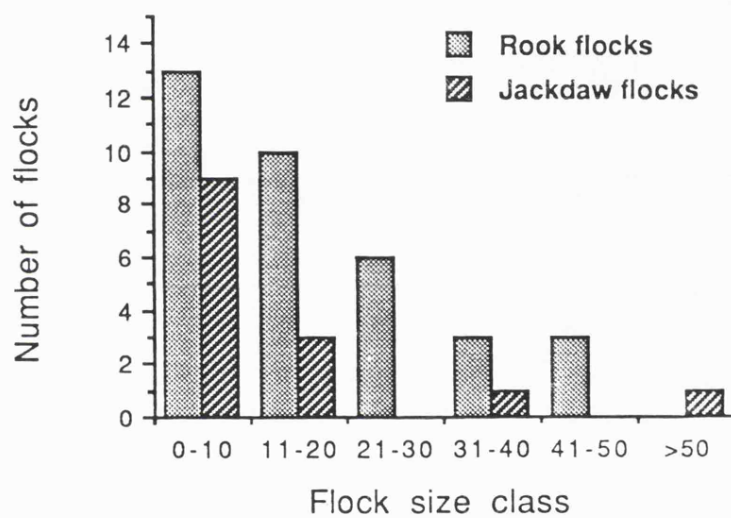
### 5.3. Social attraction

#### 5.3.1 Intra flock species distribution

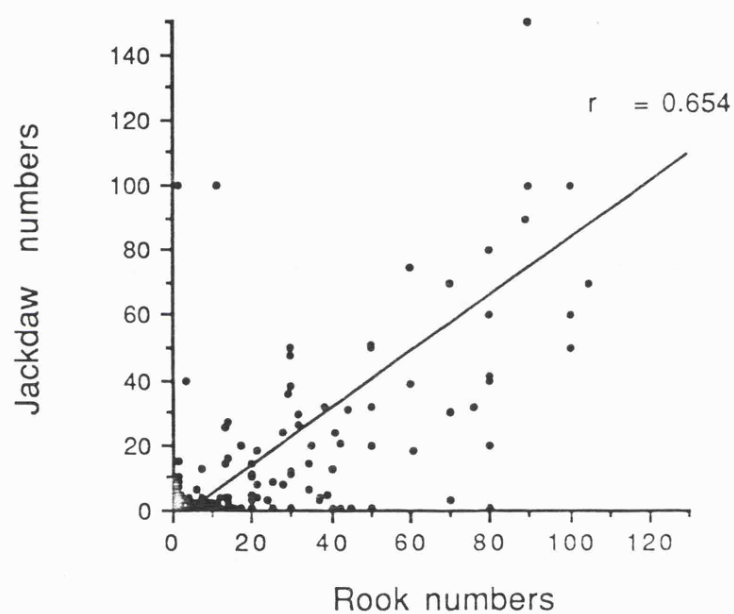
The extent of inter and intra specific social attraction was initially monitored by counting the neighbours a) of all individual birds from 35 flocks and b) of all incoming birds from 43 flocks during 10 minute sample periods. In the first case, the procedure involved the scanning of each flock, systematically noting the successive neighbours of each individual bird in turn. Perhaps the weakness of the technique was its reliance, to a point, upon a certain degree of subjectivity, as there were several occasions when I had difficulty deciding which of the next group of individuals was nearest the one under scrutiny. Perspective exacerbated the problem due to the difficulty of judging distances between individuals positioned along a common line of vision. For this reason flocks viewed



**Figure 5.2** The breakdown of single species flocks into flock size classes.  
Note few flocks comprised more than 30 individuals.



**Figure 5.3** Regression of jackdaw numbers on rook numbers in mixed species flocks, with rooks tending to predominate



either on a hillside, or with the observer elevated on a valley side, were most accurately assessed. These were the situations in which I chose to analyse flocks for signs of contagious species distribution. For the record, I began with the left hand most bird and worked across each flock with a telescope, thereby obtaining reasonably systematic and repeatable data. Thus the following hypothetical sequence of individuals,

R J J R R R R J

would have scored four RR (rook), one JJ (jackdaw) and three RJ (rook/jackdaw) combinations. Table 5.1 summarises the results for both a) and b) above.

#### 5.3.1.1 Results

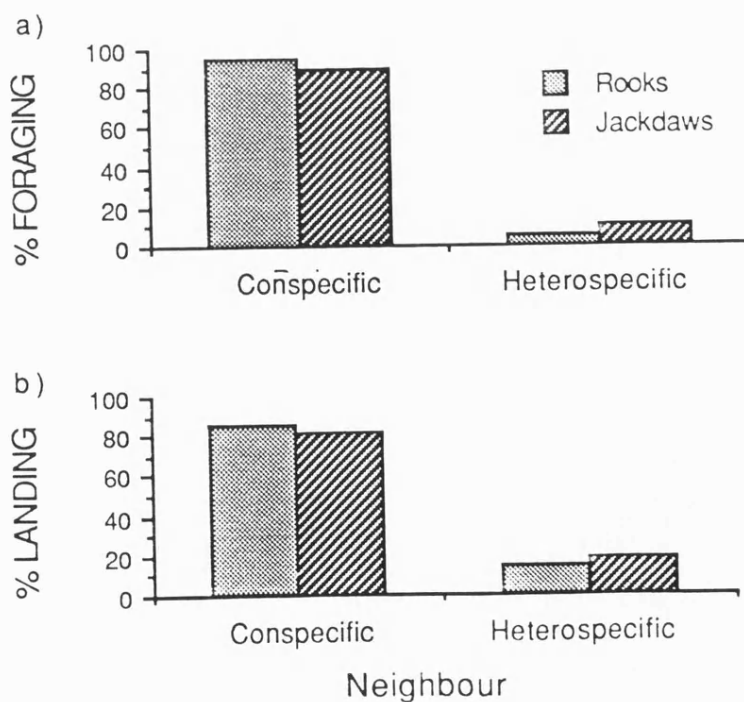
Clearly both rooks and jackdaws foraged more frequently in the vicinity of conspecifics than heterospecifics ( $\chi^2 = 721$ ,  $P < 0.001$ ,  $df = 2$ , assuming complete random mixing; Fig. 5.4a) and both species showed a significant tendency to land by members of their own species ( $\chi^2 = 167.3$ ,  $P < 0.001$ ,  $df = 1$ ; Fig. 5.4b). Seven percent mixing (RJ combinations) was further indication of an aggregated distribution, over and above the effects of paired ( $\sigma/\sigma$ ) partnerships. This is because, at the extreme, equal numbers of each species in randomly distributed male/female pairs, would be expected to produce between 33% and 50% mixed (R/J) species pairs (Fig. 5.5).

**Table 5.1** The nearest neighbours of both foraging and incoming rooks and jackdaws amongst mixed species flocks.

Nearest neighbour	Foraging <sup>*</sup>		Landing	
	rook	jackdaw	rook	jackdaw
Rook	711	82	186	29
Jackdaw	82	339	30	125
TOTALS	783	421	216	154

(<sup>\*</sup>  $p^2(RR)=0.424$ ,  $q^2(JJ)=0.123$ ,  $2pq(RJ)=0.455$ .)

**Figure 5.4** The percentage of rooks or jackdaws a) foraging and b) landing in the vicinity of conspecifics.



**Figure 5.5** A diagrammatic representation of the probability of obtaining rook/jackdaw combinations in mixed flocks of faithful rook (RR) and jackdaw (JJ) pairs (o/o).

1) Simplest case,

RRJJ

∴  
N= 3 combinations  
RJ= 33%.

2) More complex case,

RRJJRRJJRRJJRRJJRRJJRRJJRRJJRRJJRRJJ

∴  
N= 39 combinations  
RJ (19) = 48.7%

And so on.

No array of pairs can increase the coefficient of mixing beyond 50% or decrease it below 33% without inferring either greater clumping or greater dispersal over and above an array of purely sexual partnerships. If the percentage of mixed pairs lies between 33% and 50%, the result is inconclusive and no degree of interspecific social attraction or repulsion can be implicated (but see text 5.2.1.2).

### 5.3.2 Index of interspecific mixing

To try and attain more rigorous quantification of the data I applied Busse's formula (1977) which treats a distribution of birds as a complete 'string'. Busse (op. cit.) derived his index to analyse the proportion of mixing that occurred amongst groups of terns *Sterna* spp. and black-headed gulls *Larus ridibundus* L., while both feeding and nesting. Essentially, the technique calculates a preference factor  $V$ , as an expression of the degree of aggregation within a species. The analysis is based upon a comparison of two estimated values of the expected level of aggregation,  $C_e$  which assumes no mixing and  $C_r$  which assumes complete mixing, of the species concerned, with a third value  $C_o$  which is the actual observed value of species specific aggregation. The index is calculated using the following procedure:

- $n_1$  = the number of rooks (species R) in the flock.
- $n_2$  = the number of jackdaws (species J) in the flock.
- $n$  = the total number of birds,  $n_1 + n_2$ .

Observed and expected values are then generated for the frequency of the following pairings:

- RR where neighbours are rooks (conspecific)
- JJ where neighbours are jackdaws (conspecific)
- RJ where neighbours are heterospecific.

As previously stated, the flock is viewed as a single line or string, and the expected value for respective mixing, assuming the two species never mix, follows the expression  $C_e = n - 1$ , because aggregation will equal the number of each species R (or J) minus the end individual which is treated as a neighbour of the other species. Thus  $C_e$  for:

$$RR = n - 1$$

$$JJ = n - 1$$

$$RJ = 1$$

$$\text{all combinations together} = n - 1$$

The actual (observed) value of mixing, assuming the first and last birds are neighbours is  $C_o$  therefore:

the observed numbers of  $RR = C_o$

" " " of  $JJ = C_o$

" " " of  $RJ = C_o$

" " " for all types =  $C_o = n - 1$ .

[ $C_o = n$  for large flocks]

Assuming absolute indifference (random association) then formulated expressions for  $RR$ ,  $JJ$ ,  $RJ$  respectively are for  $RR$  &  $JJ$ ,

$$C_r = (n_4 - 1) \times \left( \frac{n_i}{n_4} \right)^2 \quad (n_i = n_1 \text{ or } n_2) \quad (5.1)$$

and for RJ,

$$C_r = (n_4 - 1) \times 2 \times \frac{N_1 \cdot N_2}{n_4^2} \quad (5.2)$$

The preference factor V can now be calculated for RR, JJ and RJ from the expression:

$$V = \frac{C_o - C_r}{C_e - C_r} \quad (5.3)$$

If  $V=1$ , then the species concerned is considered to be completely aggregated. If  $V=0$  then the species are completely mixed. If  $V<0$  and therefore negative, then a positive attraction for the opposite species is implied.

I tested Busse's index on data from 35 flocks, each flock having been worked through as described above. The results are presented in Table 5.2.

The results of the exercise implied that approximately 73% ( $V \times 100$ , Table 5.2) of rooks and 70% of jackdaws foraged in the proximity of conspecific neighbours. The percentage of non mixing (85.8%) was significantly greater than expected for complete random and indifferent mixing ( $\chi^2 = 23.2$ ,  $P < 0.001$ ,  $H_0 = 50\%$  RJ combinations).

Since rooks and jackdaws were strongly associated with one another, and yet their distribution within flocks was



**Table 5.2** A summary of the progression through Busse's (1977) formula for calculating of the degree of interspecific mixing within 35 foraging flocks of rooks and jackdaws.

	$N$	$C_e$	$C_o$	$C_r$	$V$
RR	1044	1043	939	653.8	0.733
JJ	622	621	504	232.1	0.699
RJ	--	1	111	779.1	0.858*
Total	1666	1665			

\*

If  $C_o$  (RJ) is small compared with  $C_r$ , then  $V$  is large.

If  $C_o$  (RR or JJ) is small in relation to  $C_e$  then  $V$  is negative.

If  $C_o$  (RR or JJ) is equal to  $C_r$  then  $V = 0$  (implying complete mixing).

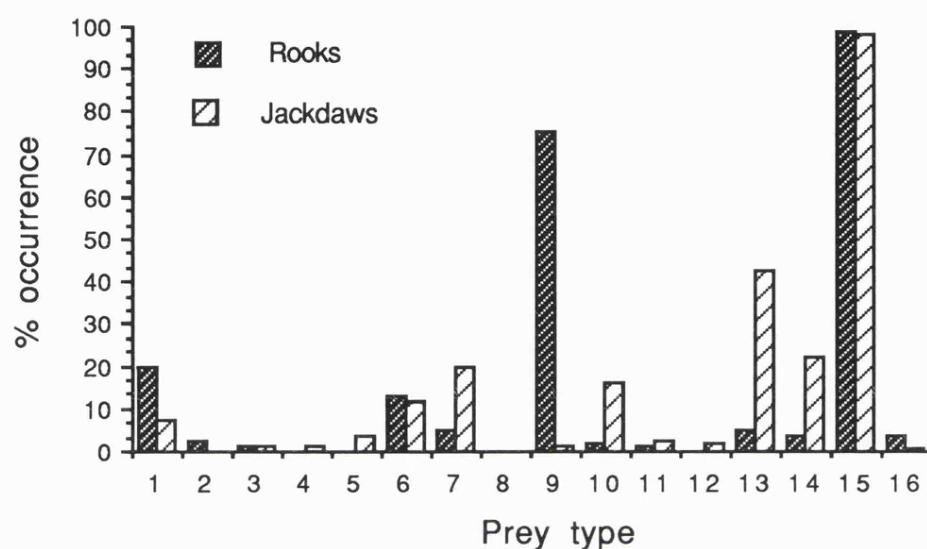
aggregated towards species specific groups, the inference was that they did not habitually use each other for fine tuning of resource acquisition, but were able to use the more specific signals of their own species to greater effect. No tendency was expressed for one or other species to occupy more central or more peripheral positions ( $\chi^2 = 8.81$ ,  $df = 2$ , N.S.,  $H_0 = 50\%$  chance of being located either centrally or peripherally), providing little evidence of serious interspecific interference, though the costs of peripheral foraging (reduced prey density, pers. obs. §6.1; higher risk of predation, Hamilton 1971) might well outweigh those costs experienced from interference in central positions.

#### 5.4 Foraging niches

Accurate evaluation of the diet content of jackdaws required more than observational information, as food items were extremely difficult to identify when being consumed and I had little confidence in the representativeness of the data. Thus strictly comparable field data with rooks (Chapter 6), permitting energy and error analysis were not available.

I had neither the means nor the mental disposition to 'obtain' jackdaw/rook stomachs for useful analysis, on a subject already adequately supplied with suitable information (Holyoak 1968). Hence I was compelled to make use of this same published information for studying

**Figure 5.6** The winter diet of rooks and jackdaws (Nov-Feb, from Holyoak 1968).



1. Miscellaneous insects
2. Lepidoptera larvae and pupae
3. Diptera larvae and pupae
4. Diptera imagines
5. Miscellaneous coleoptera larvae
6. Miscellaneous coleoptera imagines
7. Curculionidae
8. Arachnidae
9. Oligochaetidae
10. Gastropodidae
11. Carrion
12. Fruit
13. Weedseeds
14. Farm produce (excluding grain)
15. Grain
16. Acorns

niche divergence.

Holyoak (op. cit.) demonstrated seasonal variations in the selection of food items, of various corvid species (from lowland farm areas of England and Wales) based on the frequency with which stomachs contained particular prey items. It was therefore possible to draw up a visual comparison of the winter foraging niches of rooks and jackdaws, from Holyoak's data (Fig. 5.6). However quantitative methods for niches analysis were available and I was subsequently able to access more precise information, by applying a formulated index of niche overlap to this same data, above.

#### 5.4.1 Niche overlap

From the data above, I was able to compute an estimate of niche overlap for foraging rooks and jackdaws, according to Sale (1977), using Colwell and Futuyma's index (1971) which is similar to Schoener's index (1968). Thus,

$$C_o = 1 - \frac{1}{2} \sum |p_i - p_k| \quad (5.4)$$

where  $p_i$  and  $p_k$  represent (in this case) the proportion of stomachs belonging to the  $i$ th (jackdaws) and  $k$ th (rooks) species respectively, containing each specific winter food resource (of which there were 14 with all coleoptera categories combined). The indices vary

between 1 (complete overlap of resources) to zero (no overlap of resources). Linton et al (1981) tested by computer simulation, the limitations of Schoener's and three other niche indices (Morista 1959, Horn 1966, Pianka 1973). Schoener's index performed well, in accurately predicting computer generated resource overlaps, especially in the range of between 5 and 85%. Only when overlap increased above 95% did Schoener's index perform inadequately. I therefore accepted that Schoener's index would provide a reliable test of niche overlap under the conditions.

#### 5.4.1.1 Results

By calculating  $C_o$ , I obtaining a resource overlap value of ( $C_o$ ) 0.761, demonstrating, on the basis of these data, that rooks and jackdaws shared a 76% overlap in diet.

#### 5.4.2 Competition free overlap

Sale (1977) takes Colwell and Futayma's (1971) index further by quantifying 'Competition Free Overlap'. This was an important addition to the analysis as a common diet does not in itself imply the existence of competition, particularly when dietary requirements are broad. Thus, competition free overlap determines the mean overlap for a group of synthesised niches by rearranging the actual array of resources equally available to each species concerned. The synthesised

niches share the number of resources, the niche breadths and niche shapes of each species, but each species' use of resources becomes independent of the other species. Thus they are competition free. If competition free overlap exceeds the actual niche overlap, then interspecific competition has been a significant factor in arranging the resource priorities of the two species concerned. Alternatively, if competition free overlap is less than the actual overlap, then according to Sale (1971) competition is unlikely to have been a significant factor between the two species, because their niches have expanded with increased sympatry.

#### 5.4.2.1 Results

$C_{cf}$  (Sale op. cit.) was calculated from Schoener's index for 14 rearranged arrays of the same comparative data ( $p_i$  and  $p_k$ ) used above (Appendix E, Table 1). The mean and standard deviation of the 14 values of  $C_{cf}$  provided a 'Null' expectation for comparison with the previously computed value  $C_o$ , the observed niche overlap. Significant differences between  $C_o$  and  $C_{cf}$  were evaluated by t-test, according to the formula:

$$t = \frac{[C_{cf} - C_o] \sqrt{\frac{N}{N+1}}}{\sigma} \quad (5.5)$$

where  $N$  = the number of degrees of freedom (i.e. the range

of resources included (14)) and  $\sigma$  = the standard deviation of  $C_{cf}$ . For rooks and jackdaws,

$$C_{cf} = 0.326$$

$$C_o = 0.716$$

$$t = 2.576$$

$$df = 13$$

$$P < 0.05$$

The model predicts that if  $C_{cf} < C_o$  then interspecific competition should not be invoked as a significant factor operating between the two species concerned. On the basis of Holyoak's data, this conclusion is true for rooks and jackdaws.

#### 5.4.3 Conclusion

The fundamental niches of rooks and jackdaws, were broad and overlapped extensively, but despite this overlap certain food items feature prominently in the diet of each species. Other than grain (readily exploited by both species) earthworms feature as the major component of the rook's diet. Waite (1981) concluded that earthworms account for as much as 60% (by weight) of the diet of rooks, (but only 25% of intake). From my own behavioural observations I positively identified earthworms on 28% of occasions, (probably an underestimation), and while Holyoak's data (Fig. 5.7a) did not approach this figure (perhaps because

identification relied heavily upon the detection of earthworm chaetae) there was little doubt that earthworms were one of the most important dietary components.

By contrast, earthworms were accounted for in only 6.3% of jackdaw stomachs (and I could only positively identify them on 2.1% of occasions), a void filled by vegetable matter (weed seeds) and more importantly, by species of coleoptera (Fig. 5.7b). Neither of the latter two items figured significantly in the stomachs of rooks.

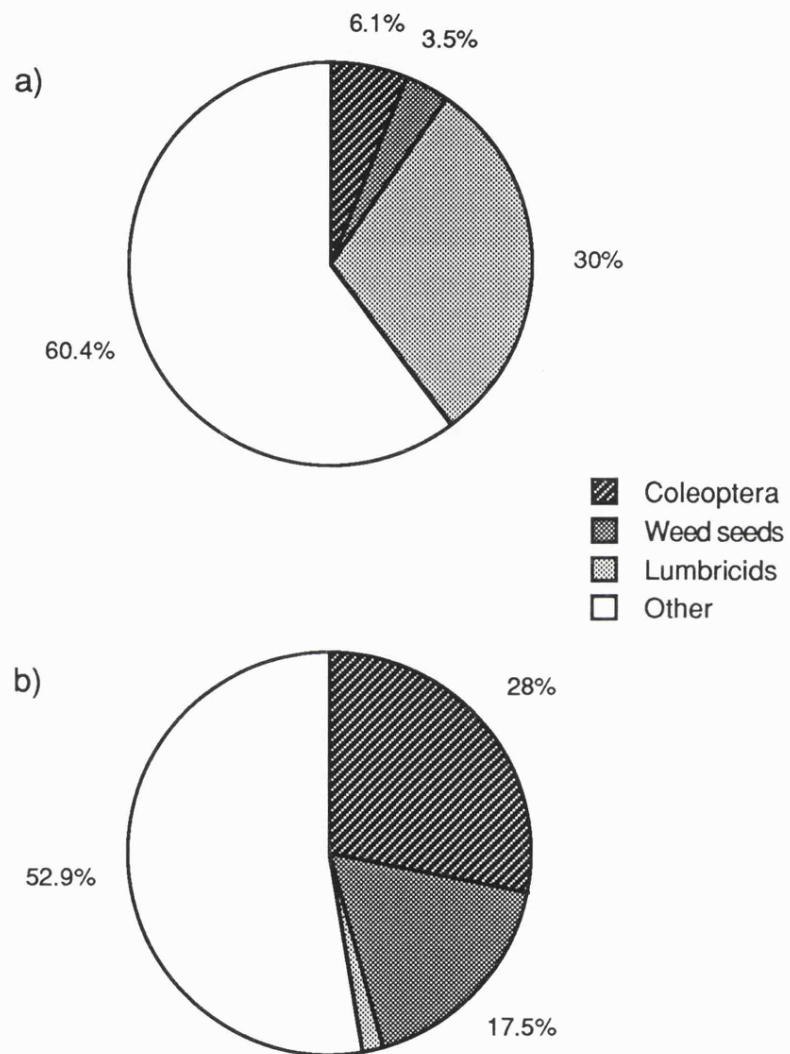
High overlap indices have also been estimated for habitat preferences in rooks and jackdaws (Loman 1980; Waite 1984b; Olsson and Persson 1979). Waite (op. cit.) then concludes that micro-habitat and prey choice are responsible for stable sympatry, as rooks, "were unique in their tendency to take prey from the beneath the soil surface (See also Olsson and Persson op. cit.) and jackdaws in taking small invertebrates".

Typically, when the resources of two sympatric species are superimposed then one species suffers local extinction to the advantage of the most dominant species (see for example, Begon et al 1986). Resource overlap does not necessarily lead to competition; only when a resource is limiting will competition occur. This assumes that each species cannot retreat into more specialised 'realized' niches.

Clearly the two species have much in common in terms of the range of prey items utilised, and on the available



**Figure 5.7** Comparing the major winter (Nov-Feb) food items of a) rooks and b) jackdaws (data from Holyoak 1968).



evidence I would interpret this common ground as a firm basis for interspecific social facilitation (or "local enhancement" see Thorpe 1963; Crook 1965; Krebs 1973), enabling rooks and jackdaws to use each other as indicators of patch quality.

## **5.5 Resource distribution**

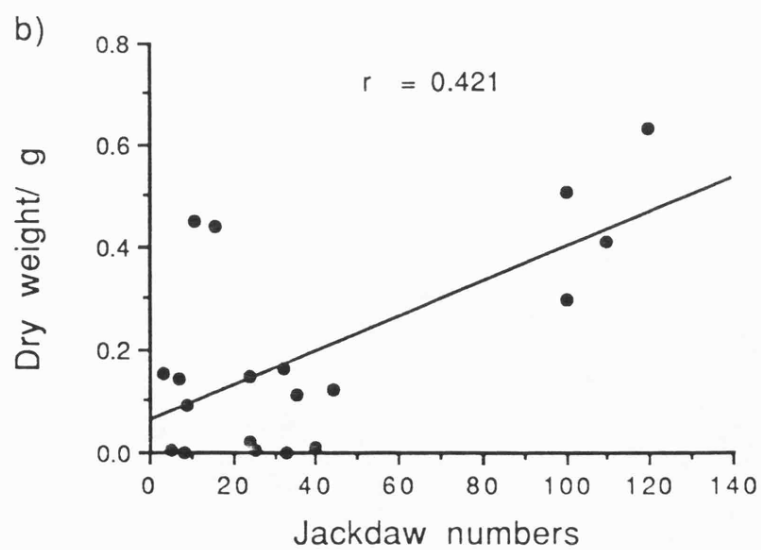
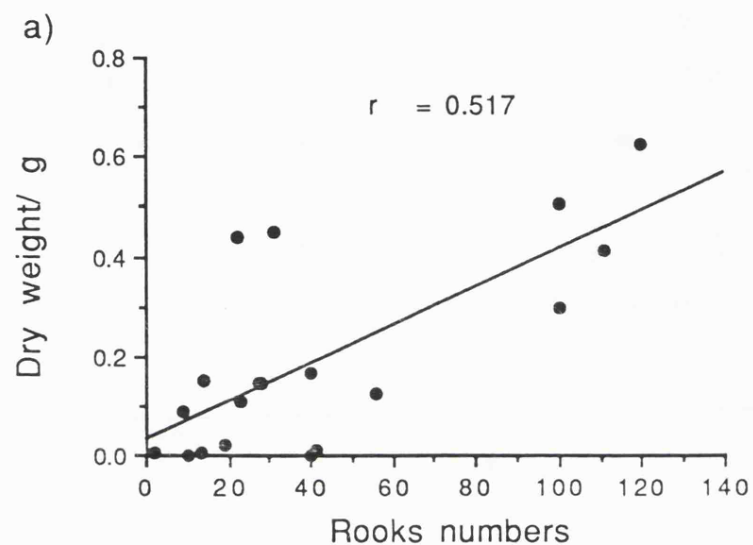
### **5.5.1 Soil analysis**

I have established already (§ 4.2) that increased flock size was predicted by a positive increase in available soil fauna (see also Waite 1981). From the soil core samples previously taken (§ 4.2) I investigated horizontal invertebrate distribution with the result that,

a) The biomass of invertebrate material taken from the top two centimeters of soil (representing a depth equally available to both rooks and jackdaws) was significantly correlated with both rook and jackdaw numbers (Pearson correlation  $r = 0.517$ ,  $P = 0.005$  and  $r = 0.421$ ,  $P = 0.024$  respectively; Fig. 5.8).

b) Both the biomass and energy content of the top 2cm of soil reflected the quality (energy) of potential prey at deeper levels, though these resources became more concentrated towards the surface (§ Fig. 4.3 & Table 4.2). In Chapter 4 I also showed that the biomass of

**Figure 5.8** Rook (a) and jackdaw (b) numbers as a function of invertebrate biomass in the top 2cm of soil. N= 19.



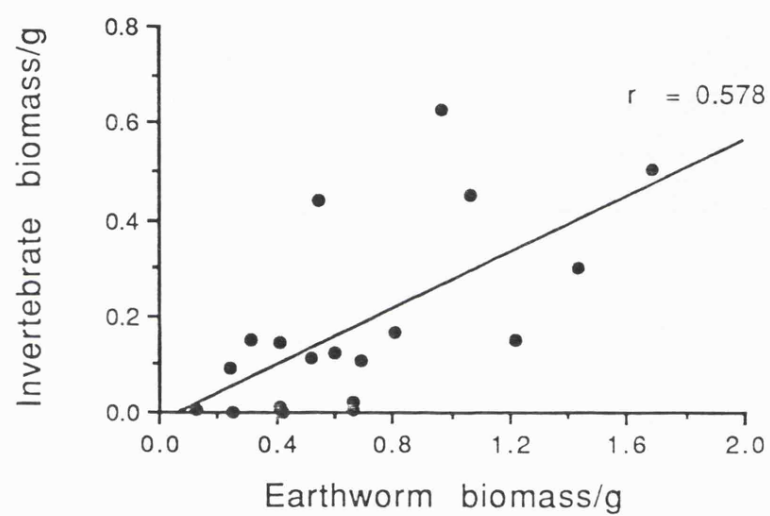
earthworms predicted ( $r^2 = 33\%$ ) the presence of other miscellaneous invertebrates (§ Table 4.2).

The latter point was important as it demonstrated that for the same collection of soil samples from the locations where flock size and invertebrate biomass were correlated, there was also variation in the potential food resources for both rooks and jackdaws (Fig. 5.9). That these resources were also more concentrated towards the soil surface (though not unusual, see Wallock 1977 pp 62-63), provided further latitude for interspecific social facilitation. Furthermore, because subsurface invertebrate distribution invariably reflected the presence of deeper soil organisms, again scope was provided for both rooks and jackdaws to use the presence of each other as indicators of local patch quality.

#### 5.5.2 Temperature

In many species of birds, where flock size enhances the location of transient and ephemeral food resources (for example, Crook 1965; Morse 1970; Krebs et al 1972; Krebs 1973; Rubenstein et al 1977), flock size correlates with temperature because temperature invariably affects invertebrate distribution (Wallock 1977, Green 1980). Thus flocks of titmice *Parus* species increase in size as the air temperature drops and prey become more scarce and more aggregated (pers. obs. Gibb 1963). Consequently, one might expect to see similar, temperature related flock

**Figure 5.9** The variation in biomass, of potential jackdaw prey ("invertebrates") with rook prey (earthworms) in the top 2cms of the soil.



size relationships, in corvids that we know habitually feed on invertebrate fauna. In fact the relationship between corvid flock size and ambient air temperature was negative, though the correlation was not significant. Temperature explained only 2% of the variation in corvid flock size.

Even so, one could still predict the formation of large flocks on very cold days, and expect smaller flocks in summer (§ 3.4)(Patterson et al 1971). However, the local distribution and abundance of food was not temperature dependent but was controlled, instead, by the activities of farmers. Manure may be spread on any day, and its impact on crows and also on soil fauna, has already received attention in Chapter 3. Hence, the natural effects of temperature are damped by human activities and I believe this explanation accounts for the poor flock size/ temperature relationship observed. In Chapter 4, temperature correlated significantly with soil invertebrate energy content. However, the marginal influence of temperature was not enough to significantly alter the relationship between flock size and the available prey energy content of the foraging site (§ 4.2).

## **5.6 Interference**

### **5.6.1 Published information**

Lockie (1956b) considered aggression to be a common

feature of mixed corvid flocks, though his figures tended not to bear this out. He recorded a maximum mean value of approximately 4 encounters per minute (during February 1953) with pooled means for two winters averaging only 2 encounters per minute. His flock sizes ranged from between 15 and 40 individuals and encounter rates were a combination of both inter and intraspecific confrontations. (I assume that intraspecific aggression was the most common of the two, as was true in this study, and is inferred where intraspecific competition is expected to be greater than interspecific competition (Begon et al 1986), that is where intraspecific niche overlap equals 100%.) An average of 2 encounters per minute, in a minimum flock size of 15 birds (0.13 encounters/bird/min.) does not signify an intensive level interspecific aggression.

Höglund (1985) interprets 17 encounters, in 9 days, among a total of 1107+ jackdaws and 562 rooks, as evidence of significant rates of interspecific interference (0.0017 encounters per jackdaw per day!). Höglund also concluded (from these same data) that kleptoparasitism (one species stealing procured food from another, Rothschild and Clay 1952) "often" occurred, despite not all 17 encounters having being kleptoparasitic.

### 5.6.2 Empirical information

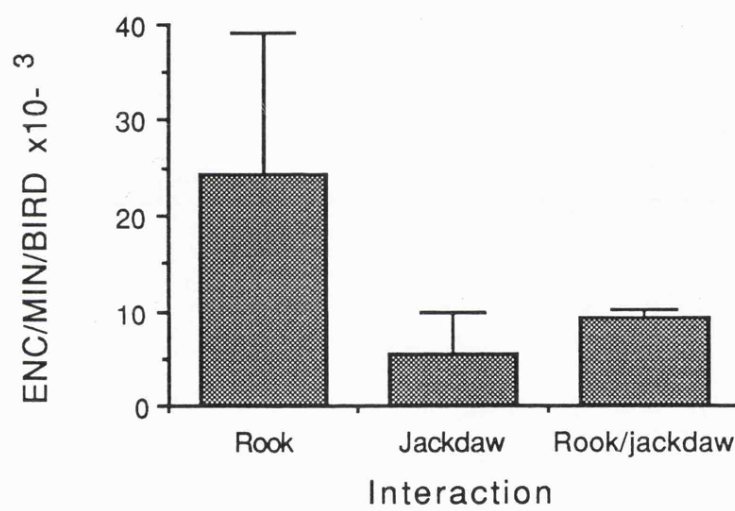
In this study, intraspecific rook aggression varied within similar margins to those of Lockie's (Fig. 5.10) though jackdaw agonistic behaviour was present at only very low rates. Interspecific encounters were also rather infrequent, at a rate of only 0.009 encounters/minute/bird (Fig. 5.10), except when food was restricted or concentrated (as observed during hard weather). Rooks always dominated encounters with jackdaws, and while jackdaws occasionally attempted to interfere with feeding rooks (jackdaws, have been noted for their kleptoparasitic tendencies in seabird colonies (Birkhead 1974)), the former were never observed to succeed in accomplishing anything advantageous. Thus, from my observations and my interpretations of published data (Lockie 1956b; Höglund 1985), interspecific aggression between rooks and jackdaws, while existing, did not emerge as a serious cost of day to day foraging.

### 5.6.3 Conclusions

It was unlikely that jackdaws would have posed a competitive threat to rooks as the former had not the morphological apparatus (in a short bill) to physically exploit earthworms as efficiently as rooks. The converse however, was not so readily explainable, as in theory, rooks were capable of exploiting most of the food items of jackdaws. There were however, two reasons why



**Figure 5.10** Rate of intra and interspecific interference in and between rooks and jackdaws. (Error bars = txSE)



this source of conflict was unlikely to prevail.

Firstly, the typical foraging behaviour of jackdaws, was one of quick, rapid movements, largely selecting prey from the grass roots and stems (e.g. Waite 1984b, per. obs.) Rooks were more methodical feeders, spending much of their time searching and probing on and below the soil surface (e.g. Coombs 1978, Goodwin 1976, Waite 1984b, pers. obs.). Such feeding techniques implied, that jackdaws were more efficient handlers of small prey, than rooks (In the following chapter this point is consolidated, in that small prey items - those less than  $\frac{1}{2}$  the length of a rooks bill - were energetically unprofitable and under-selected by rooks). Hence the two species were not competing for an identical resource.

Secondly, kleptoparasitism is an inefficient strategy when waged against potential victims, that handle and consume prey rapidly (Grant 1971; Dunn 1973; Fuchs 1977). Barnard and Thompson (1985) established this point with black-headed gulls *Larus ridibundus* and plover species *Vanellus vanellus* and *Pluvialis apricaria*. Lockie (1956b) also found that avoidance behaviour, in corvids, was more common in individuals feeding on conspicuous food items. Thus, while mixed-species associations are a necessary prerequisite of kleptoparasitic behaviour, small prey items and short handling times are not (Brockmann & Barnard 1979).

Hence, while prey is not limited in supply, there is evidence to strongly imply that aggression, interference and competition are not serious consequences of rook/jackdaw associations.

## 5.7 Vigilance

### 5.7.1 Overall flock vigilance

The advantages of flocking in terms of improved overall vigilance (for whatever reason) is now largely accepted as a consequence of group behaviour (e.g. Pulliam 1973; Diamond & Lazarus 1974; Powell 1974; Caraco 1979; Lazarus 1979; Jennings and Evans 1980; Inglis and Lazarus 1981). I decided, then, to investigate some fundamental intra and interspecific flock responses to vigilance in rooks and jackdaws, to see whether the theory was applicable to corvids.

I tested the theory six times for each flock size class (different flocks in each case, with the larger flock size class varying between 8 and 14 birds, mean = 11.5), for which the results are presented in Table 5.4.

Mean non vigilant activity for two birds equalled 48.2% and for the larger flock size class 2.3%. Thus, it was clear that pairs and individual birds were less vigilant and consequently more vulnerable to predatory attacks, than larger aggregations (see Kenward 1978).

**Table 5.4 Overall flock vigilance in foraging rooks.**

Flock size	Observation time (mins.)	% total time during which non vigilant activity was seen
2	3.6	56.0
2	3.0	42.0
2	2.8	34.2
2	4.0	39.0
2	4.0	75.0
2	3.1	43.0
		$\bar{x} = 48.2\%$
14	4.0	2.5
10	2.6	0.1
10	4.0	6.3
14	4.0	0.9
13	6.3	0.0
8	2.6	4.2
		$\bar{x} = 2.3\%$

### 5.7.2 Intraspecific vigilance

Focal samples (§ 1.4.2) demonstrated that individual vigilance was negatively correlated with flock size (Spearman's  $r_s = 0.461$ ,  $N = 119$ ,  $P = 0.01$ ), and this result was consistent with previous studies of avian vigilance (e.g. Caraco 1979b *Junco phaeonotus*; Betram 1980 *Strutio camelus*; Elgar & Catterall 1981 *Passer domesticus*; Waite 1981 *Corvus frugilegus*).

### 5.7.3 Interspecific vigilance

#### 5.7.3.1 Percent time spent vigilant

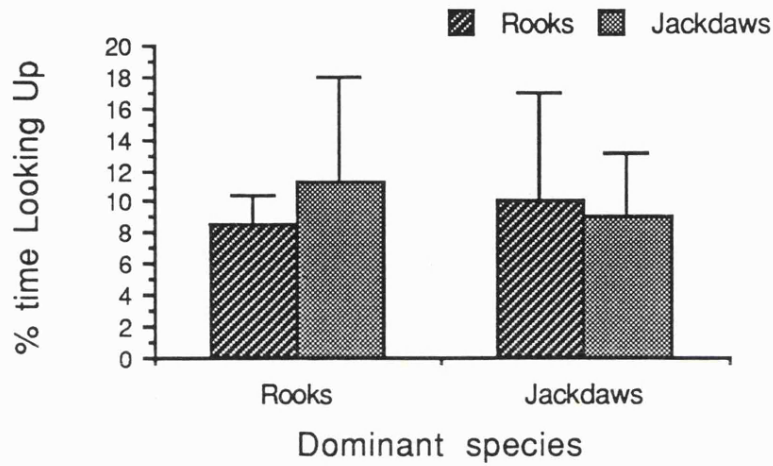
There was no significant difference in the time spent vigilant of either rooks or jackdaws when outnumbered by heterospecifics, compared to each species' normal vigilance times (Fig. 5.11a). For example, small numbers of rooks had similar vigilance times in groups of jackdaws ( $\bar{x} = 32.1$ ,  $n = 45$ ) as in rooks ( $\bar{x} = 28.4$ ,  $N = 113$ ).

#### 5.7.3.2 Flock proportions

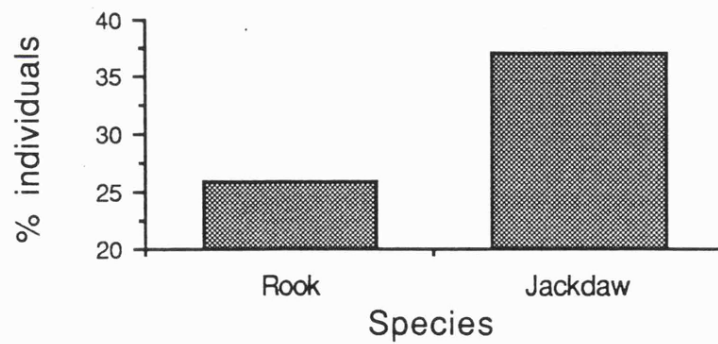
Because of their less methodical foraging technique, jackdaws were more likely, by chance, to have been more vigilant than rooks and therefore perform the function of an early warning alarm to the approach of predators. To test for relative levels of vigilance between the two species, I completed 42 scan samples of

**Figure 5.11** A comparison of three components of rook and jackdaw vigilance. (Error bars = txSE)

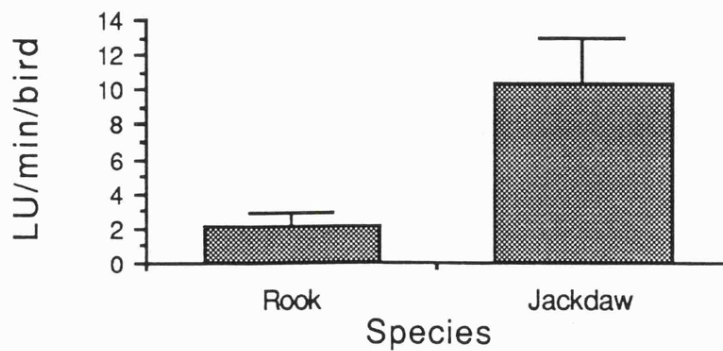
a) Vigilance time in relation to rook or jackdaw proportions



b) % each species vigilant from 42 flocks (N=224)



c) Look Up rates in rooks and jackdaws.



foraging flocks, recording the proportion of each species 'looking up' during each sample. From these scan samples the following results were obtained:

26% rooks and

37% jackdaws were recorded as engaging in vigilant activities (N= 224 individuals; Fig. 5.11b).

#### 5.7.3.3 Vigilance rates

For two close mean flock sizes (28 in rooks and 32 in jackdaws), jackdaws had significantly higher average rates of looking up than rooks, (Fig. 5.11c).

#### 5.7.3.4 Response times

Unfortunately, I was unable to complete one further test of interspecific differences in vigilance. I began to video the responses of individuals from mixed species corvid flocks, to the approach of a human 'predator'. On analysing the videos I looked for the species that first responded to the 'predators' approach. However, should I have simply recorded the first birds to take flight, I would not have proved anything beyond the capability of jackdaws, as lighter and more agile birds, to attain flight more rapidly than rooks. Instead, the initial response to the detection of an encroaching predator was to crouch in preparation for flight. Thus, by studying videos carefully I was able identify which

species was, in each case, first to respond in this way.

From only seven flocks the results were inconclusive, with jackdaws responding first on four occasions and rooks on three.

#### **5.7.4 Vigilance conclusion**

Both rooks and jackdaws modified their vigilant behaviour in a manner recognised in previous flock studies. Hence, individual vigilance was reduced (Betram 1980; Studd et al 1983), while overall flock vigilance improved with increased flock size (Kenward 1978; Caraco 1979).

The results of interspecific differences in vigilant behaviour were inconclusive, though jackdaws appeared to be consistently, the most responsive species.

#### **5.7.5 Consequences**

Natural selection should still favour rooks or jackdaws, that retain a degree of anti-predator awareness, because the threat of predation for such conspicuously exposed birds, cannot easily be dismissed. The cumulative risks of predation, involve the following:

- 1) Corvids are still widely persecuted throughout the country by farmers and land owners, as a result of damage done to agricultural crops or game stocks.



2) British rooks and jackdaws may originate from the continent (Busse 1969), where large avian predators such as goshawks *Accipiter gentilis* and eagle owls *Bubo bubo* are more common.

3) Foxes *Vulpes vulpes* (per. obs.) and female sparrowhawks *Accipiter nisus* (Newton pers. comm.), both common in Britain, occasionally prey upon corvids (jackdaws in the latter case), while increasing numbers of peregrines *Falco peregrinus* and in some areas goshawks add further to the threat.

However, Waite (1981) noticed that small rook flocks had similar individual vigilance rates to large flocks for a given prey density. He therefore, proposed that the normal increased per capita vigilance, observed in small groups of rooks, was the result of birds looking for better places to feed, rather than for predators. Thus, while the functional aspects of both mixed and single species flocking may be more closely correlated with foraging requirements, there is, in an evolutionary sense, little room for anti predator complacency. Hence, predation per se may not be a fundamental function of flocking but nevertheless, a significant consequential benefit.

## 5.9 Experimental tests

I prepared the ground for several experimental tests of

the rook/jackdaw association so far discussed. The intention was to analyse interactive responses following the provision of two patches of food, of variable density, located with the same field. I was then to have recorded the sequence of species arrival at each patch and test the following hypotheses. a) if the arrival of the first bird had been a rook it would have attracted to within close proximity (that is, the diameter of the patch) rooks rather than jackdaws. b) That rooks would oust jackdaws on food limited patches (thereby affecting flock composition), but not on patches of sufficient food density, limited in physical area. c) That both species distribute themselves between patches according to the 'ideal free distribution principle' (Fretwell 1972).

One other advantage of providing 'prey' was that exact energy values would have been known and the relative competitive abilities and energy intake rates of identifiable (tagged) individuals could then have been established.

However, the birds rarely responded to the placement of food by alighting on predictable occasions (I encountered similar problems when trying to trap corvids in winter). Pre-baiting often resulted in the bait still being present after two or three days, thus, as with the trapping, I suspected that when food was plentiful, corvids were not easily tempted by 'supplied' food. On two occasions, flocks of rooks and jackdaws arrived at dawn to a field used the previous day, and settled by two

polystyrene decoys. After approximately 30 minutes duration, birds moved away and fed, the first occasion on the same field and the second occasion elsewhere. On both occasions they ignored the food provided (white bread, rolled oats and food scraps).

I had some success in attracting birds to large quantities of bread, mixed in with manure and straw provided by one of the local farmers. The same day was also very cold. However, this method was very labour intensive and time consuming, and the day was characterised by long periods with no birds present - typically after every disturbance.

In retrospect, decoys were of some value and were used often in traps during the breeding season, certainly without any negative effect. Food patches placed in well utilised areas, on cold days, with decoys and baited manure would probably produce results, though not quickly.

## 5.10 Discussion

In the past, explanations have been sought but found wanting, to account for the conspicuous sympatric behaviour of rooks and jackdaws. However, conditions would seem to overwhelmingly favour the association, as the two species clearly share much in common in terms of foraging requirements. Meanwhile, differences in:

- a) morphology and feeding technique (Waite 1984b, pers.obs),
- b) specific prey selection (this study)
- c) micro-habitat (Waite 1984b),

serve to reduce the costs of competition to a minimum

Thus, the association was adequately explained in terms of established group theory, and particularly as a consequence of concurrent food resources ( $r_s^2 = 41\%$  excluding common resources such as grain, animal feeds and other occasional super-abundant food stocks). Responses to the distribution of patchy and ephemeral prey were subsequently, of mutually benefit to both rooks and jackdaws. Consequently, decisions by individuals of either species to alight within the flocks of the second species, were likely to incur the net benefits of improved food location (this study) as well as reduced vigilance costs (Feare et al 1974; Waite 1981, this study).

Since the co-occurrence of food resources can be responsible for maintaining such a well established interspecific group structure, need we attempt to explain further foraging tactics within either of these two species? After all, intraspecific individual foraging requirements are of even greater similarity.

However competition for common resources may be an important cause of conflict between conspecific individuals and may be responsible for species

dispersion. Hence the need to investigate intraspecific social matrix, for the differential responses to competition that might effect flock structure.

## 6 AGE RELATED FORAGING STRATEGIES

### 6.1 Introduction

Although in general, individual members of flocks have been shown to acquire considerable benefits from social behaviour (Crook 1965; Krebs et al 1972; Caraco 1979; Waite 1981), subsequent work by Goss-Custard & Durell (1981) indicated that flock members may benefit differentially, according to their age. Thus, the inability of immature oystercatchers *Haematopus ostralegus* to compete with adults caused them to restrict their feeding to the less profitable areas of the shoreline. Such inequalities in the pay-offs available to individuals from gregarious foraging, have therefore been demonstrated to influence the distribution and composition of foraging flocks.

Rooks are familiar birds of open farmland in Britain, and the tendency for age composition to vary with flock size is well known (Stewart 1919; Burkitt 1936; Dunnet et al 1969). Burkitt also noted the tendency in autumn and winter for juveniles to group together and to occupy only a "fraction of normal rook flocks". He established that young rooks were more prevalent in smaller flocks (less than 40 birds), and occasionally formed small flocks of their own. However causal mechanisms explaining the dispersion of young have been less readily identified in rooks. Burkitt (1965) postulated that

groups of juveniles may form passively due to adults being otherwise preoccupied with autumn rookery and pair bond activities associated with the species (Marshall & Coombs 1957). Under these circumstances Burkitts's explanation may be true, though it fails to explain the continuation of the trend throughout the following winter.

Swingland (1977) showed that rooks competed amongst each other when roosting and so he demonstrated the ability of adult male rooks to dominate other flock members, particularly at the expense of subordinate immature birds. Post fledging, juvenile rooks are highly dependent upon parents for finding and obtaining food (Dunnet et al 1969, and pers. obs.). This dependence wanes as immatures approach maturity, leading eventually to a conflict between the benefits gained through associating with experienced adults and the simultaneous costs of interference from dominant conspecifics. The present study subsequently strove to highlight the conflict described above, by identifying any significant departures from adult foraging behaviour that immature birds may make. The problem was approached from three main directions.

(1) Time budgets of both adult and young rooks were compared for differences in their respective behavioural patterns, (2) the daily energy budgets of both adult and immature rooks were estimated, and (3) the observed distribution of immature birds, across a range of flocks

sizes, was compared with previous studies and with expected proportions derived from the present data.

## 6.2 Methods

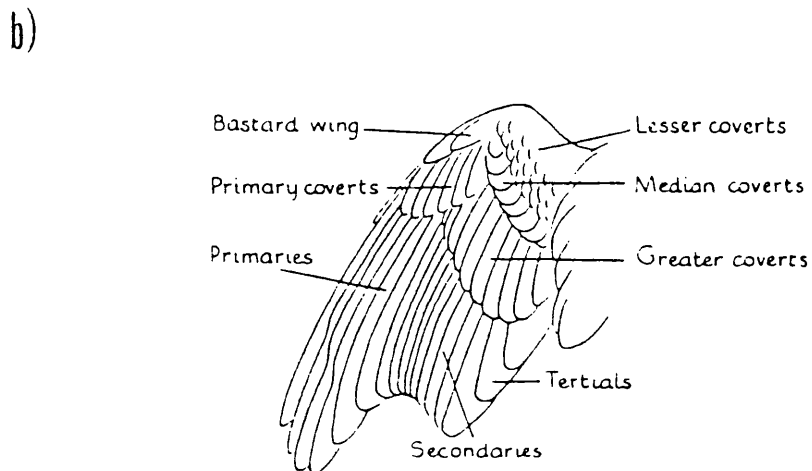
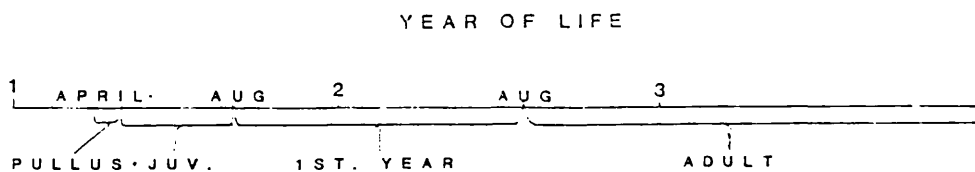
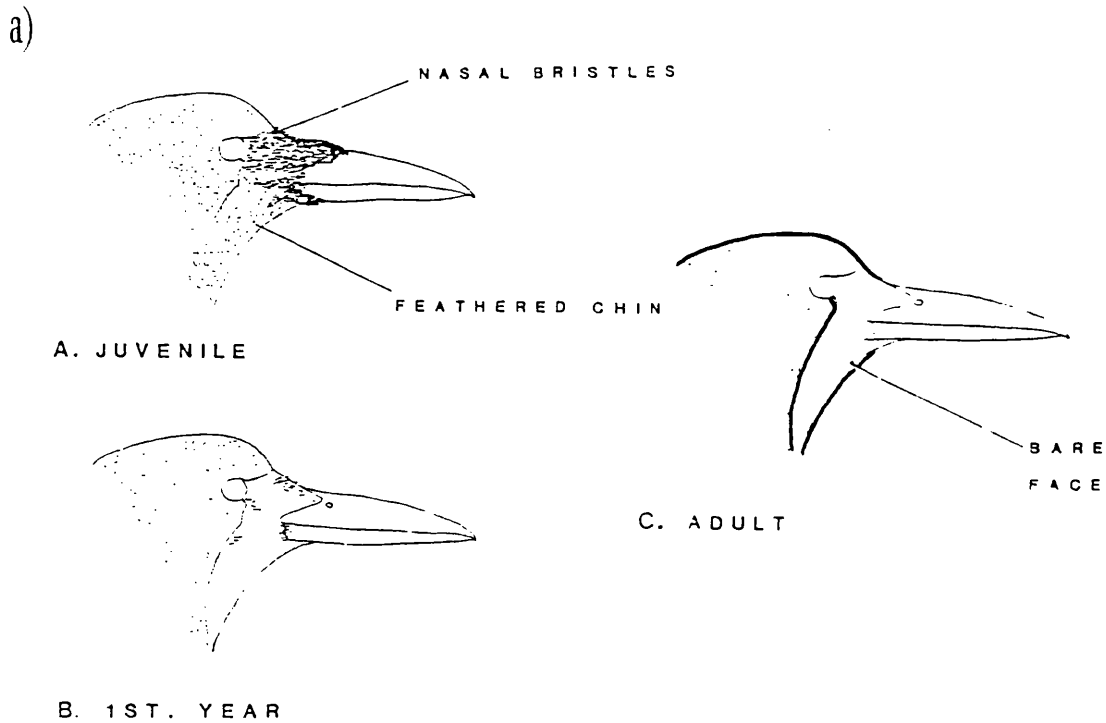
### 6.2.1 Field identification

For the first 9 to 10 months of life, immature rooks retain nasal bristles and facial feathering. These features are the main identification characters which separate immature rooks from adults in the field (Fig. 6.1a), (Goodwin 1976; Dunnet et al 1969; Holyoak 1967). The moult of immatures during the first calendar year sees the replacement only of lesser, median and inner greater coverts (Fig. 6.1b). The rectrices and remiges (tail and flight feathers) are moulted sequentially during the second summer of life and until that time their brownish and worn appearance contrasts with the freshly moulted body feathers and wing coverts. These body characters are not always easy to distinguish in the field but in good light they present no problem. From June onwards of the second calendar year the rectrices and remiges are gradually replaced and the nasal bristles and facial feathering lost (Coombs 1978, Svensson 1985). After this period, adults are inseparable from young birds.

Although immature rooks can be separated from adults



Figure 6.1 a) The facial characteristics of rooks in relation to age. b) Wing feather sequence.

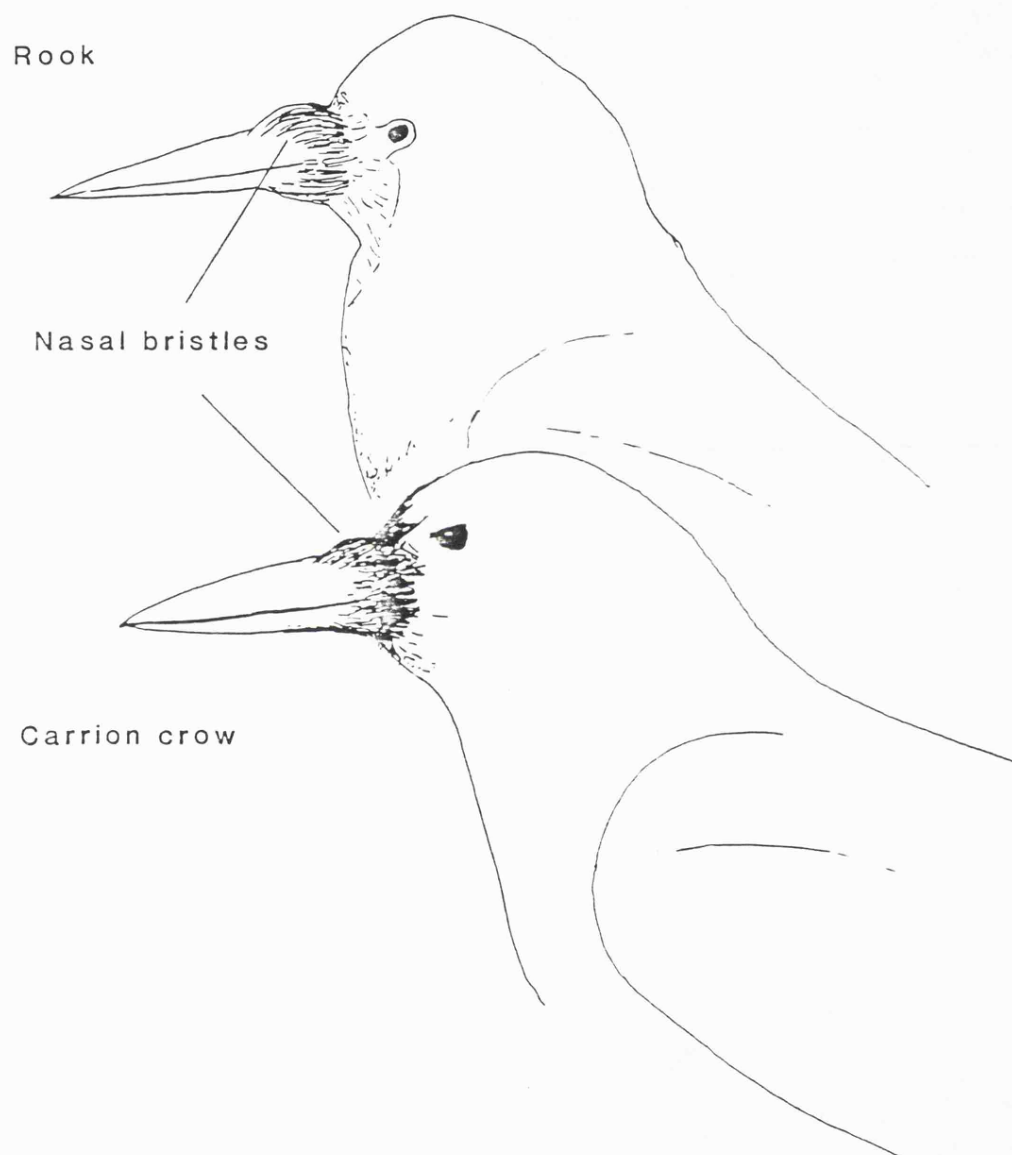


with confidence throughout the first 10 months of life, a more testing problem lies in the separation of immature rooks from immature carrion crows, both of which regularly frequent the same flocks (pers. obs.). With practice the two are easily distinguishable on the basis of posture, gait and silhouette. In more detail, carrion crows look neater and less ungainly than rooks and their bills more robust and less pointed. The bill of a young rook, perhaps because of its more slender shape, appears to project further from the head than the bill of a carrion crow. This narrow outline also serves to emphasise the bulge of the nasal bristles at the base of the bill (Fig. 6.2). Cases of mis-identification were unlikely on closely watched, focal birds. However, if a flock was scanned or counted too quickly or viewed from a distance then mis-identification was possible. Immature carrion crows tended to appear in flocks of rooks in low numbers and were usually accompanied by an adult. The latter point was more relevant before December, after which time the immatures of both rooks and carrion crows had become more independent. For this reason the majority of immature rook observations were made between October and December inclusively.

#### **6.2.2 Procedure**

The behaviour of adult and immature rooks was recorded from 119 foraging flocks, between 14th December 1986 and

Figure. 6.2 Demonstrating the respective facial characteristics of young rooks and carrion crows.



12th February 1988, though most of the data were collected in October, November and December of each year (see above). All behavioural information was collected using the focal sampling technique described in section 1.4.2. Focal birds were selected arbitrarily from within flocks and their behaviour studied in detail. Prey was identified where possible, with particular emphasis being placed upon the length of captured earthworms.

### 6.2.3 Prey identification

Prey categories were separated as follows: grain; invertebrates other than earthworms, and earthworms. Prey items were classified according to their length relative to the size of the birds bill (l) that is,  $<\frac{1}{4}l$ ,  $\frac{1}{4}l$ ,  $l$ ,  $1\frac{1}{4}l$ ,  $2l$  ( $l = 5\text{cm}$ ). The corresponding handling time of each prey item (from capture to swallowing) was also noted. Invertebrates other than earthworms were very difficult to identify in the field, the vast majority falling below the  $<\frac{1}{4}l$  class. Most were separated from earthworms by their silhouette.

Data were tested for correlations between specific behavioural events, (§ 1.4.2) such as flock size and density and prey selection. Immature rook distribution data were gathered from routine circuit transects (§ 1.4.1).

#### 6.2.4 Evaluation of errors

Errors accumulated when estimating earthworms size classes were calculated experimentally by simulating worms with varying lengths of string. Then, by having a colleague arbitrarily hang lengths of string from clothes pegs (from a distance of 8.3 meters - equivalent to 250 meters with 30x magnification) I then proceeded to assign the lengths of string to the classes;  $<\frac{1}{2}$ ,  $\frac{1}{2}$ , 1,  $1\frac{1}{2}$  and 2 lengths of the pegs (simulating the birds bill). The estimates were then compared with the true size classes of the string and the percentage of mis-classification calculated. Forty eight pegs were tested. The results are presented in Table 6.1 below.

Small lengths ( $<\frac{1}{2}$ ) were infrequently assigned to the wrong size and indeed the extremes were most easily classified. A quarter of the time, lengths within the  $\frac{1}{2}$  bill length and  $1\frac{1}{2}$  bill length categories were mis-classified. Most of the former were placed in the 11 category, while the latter was equally over and under estimated. The effect of such errors meant that the identification of prey was largely confined to three categories, small, medium and large. It was unlikely that one could have attained greater accuracy with this method of sampling (see Barnard and Thompson 1985), especially as earthworms continually expanded and contracted in length. Even so, it was important to try and identify prey items to as great an accuracy as possible.

**Table 6.1** Percentage error accumulated while attributing variable lengths of string to five length classes, from a distance of 8.3 metres. See text above.

string length	percentage mis-classification	N
<½l	6.25	9
½l	25.0	16
1x1	12.5	12
1½l	25.0	14
2l	10.0	7

### 6.3. Results

#### 6.3.1 Individual time budgets

Correlations between flock size and individual behavioural activities, of both adult and immature rooks, are presented in Table 6.2. Significant, positive relationships could be attributed, in adults, to the percentage of time spent 'Pecking' and 'Feeding' (FE) (Fig. 6.3a), while 'Searching' and individual vigilance ('Looking up' LU) was significantly reduced in larger flocks. In immature rooks, only 'Looking up' (negative), 'Walking' and 'Encounter' rate (ENC) were significantly correlated with flock size. The 'percentage of time spent feeding (FE)' (Fig. 6.3b) failed to correlate significantly with flock size, though when mean values were plotted for three flock size classes (<6, 10-40, >50 (Fig. 6.3c), FE increased in mid-range flock sizes.

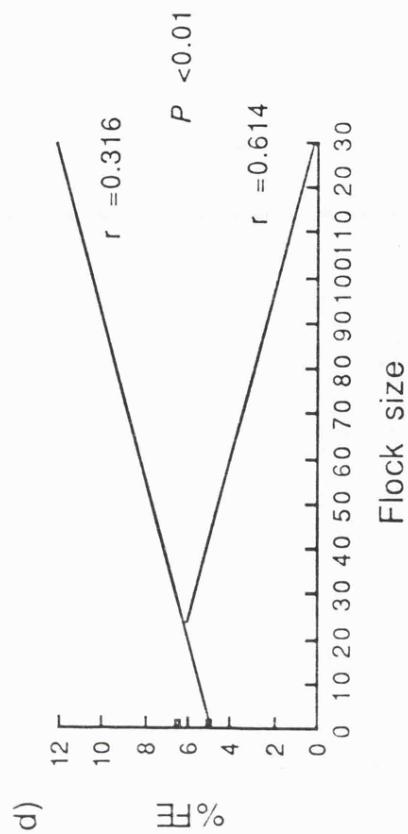
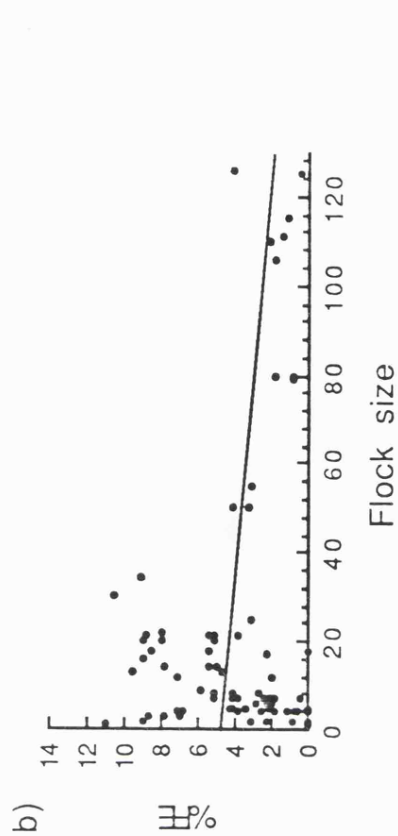
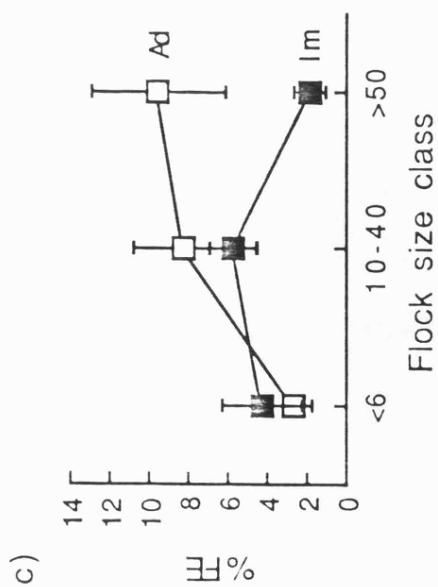
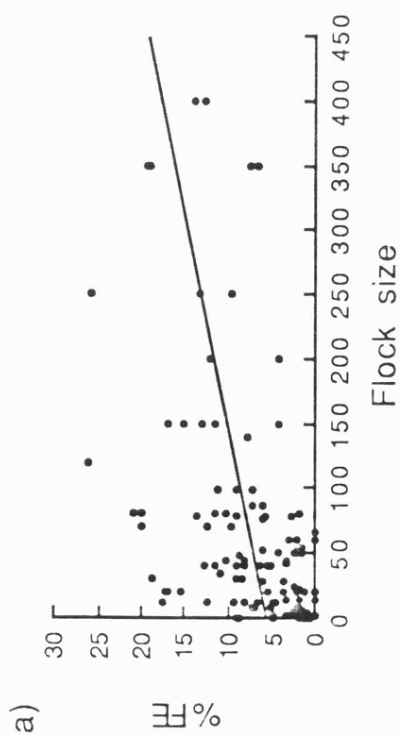
Thus having split the immature data set according to whether flock size was greater or less than 30 birds, regression coefficients of FE against flock size were calculated (after arcsin transformation of the data), and t-tests performed between the two regression coefficients for immatures, and the adult regression coefficient (Fig 1d) according to the following formula,

$$t = \frac{b_1 - b_2}{\sqrt{SE_1^2 + SE_2^2}} \quad \frac{1}{2} \quad (6.1)$$

**Table 6.2.** Spearman rank correlations ( $r_s$ ) relating the time spent on specific behavioural activities to flock size, in foraging rooks.

Behavioural activity	Adults			Immatures		
	$r_s$	P	N	$r_s$	P	N
Feeding	0.349	0.000	119	0.086	N.S	81
Looking up	-0.644	0.000	119	-0.191	0.044	81
Walking	0.044	N.S	119	0.212	0.029	81
Sitting	0.012	N.S	119	-0.008	N.S	81
Searching	0.246	0.004	119	-0.076	N.S	81
Encounters	0.595	0.000	119	0.398	0.000	81





**Figure 6.3** Regressions of % time spent feeding in a) adult and b) immature rooks. c) emphasises the differences between a) and b), while d) compares a) and b) statistically.  
(Error bars=  $1 \times SE$ )

where  $b$  = regression coefficient and SE the standard error.

In flocks of less than 30 individuals, significant differences between adult and immature regression coefficients were not detected. However, in flocks comprising more than 30 individuals, regression coefficients were significantly different (Table 6.3; Fig 6.3d). This led me to the conclusion that while adults continued to increase their feeding time in relation to increased flock size, immature feeding time decreased. Immature rooks subsequently failed to benefit from longer feeding times, while foraging in large flocks.

When foraging in larger flocks, both adults and immature rooks were subjected to relatively high encounters rates (interference), though immatures were less affected (Fig. 6.4a). (Increased interference was similarly correlated to an increase in flock density Spearman's rank correlation  $r_s = -0.435$ ,  $P < 0.001$ ,  $N = 119$ ). In immatures the percentage of time spent 'Looking up' was also less strongly correlated with flock size than in adults (Table 6.2 and Fig. 6.4b).

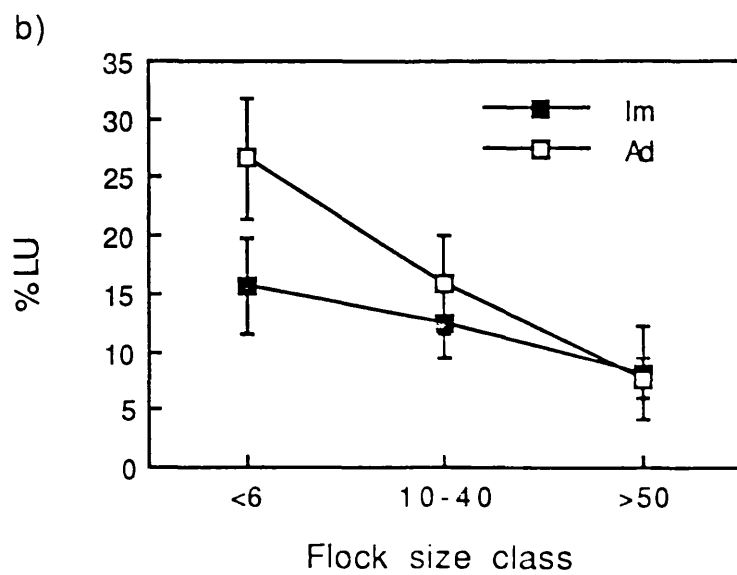
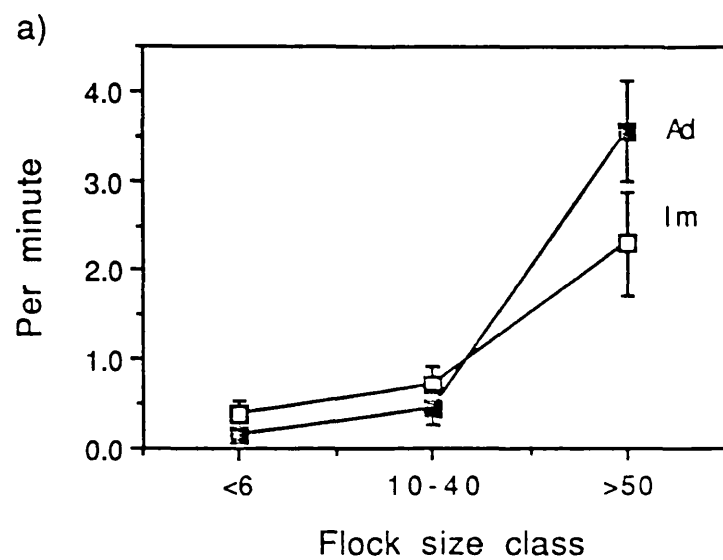
### 6.3.2 Prey choice

The mean unit energy content of earthworms (23.21

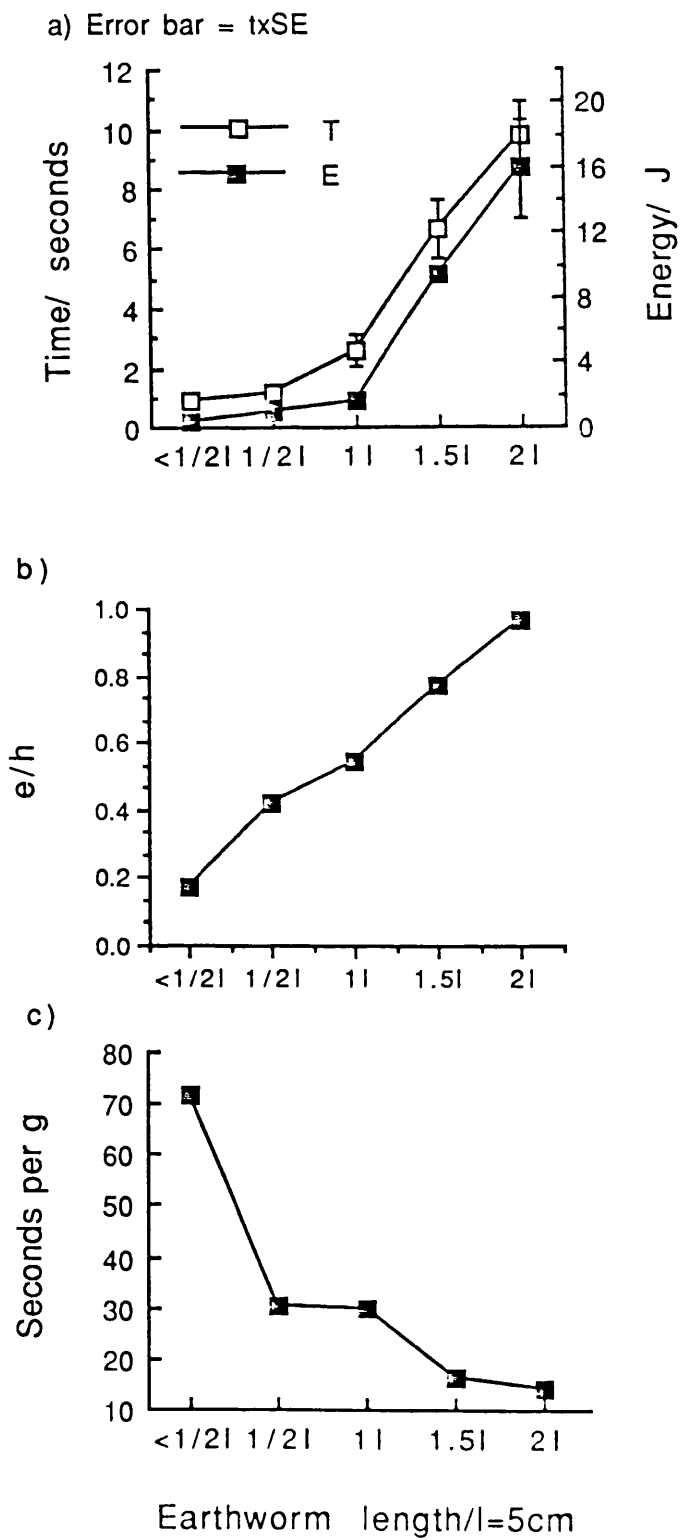
**Table 6.3** Regression coefficients (b) and t-test values (t) comparing the relationship between 'percent time spent feeding' and flock size in adult and immature rooks.

Relationship	r	P	b	t	P
Adults	0.280	0.002	0.00036	00.0	N.S.
Immature (flk <30:)	0.316	0.050	0.00383		
Immature (flk >30)	0.614	0.025	-0.00125	35.1	<0.001

**Figure 6.4** a) encounter rate and b) the % time spent looking up in adult and immature rooks in three flock size classes (Error bars = tx SE).



**Figure 6.5** a) Handling time and energy content, b) prey profitability (e/h) and c) unit handling time per cm as functions of earthworm length. l= 1bill length ~ 5cms.



Joules/mg, SE= 0.32, N= 27: full gut, Table 4.1) was consistent with those of Bolton and Phillipson (1976). The relationships of both energy content (e) and rook handling times (h) with earthworm length are presented in Fig. 6.5a, with the resulting trade off, e/h, (Fig. 6.5b) showing an increase in the profitability of prey with increased earthworm length. The variation in handling time per unit weight, showed that rooks were particularly inefficient at handling small prey ( $\leq 1$ ) (Fig. 6.5c)

This unprofitability was reflected in the earthworm size selection of rooks. Earthworm size selection closely followed the abundance and availability of items in the soil (Spearman's  $r_s = 0.900$ ,  $P = 0.001$ , Fig. 6.6a), but a significant departure from the relationship existed for earthworm size classes of less than 1. There was also a slight departure for earthworms of 1 length category, though in view of the errors calculated above I was not justified in using this information as evidence for positive selection for this size class. Suffice to say, that rooks were rejecting small and unprofitable prey items.

Figure 6.6b demonstrates that there was, nevertheless, a shift towards the selection of smaller prey items in larger flock sizes ( $\chi^2 = 14.7$ ,  $P < 0.01$ ,  $df = 4$ ; cf Waite 1981), perhaps reflecting the birds' tendency to be less selective of prey when foraging in competition with conspecifics. If so, then the improvements in foraging

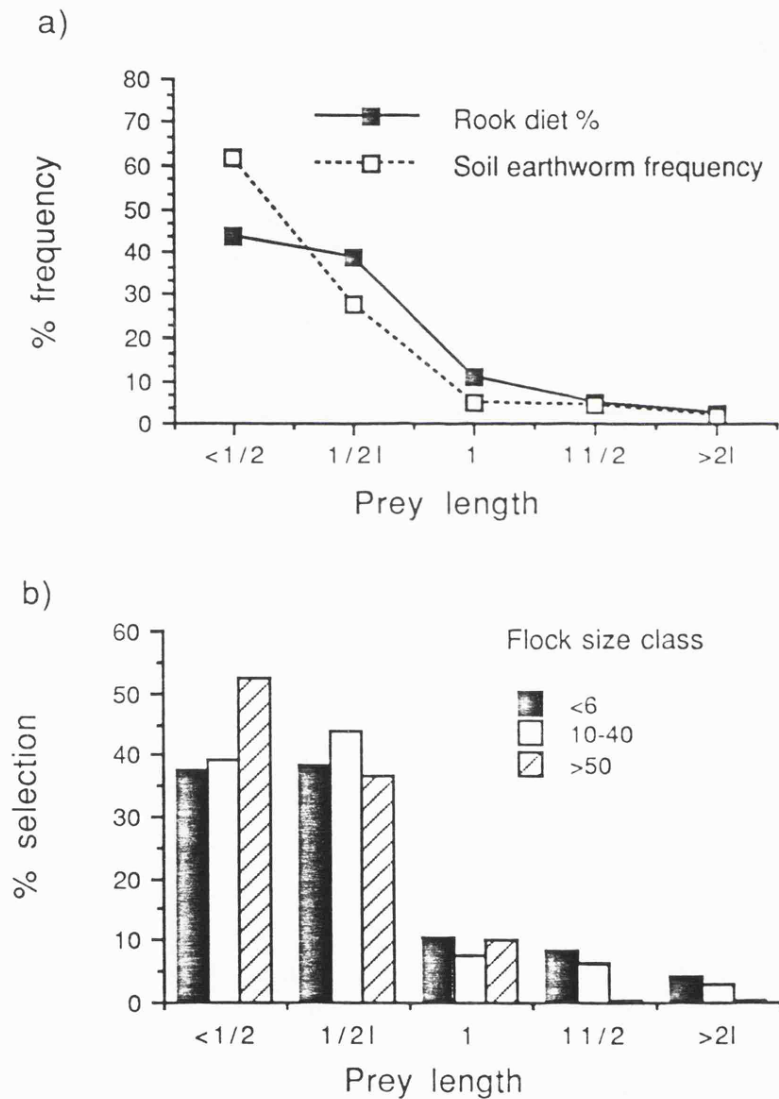
**Table 6.4 Earthworm soil abundance and selection by foraging rooks.**

Size class xl*	Percentage in		Number in	
	the soil	rook diet	the soil	rook diet
<½	62.0	43.9	178	122
½	26.2	38.8	74	108
1	7.7	10.7	22	30
1½	3.0	4.6	6	13
≥2	2.1	2.6	6	5

\* Earthworm length was measured against the birds bill (1). Size classes are multiples of '1'. (1= 5cm).

$\chi^2 = 44.35$ , d.f= 4,  $P < 0.01$ .

**Figure 6.6** a) compares rook earthworm size selection with the availability of each size class in the soil. b) shows a shift towards selection for smaller earthworms when rooks foraged in larger flocks.  $l=1$  bill length,  $\sim 5\text{cms}$ .





efficiency, normally associated with large flocks may have slight costs in this respect.

### 6.3.3 Handling times

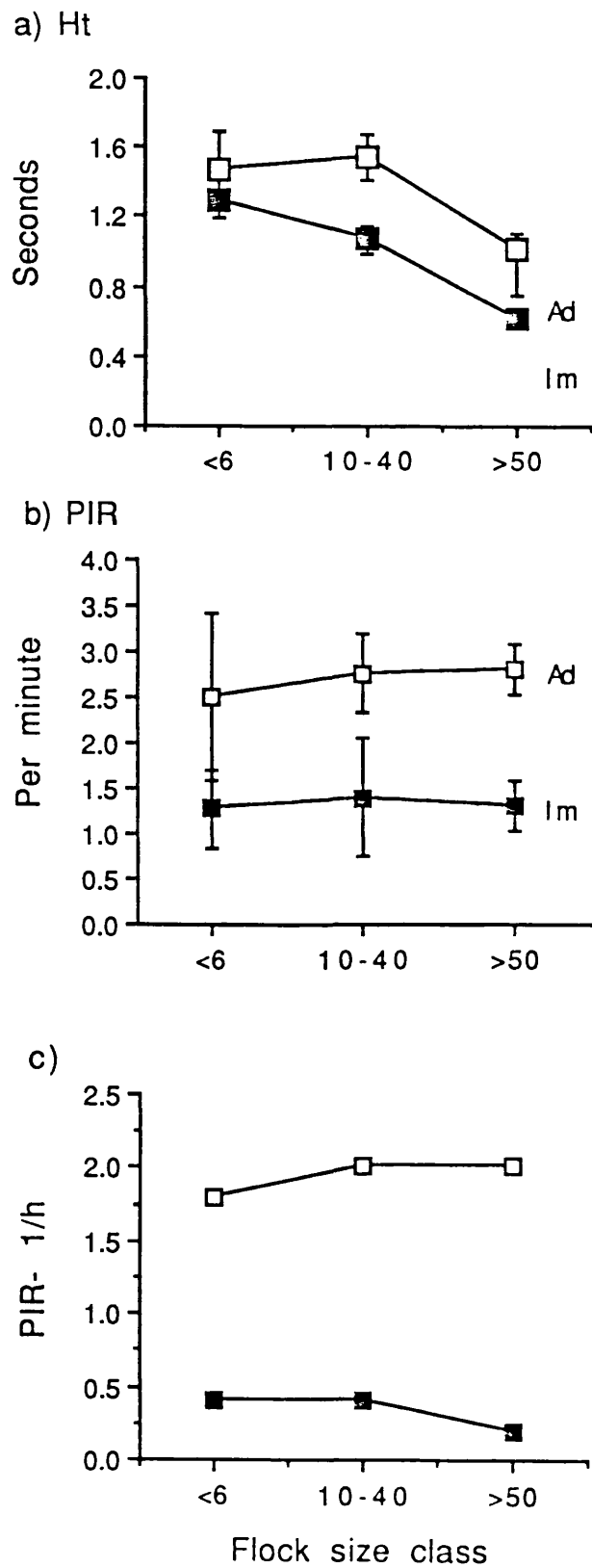
The mean prey handling times of adult and immature rooks were only slightly but significantly different; 1.34 seconds (SE= 0.056, N= 300) and 1.11 seconds (SE= 0.061, N= 192) respectively ( $z = 2.629$ ,  $df = 526$ ,  $P < 0.01$ ). However, the greatest source of error was my determination of actual prey size. Thus despite the handling times of adults and immature being significantly different both means corresponded to the handling times for the same earthworm size class of  $\frac{1}{2}$ l (X= 2.5cm), with an equivalent mean energy value of 920.4J (SE= 117, N= 156; Fig 6.5a).

In both adult and immature rooks, handling times were shorter in larger flocks (Table 6.5) although adult handling times were consistently higher than those of immatures (Fig. 6.7a).

### 6.3.4 Prey intake rates (PIR)

Mean prey intake rates across all flock sizes, were significantly higher in adult rooks than immatures; 2.5 items/minute (SE= 0.23, N= 134) in adults as against 1.3 items/minute (SE= 0.30, N= 81) for immatures;  $z = 3.20$ ,

**Figure 6.7** The differences between adult and immature rooks in their prey a) handling times (Ht) and b) intake rates (PIR). c) is the trade off between b and c. (Error bars =  $\pm$ SE.)



df= 198,  $P < 0.002$ . Adult prey intake rates were also consistently higher than immature prey intake rates across for three different flock size classes (Fig. 6.7b).

Adult prey intake rates increased marginally with flock size, though the same was not true of immature birds ( $r_s = 0.211$ ,  $P = 0.007$ ,  $N = 134$ ; and  $r_s = 0.058$ , NS,  $N = 81$  respectively).

Figure 6.7c shows the trade off between prey intake rate (PIR) and handling time (h) for adult and immature rooks in large, medium and small flock sizes. The trade off was represented by the expression,

$$\text{Net gain} = \text{PIR} - \frac{1}{h} \quad (6.2)$$

because short handling times represented the cost of selecting smaller prey items (Fig. 6.4c) and therefore a decrease in energy intake. Once again, in contrast to immatures, adults benefitted in larger flock sizes.

### 6.3.5 Feeding success

The success rate of adults was improved slightly in larger flocks (Table 6.5) while immature feeding success remained unaffected. Success rate was measured by dividing the number of feeding events by the number of pecks.

**Table 6.5** Handling times, feeding rates, success rates and ratio of adult and immature rooks in relation to flock size.

	Adults			Immatures		
	$r_s$	P	N	$r_s$	P	N
Handling time	-0.278	<0.001	300	-0.128	0.038	192
Feeding rate	0.211	0.007	134	0.058	N.S.	81
Success rate	0.159	0.033	134	-0.044	N.S	81

### 6.3.6 Résumé

In larger flocks adult rooks spent more time feeding, at a faster prey intake rate and with a higher success rate than in smaller flocks. Immature rooks, in contrast, failed to compensate for a reduction in handling time (again assuming handling time represents prey size) with an increase in either prey intake rate or the proportion of time spent feeding.

## 6.4 Energy assimilation and expenditure

### 6.4.1 Intake

In the following section I estimated the daily Gross Energy Intake (GEI) and daily energetic costs of adult and immature rooks in order to compare energy net intake. Daily GEI is equal to, the energy content of an average prey item multiplied by the capture rate of prey, multiplied by the total amount of time spent feeding. Thus, the energy content of an average prey item was calculated above to approximate 920.4 J (Table 4.1). The mean PIR of adult rooks was calculated at 2.5 items per minute and mean daily foraging time, as 330 minutes a day (SE= 10.4, N= 26; Table 3.1). The gross energy intake (GEI) of adult rooks was therefore estimated as:

$920.4 \times 2.5 \times 330 = \underline{759} \text{ kJ per day (SE= 73.8, N= 134, see section 1.8), and the GEI of immature rooks as:}$

$920.4 \times 1.3 \times 330 = \underline{395}$  kJ per day (SE= 92.0, N= 81).

A significant decrease in prey intake rate therefore restricted substantially, the gross energy intake of immature rooks ( $z = 3.08$ ,  $P = 0.01$ ). To reiterate, note that, despite mean handling times of immatures and adults being significantly different, both values corresponded to earthworms of the same length category and therefore earthworm energy value remained the same in both calculations.

Clearly a significant decrease in prey intake rate considerably restricted the gross energy intake of immature rooks. Immature GEI fell below Feare et al's (1974) estimation of the basic energy requirement for a captive rook of 567.6 kJ /day, that is, less than the fundamental quantity of energy required to maintain a rook's body weight. Within the margins of error, small fluctuations in prey intake rate could make up the difference. The present estimate was also based on the assumption that rooks were feeding on earthworms, to the exclusion of other prey items. Earthworms certainly play a major role of in the diet of rooks (Holyoak 1968; Waite 1981), but during hard weather alternative resources (farm produce for example) may be more efficiently harvested (pers. obs.).

#### 6.4.2 Energy requirements

By comparing GEI with estimated living costs one could judge the influence of prey intake rate on the net energy increment or deficit of foraging birds. Kendeigh (1970) developed a formula to calculate the Existence Energy Requirement (EER) of a number of passerine and non passerine birds based on their weight. EER was defined as the daily amount of energy required by a bird to maintain its standard metabolism as well as locomotive, behavioural and physiological activities. For a temperature of 0°C the formula was as follows:

$$\text{EER} = 4.33 \times W_g^{0.53} \text{ Kcals} \quad (6.3)$$

where  $W_g$  is the wet weight of the bird in grams. The formula can be modified for a temperature of 30°C (see below) but for a temperate, winter study of foraging rooks it was felt that 0°C was more appropriate. Hence, for 'average' rooks of 420g (this study) EER was evaluated at:

$$\text{EER} = 444.6 \text{ kJ (106.4 kcals)}$$

However, the energy requirements of wild birds would be greater still, as extra energy would be expended on activities such as flying and foraging.

#### 6.4.3 Net intake

Unfortunately estimations of energy expenditure for various bird activities vary enormously. For example Puchas' (1980) estimates of foraging costs were only one third greater than the roosting value. The estimates used by Barnard and Thompson (1985) were three times greater. Similarly Puchas' estimates of flying costs (from calculations on the dickissel *Spitza americana*, King 1974) were only half those used in this study. Other studies have used from between 5 (Orlans 1961) and 15x BMR (King 1974) to estimate the energetic costs of free flight, though 8-9x BMR was estimated for the fish crow *Corvus ossifragus* in level flight (Bernstein et al 1972).

Accurate evaluation of energy expenditure in wild rooks was hindered by inconsistency in the published data above. Nevertheless, as in previous studies, I measured the energetic costs of free living birds, using multiples of the Basal Metabolic Rate (BMR) to calculate the specific quantities of energy expended on various behavioural activities (King 1974; Barnard & Thompson 1985). BMR (kjoules/24 hours) is calculated from the equation (Barnard & Thompson 1985):

$$\text{BMR} = (78.3 \times w^{0.723}) \times 4.18 \quad (6.4)$$

Where W is the weight of the bird in kilograms and 4.18 simply converts calories into joules. For an average



rook weighing 420g (this study), BMR equals 174.8 kJoules/24 hours ( $7.28 \text{ kJ h}^{-1}$ ).

Barnard and Thompson (1985) made estimates of the total energetic demands of daily foraging in lapwings *Vanellus vanellus* and golden plovers *Pluvialis apricaria*, by using the following BMR multiple values of each behavioural activity: Foraging = 3x BMR, Flying = 12x BMR (this value corresponded well with the free-flight empirical estimates of power consumption by Berger & Hart 1972, from their equation  $\text{kcal/hr} = 45.5 \text{ Wkg}^{0.73}$ ), Loafing/preening = 2x BMR, and Roosting = BMR. The adjusted BMR values were further multiplied by the daily duration (in hours) of each activity to give total 24 hour energetic costs. The procedure layed out in Table 6.6, for the computation of the net energetic 'gains' of daily rook life, follows that of Barnard & Thompson (1985) and was selected to provide conservative estimates.

On the basis of these calculations it was clear that immature rooks were not able to maintain their body condition as efficiently as adults, though it would be unlikely for immature rooks to accumulate this kind of energy deficit regularly. Much of the inaccuracy of the calculation existed in the formulation of energetic costs. But as both adult and immature estimates were calculated on an identical basis, the relative differences were of greater importance than the absolute values. Clearly age specific differences existed.

**Table 6.6.** Estimated winter 24 hour energetic\* intake and expenditure of free living adult and immature rooks at 0°C (mean day length of 9.5 hrs).

BMR (kJoules/24 hrs)	174.8		
(per hour)	7.3		
GEI (kJoules/24 hrs)	759 (adults)		
	395 (immatures)		
	24 hour costs	Activity duration (hours)	Cost xBMR
Roosting	102.2	14.0	1
Foraging	120.5	5.5	3
Flying	140.2	1.6	12
Loafing/preening	42.3	2.9	2
Total costs	405.2		
	kJoules assimilated /24 hours (84.5%** GEI)	Net energy gain (Assimilation minus total costs)	
Adults	641.4	236.2	
Immatures	333.8	-71.4	

\* In kJoules. To convert to Kcalories + 4.18.

\*\* 84.5% assimilation efficiency (Feare et al 1974).

In consequence, low prey intake rates and subsequent possible energy intake deficits in large flocks were likely to increase the pressure on immature rooks to investigate alternative foraging strategies, thereby affecting the distribution of immature rooks among foraging adults.

#### 6.4.4 Energy intake and flock size

The value of GEI in Table 6.6, corresponded to the 24 hour intake of energy based on a mean of 5.5 hours foraging time. It was not possible to calculate the precise variation of 24 hour foraging time (and therefore GEI) as a function of flock size because flock sizes fluctuated continually throughout the day. However, by using mean prey intake rate for three flock size classes (<6, 10-40 and >50) I could calculate corresponding GEI values. The results are summarised in Table 6.7. Figure 6.8a demonstrates the relationship of GEI with flock size.

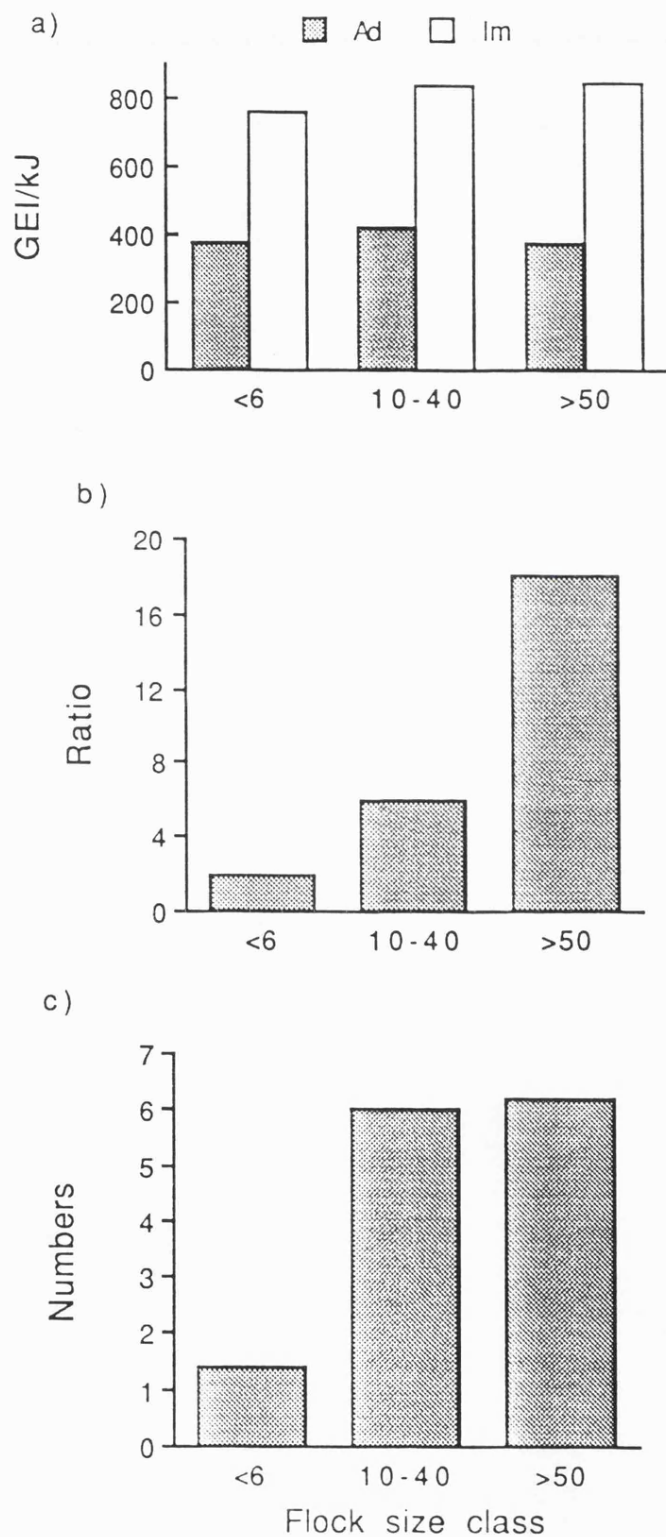
Notably, the GEI of adult rooks increased with an increase in flock size, while immature rooks improved their intake of energy in the smaller, and middle ranked flocks (which even exceeds the expenditure of energy calculated in Table 6.6). This exercise again served to consolidate the point that immature rooks were foraging less efficiently in large flocks, inferring once again that immatures could improve their net energy gain by foraging in smaller flocks.

**Table 6.7** The relative proportional gross energy intakes of adult and immature rooks in small medium and large flock sizes.

	Flock size class		
	<6	>10-<40	>50
<b>Adults:</b>			
PIR	2.50	2.75	2.78
GEI	759	835	844
<b>Immatures:</b>			
PIR	1.25	1.40	1.30
GEI	380	425	395

**Figure 6.8**

a) Gross energy intake (GEI), b) Adult:Immature ratio and c) immature numbers in relation to flock size.



## 6.5 Immatures dispersion

Consistent with previous studies (Burkitt 1936; Dunnet et al 1969; Purchas 1980), the ratio of adult rooks to immatures increased considerably in large flock sizes (Spearman's  $r_s = 0.826$ ,  $P < 0.001$ ; Fig. 6.8b). The actual numbers of immature rooks peaked in flocks of 15 to 20 birds after which no further significant increases were observed (Fig. 6.8c). The overall mean winter flock size within the study area equalled  $84 \pm 16.6$  (rooks), with a mean adult:immature ratio of 20:1. The population dispersion of immature rooks was therefore biased towards smaller than average flock sizes.

## 6.6 Discussion

The present results showed important variations in the competitive ability of adult and immature rooks which affected substantially the intake of energy. Distribution of adults and immature was also dissimilar, and though a causal relationship cannot be proved there was evidence that dispersion was a function of competitive inefficiency. Certainly poor immature foraging success can have major consequences on their survival, as recently demonstrated by Patterson et al (1988). Thus we would expect them to respond to deteriorating circumstances by searching elsewhere.

Our results here were consistent with those of Waite's

(1981) who demonstrated that larger rook flocks tended to occur on areas of high prey density, and that a subsequent increase in prey intake rate followed. Such intake rates were slightly countered by a shift toward smaller prey, with a subsequent levelling off of Gross Energy Intake. However, immature birds failed to conform to the overall pattern, as immature prey intake rates were not improved in large flocks, and gross energy intake suffered as a consequence.

Inexperience was not the only factor responsible for the poorer immature performances. Feeding, handling times, vigilance and interference all showed trends of variation with increasing flock size that were dissimilar to those of adults. For example, despite a similar increase in prey biomass, immature rooks, in contrast to adults, spent more time walking and less time feeding in large flocks. The increase in walking (while encounter rate (ENC) was lower than that suffered by adults) implied that immatures were avoiding contact with other individuals, though this assumes that immature birds were able to identify dominant individuals before contact was made.

In consequence, the evaluation of 'patch quality' must be judged not only on prey density but also on the physical costs of competition with adult birds. Immature rooks must weigh these costs against the experience that adults may provide in locating food, and the improvements in anti-predator vigilance that exist in larger flocks. Hence, fewer adults would reduce the cost of immature

repression, while still providing the foraging experience that immatures require, both to survive and to refine their own foraging skills. The compromise is a medium-small flock, and in Fig. 6.9 there is a summary of the cost/benefit assessment of adult and immature rooks on the basis of the evidence available from this study.

As predicted by the behavioural information, young rooks in Leicestershire (and elsewhere Burkitt 1936; Dunnet et al 1969) were more prevalent in smaller flocks, where the adult:immature ratio was lower.

Hence two major components of immature foraging behaviour were detected. The first component comprised the inability of immatures to forage efficiently in large flocks. The second component constituted the observed distribution of immature rooks in favour of smaller (but never solitary) foraging groups.

Patterson & Grace (1984) demonstrated, that local immature (tagged) rooks tended to disappear throughout the winter, to be replaced by young from elsewhere. As some tagged birds later reappeared, the implication was that immatures were dispersing rather than dying. Adult dispersal is low in rooks that have reached breeding status (pers. obs.), thereby placing emphasis on the importance of post-natal dispersal. Thus, it may have been that foraging inequalities had a causal effect on immature dispersal.

The recognition of age specific variations in the



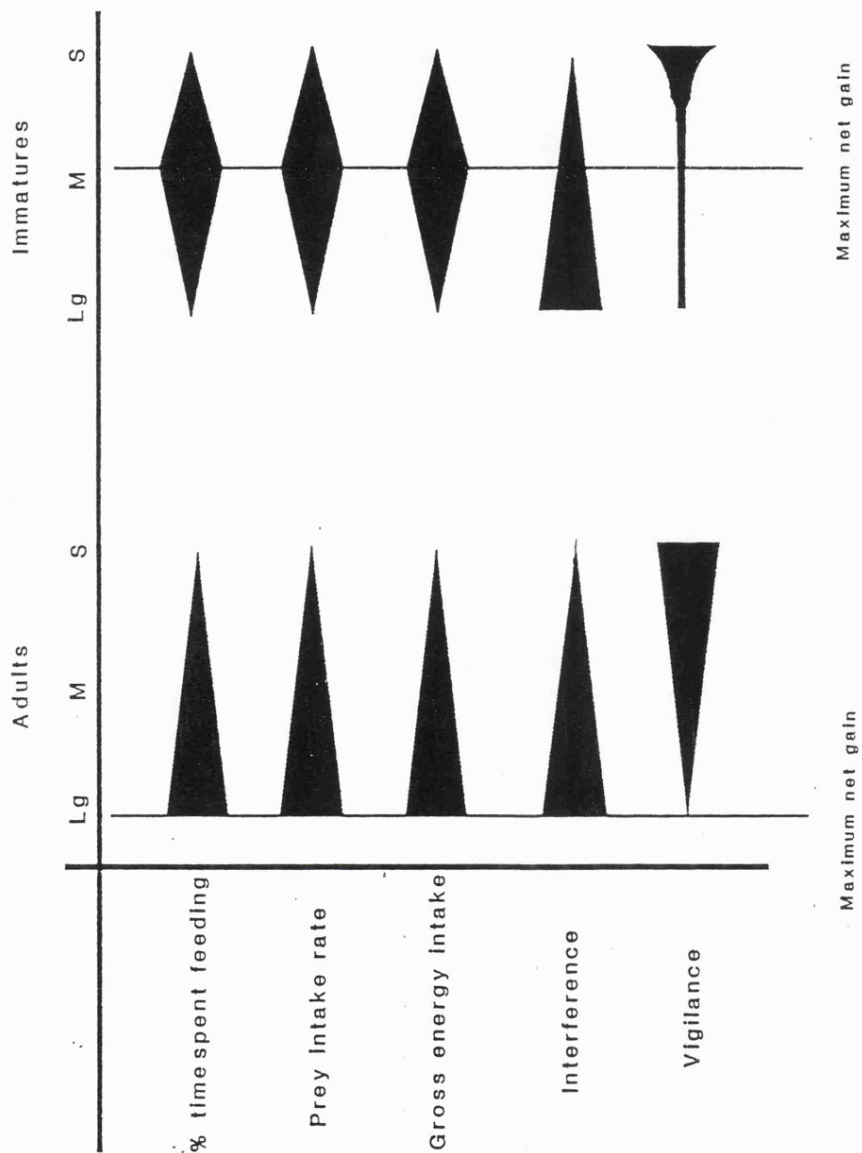


Figure 6.9 A diagrammatic summary of the cost/benefit pay-offs for adult immature rooks as functions of flock size. Maximum net gain is achieved at medium flock sizes for immatures and large flock sizes for adults.

foraging strategies of birds is an important step towards demonstrating that flock distribution and composition may be significantly affected by differential foraging ability and experience.

## 7 THE GENETIC AND SOCIAL STRUCTURE OF JACKDAW FLOCKS

### 7.1 Introduction

In Chapter 6 I showed that differential foraging behaviour in rooks, varied according to the social status of individuals, in this example age was the criterion of status. The results suggested that intraspecific competition may be partly responsible for pre-breeding or post natal dispersal. However, to reiterate, the greatest tolerance towards foraging immatures should have been shown by parents, whose lifetime reproductive success depended upon the survival of all their kin, and in particular offspring and siblings. Furthermore, if the transition from dependent juvenile to independent immature was gradual, small parent/sibship groups might have been expected to prevail in winter flocks. The conflict was one of dispersal versus altruism and the relative per capita trade-offs from both.

In this study, tagged jackdaws (like rooks) tended to be encountered within relatively contained regions of the study area (§ 3.1). Röell (1978) too, identified a common core of birds in Dutch flocks, and identified birds as resident or nonresident. Resident individuals were subsequently found to be more tolerant of each other, both when feeding and when breeding. If kin ties were important in consolidating such behaviour, then

higher than average levels of relatedness should have been detectable within the core groups.

While tagged jackdaws only represented ~20% of the Billesdon jackdaw population, their continued co-presence within certain areas of the study site indicated that they were representative of the local core flock. Therefore enough tagged individuals were present, from September 1987 onwards, to attempt to accumulate data on co-foraging activities, with a view to subsequent kinship analysis. Sexual differentiation was important, as detection of higher than average rates of kinship, would otherwise be frustrated by the presence of unrelated paired individuals. The details concerning the accuracy of sex determination is discussed at more length in Chapter 9.

Foraging groups could be established as either, discrete colonies, or as separate groups within each colony (flocks, and aggregations within flocks). As birds may not perceive affiliations in precisely the same manner as ourselves, I measured intra-flock foraging at two levels. The first criterion was a measure of frequently close co-foraging birds. The second criterion was simply a measure of individual presence or absence within flocks and the identification of representative core members.

With respect to statistical analysis, z and t tests

were not strictly appropriate to the fingerprint analysis as mean coefficient of band sharing values are calculated from repeated pairwise comparisons. Hence, data was non independent, as each individual bird was compared several times within each analysis. The same criticism was true of 'Goodness of fit' applications. I used the tests to give comparative quantitative measures of significance but only at the  $P < 0.01$  level.

## 7.2 Colonial relatedness

### 7.2.1 Procedure

Seventy-eight post juvenile jackdaws were trapped, bled and tagged at the Billesdon study site over the course of two breeding seasons - 1987 and 1988. Parameters assisting the aging and sexing of each bird were measured prior to their release (§ Chapter 1).

Fifteen jackdaws were trapped at Rutland Water Nature Reserve (SK 886 086) and blood samples taken from each one. Jackdaws and rooks at Rutland Water roost together locally at Burley Wood (SK 890 100) and form a quite separate colony to those at Billesdon Coplow some 30 kilometers to the west. No further information was known about the trapped Rutland Water birds, though sex determinant features were measured.

DNA 'fingerprints' (Chapter 2) were prepared from nine arbitrarily selected male jackdaws from the Billesdon

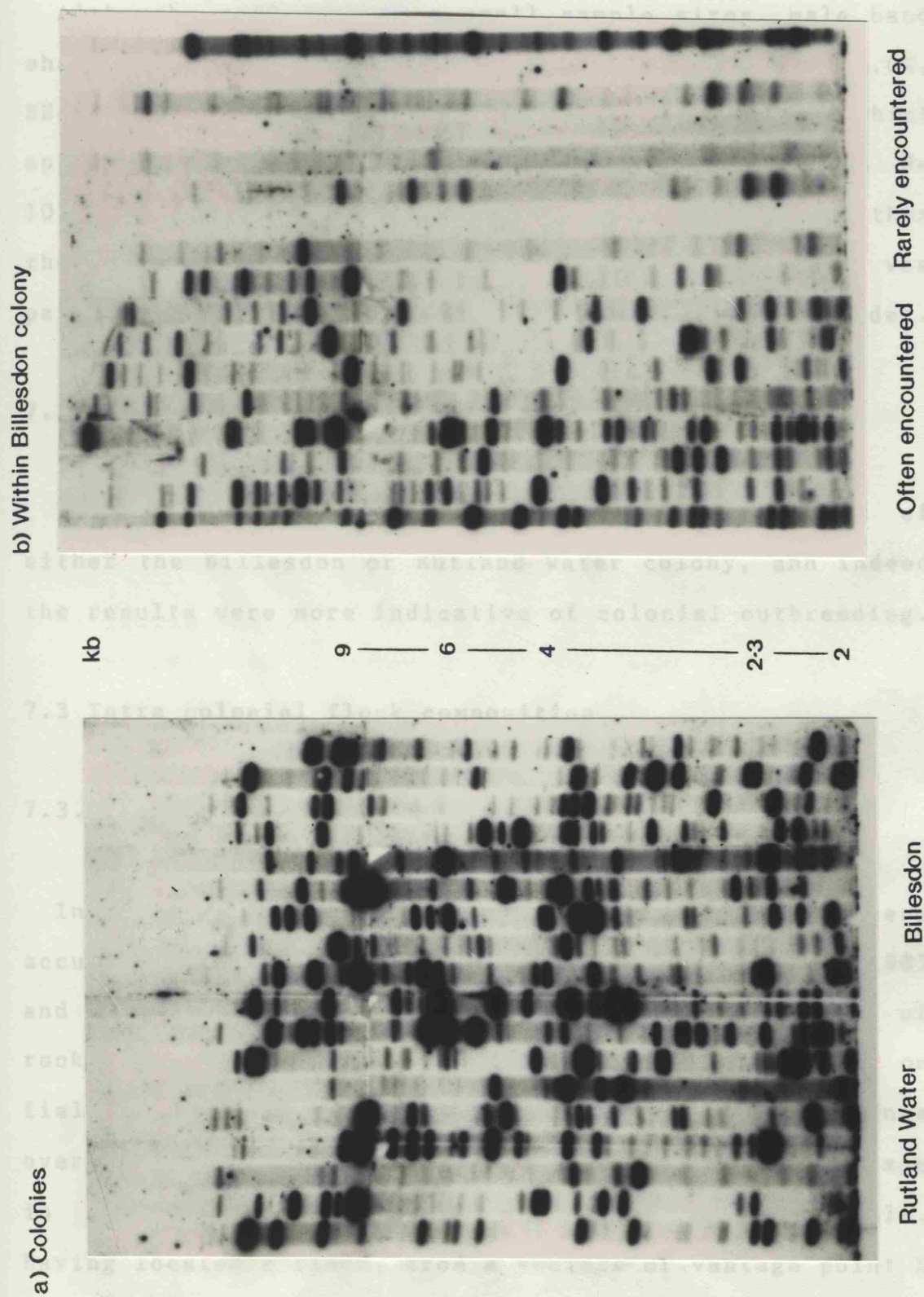
population and nine Rutland Water birds (Plate 7.1a). Male birds were selected because it was thought from expectations of female biased dispersal (Greenwood 1980), that males would be most likely to produce detectably higher levels of relatedness. However, only 15 birds were trapped at Rutland Water, the sample therefore comprised both sexes.

### 7.2.2 Overall results

I calculated the mean coefficient of band sharing (see 2.3) occurring across and within the two populations above (Table 7.1; Table 1 Appendix G). Despite very low average band sharing in the Billesdon colony, intra colony band sharing was not significantly different from inter colony band sharing (by z-test). While I was conservative in my scoring of shared bands, band co-migration was rare within any three or more individuals, and generally indicative of considerable outbreeding (Plate 7.1a). As demonstrated in Plate 7.1a, bands were well dispersed, and conserved loci rare.

The mean rate of band sharing in other animal species varies considerably, from ~25% in humans (Jeffreys et al 1985a) to ~10% in house sparrows *Passer domestica* and dunnocks *Prunella modularis*. Jackdaws band sharing was lower still at 8.3% (Billesdon Colony).

Plate 7.1 Inter and intra colonial DNA fingerprint analysis in jackdaws.



### 7.2.3 Sex differences

Although, suffering from small sample sizes, male band sharing in the Rutland Water population was lower (7.0%, SE= 1.43, N= 6), than female band sharing which approached that of other species (9.89%, SE= 1.47, N= 10). As the Billesdon sample contained only males, then there was some evidence here, that outbreeding was particularly and unusually, prevalent in the male gender.

### 7.2.4 Conclusion

Inbreeding was not evident from random samples of either the Billesdon or Rutland Water colony, and indeed the results were more indicative of colonial outbreeding.

## 7.3 Intra colonial flock composition

### 7.3.1 General procedure

Intra colonial foraging association data were accumulated during two weeks in September/ October 1987 and 1988 respectively, when substantial aggregations of rooks and jackdaws were readily locatable feeding on fields 3, 20, 21-28 (Fig. 1.2). Their continued presence over two weeks (one week each year) was a great advantage in reducing the search time for tagged individuals. Having located a flock, from a vehicle or vantage point X (Fig. 1.2), I proceeded to collect data as follows:



**Table 7.1** Mean (%) fingerprint band sharing a) in two populations of jackdaws and b) in flock foraging jackdaws. SE = standard deviation.

	Pairwise comparisons				
	%(SE)	N		%(SE)	N
a)					
Billesdon population	6.6(0.75)	36	}	7.1(0.6)	81
Rutland population	9.0(0.8)	36			
b)					
Frequently encountered	12.7(1.4)	36	}	8.3(0.9)	35
Infrequently encountered	—	—			
Males	10.5(3.0)	10	}	10.0(1.3)	28
Females	10.0(1.5)	16			

1) Initially, tagged birds, foraging within ~15 bird lengths of each other (<5 meters) were located and identified from systematic scan samples (§ 1.4.3). I concentrated on identifying, closely foraging birds to the exclusion of other tagged individuals. This procedure had two effects. The first was to identify regular partnerships. The second was to provide information on commonly co-flocking individuals (a core group), as representatives of the first case tended to be representative of the latter case. Just occasionally this was not true, and some affiliating individuals were seen often together but not often with other tagged birds (data from 144 'flocks').

2) Having identified all closely foraging birds (or if there were none), I continued to identify all other tagged birds, regardless of their position relative to others individuals. Thus, individuals were scored according to the number of occasions each was encountered (data from 140 'flocks'). This provide a second measure of the core group composition.

3) Frequent flock disturbances often made identification a lengthy and frustrating business. However, disturbed flocks, once reassembled, were again treated as in 1) and 2) above. Flocks that continued feeding without disturbance were only rechecked for tagged individuals after 30 minutes had elapsed, thereby

allowing time for complete remixing of the birds.

### 7.3.2 Intra flock co-occurrence

For convenience, point (2) above is considered first, as in retrospect, I felt that the collection of data was not sensitive enough to identify true levels of foraging association. Incomplete identification of tagged birds meant foraging associations were under-represented. Single, tagged individuals, were more often fully identified than all members of larger tagged groups (because of flock disturbances). Hence, solitary occurrences were likely to have been over-represented in the data, though not identified as such in the analysis. Including the dilution of non-tagged birds, the chance of detecting relatedness with this procedure was only slightly higher than that for the colony estimate above.

Nevertheless, the nine most frequent and nine least frequently recorded individuals were selected for cross comparison of fingerprint band sharing (Plate 7.1b, Fig. 7.2 and Table 3 Appendix G). I compared the mean coefficient of band sharing, in those individuals most often encountered, with mean band sharing between regular and non regularly occurring birds (Table 7.1b).

### 7.3.3 Overall results

Unfortunately five tracks failed to produce

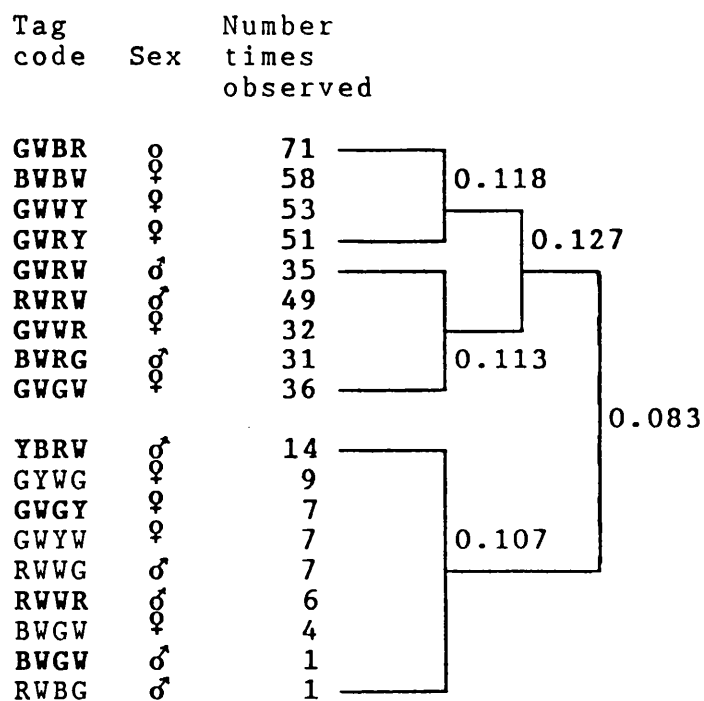
fingerprints of workable quality, but from pairwise analysis of band sharing across the remaining 13 tracks (Table 7.1b), mean band sharing was higher in the 'core' group ('frequent co-foragers'), than between core and non core individuals ('infrequent co-foragers'). Subunits of the co-occurring groups, were also correlated with the level of association (Fig. 7.1). However, the two categories were only different by virtue of the variance ratio (F-test), rather than the true means. Thus, the two mean values could have been very similar but with one value having been drawn from a set of individuals with a greater variation of relatedness. Furthermore, fingerprint band sharing was more difficult to score with precision as inter track distance increased. This may have been partly responsible for the low mean band sharing of infrequent co-foragers.

There was consistency here, with the hypothesis that higher levels of relatedness exist in co-flocking jackdaws but the results were largely inconclusive.

#### 7.3.4 Sex differences

The variance ratios of intra and intersexual band sharing were not significantly different (nor the means) and in the event, I chose to pool the values to give a population mean band sharing level of 10.85%, SE= 0.82. I felt that with males, females and intersexual cross comparisons included, this value was a better representation of average band sharing within the colony

**Figure 7.1** Dendrogram of frequently (upper nine) and infrequently recorded co-foraging jackdaws. Decimal values indicate the pairwise coefficient of fingerprint band sharing 'x'. Non bold tag codes represent those individuals not included in the analysis.



and certainly more conservative than the colony value detected for the random selection of males in 8.2 above. I will refer to this mean value, as the 'average' level of band sharing in the colony.

### 7.3.5 Close co-foraging

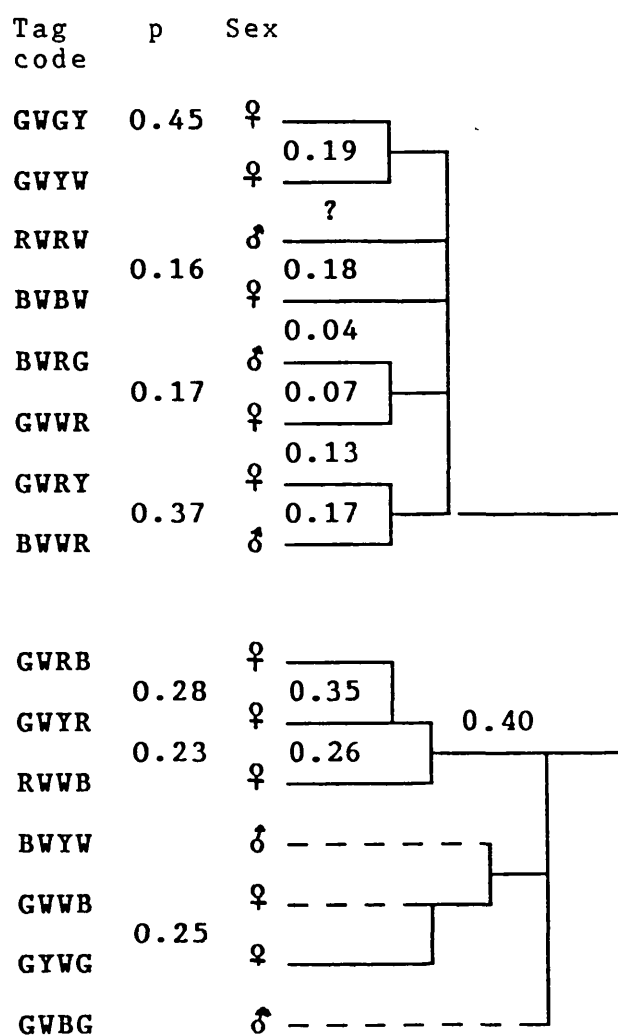
#### 7.3.5.1 Analysis

From the matrix mentioned in 7.3.1 above (Table 2, Appendix G) I was able to construct a dendrogram (Fig 7.3) using association indices calculated according to the equation (Lehner 1979),

$$p = \frac{n_{X+Y}}{n_X + n_Y} \quad (7.1)$$

where  $p$  the indices of association equals the number of time individuals  $X$  and  $Y$  were discovered within 15 birds lengths of each other, divided by the sum of the total number of occasions on which each bird was recorded in any association. This was a slight modification of the original formula, in which  $n_X + n_Y$  represented the number of occasions on which birds  $X$  or  $Y$  were respectively observed. The reasons for the modification were related to the points discussed in section 7.3.2, namely, that flock occurrences were frequently under-represented. In the present form, the expression, "the number of associations of  $XY$ , per total associations of  $X+Y$ ", was a

**Figure 7.2.** Dendrogram representing the closest 15 co-foraging jackdaws from 144 flocks. Decimals = x the coefficient of band sharing between successive jackdaw pairs. p= association indices (see text 7.2.3.1). The dashed lines are birds not included in the fingerprint analysis.



more rigorous test, than "the number of associations of XY, per total occurrences of X+Y". In the former case, virtually all involved birds were positively identified. The same was not true of intra flock occurrences, because while X was being identified Y may have been briefly present elsewhere in the flock. nY would then have been underestimated and p overestimated.

In fact, the data were skewed, with many pairs scoring similar and typically low association indices. The effect was that only a few pairs generated indices high enough to be of practical interest. Hence, 15 such individuals were chosen for fingerprint analysis, comprising 10 females and five males. (Fig. 7.3).

As many close co-foraging jackdaws were also regular flock foragers overall band sharing levels provided a second and more reliable analysis of the flock core group genetic structure.

#### 7.3.5.2 Close co-foragers

Again three tracks failed to produce fingerprints of workable quality (birds RWWR, BWGW and RWBG, two males and one female) hence kinship analysis was restricted to 11 individuals (Plate 7.2 and Table 4 Appendix G).

Mean coefficient of band sharing for the seven highest associating pairs was relatively high but not significantly higher than the mean colony value (Table

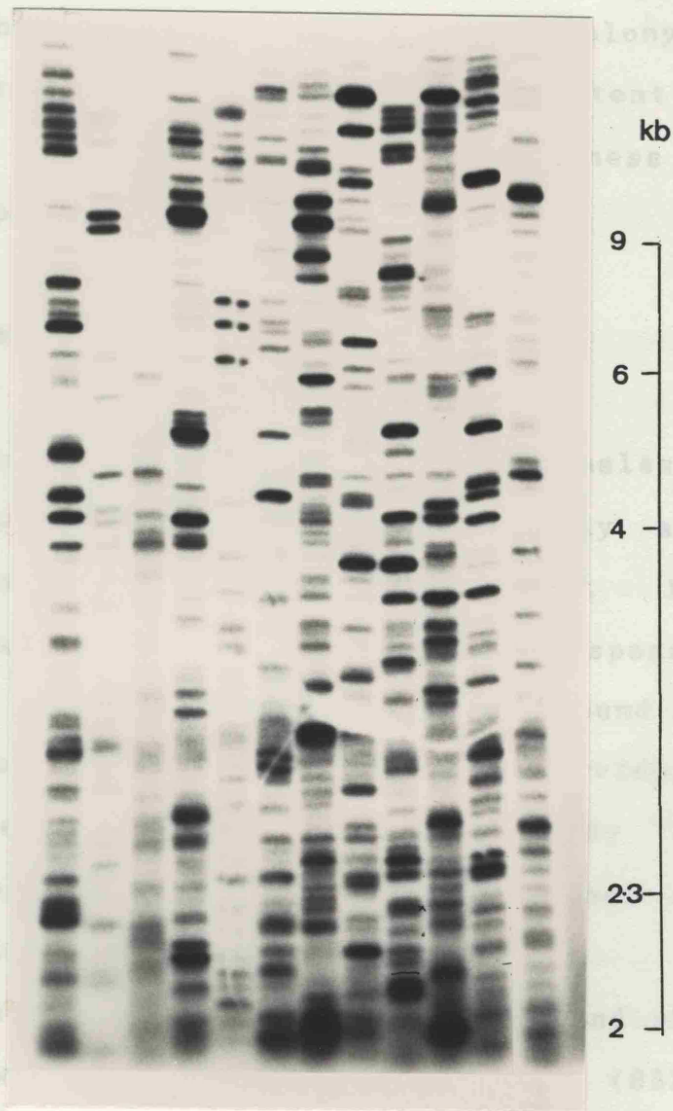


**Table 7.2** Analysis of mean DNA fingerprint band sharing in closely affiliating, foraging jackdaws. Mean band no. per track,  $n_b = 29$ .

	%	SE	N	$t^*/z$	P
-----					
Close partnerships regardless of sex	24.9	4.27	7	0.44 <sub>*</sub>	N.S
Females	21.8	1.25	35	5.75	<0.01
Male/female	14.9	1.43	25	2.10	<0.05
Males	8.7	6.00	3	0.06 <sup>*</sup>	N.S.
-----					

Significance tests were measured against the colony mean percentage of band sharing (10.85%).

Plate 7.2 DNA fingerprint of close co-foraging jackdaws



Sex ♀ ♀ ♂ ♀ ♂ ♀ ♀ ♂ ♀ ♀ ♀ ♀

Nestholders = ♀

7.2), despite a difference of ~14%. However, the variance about each mean was substantial. For instance, band sharing in the three male/female pairs (18%) was somewhat lower than the four female/female pairs (25.8%), a discrepancy that was possibly responsible for this high margin of overall variance. Nevertheless, band co-migration at conserved loci were considerably more prevalent than previously observed in the colony and band sharing levels were again consistent with the hypothesis of increased levels of relatedness in close foraging groups.

#### 7.3.5.3 Female/female band sharing

Systematic pairwise comparisons of all females revealed that mean band sharing was significantly above the population 'background' level (Table 7.2). But three females in particular could have been responsible for these results, because, allowing for background levels of band sharing of approximately 10%, two individuals (GWRB and RWWB) were related to a third (GWYR) by ~25% while the first two shared 15% of remaining bands (possibly cousins for example).

However, there were levels of over 15% band sharing in 29 of 35 pairwise female/female comparisons (83%), while only two pairwise comparisons (6%) lay below the 'population mean'. Intrasexual band sharing was therefore consistently high within co-foraging females.

Interestingly, five of the females tested were

nestboxes holders in either 1987 or 1988 and between them fingerprint band sharing averaged 19.4% (9% above the colony average). I do not know whether this was a significant feature that implied a selective advantage for philopatric females, or a coincidental artifact. But it raises the question of whether the relatively high levels of band sharing detected in females were a function of breeding demands (selecting for low female dispersal) or high male dispersal.

#### 7.3.5.4 Male/female relatedness

The mean of 25 pairwise male/female comparisons was not significantly different from the population mean (Table 7.2), but was significantly lower than female/female band sharing ( $z = 2.68$ ,  $P = 0.01$ ). One expects male/female associations to be the result of pair formation, with the corresponding levels of relatedness approaching the base level of band sharing. However, I only confirmed two tagged pairs from two seasons trapping (GWBR/GWRY and GWGW/RBYR), while closely related male/female birds were also present (for example RWRWo & GWGW<sup>0</sup>,  $x = 0.45$ , Plate 7.1b). As the pairwise male/female comparisons of Plate 7.2 could have included any combination of relationships, the results were subsequently difficult to interpret as one had no reliable notion of expected levels of relatedness. Nevertheless closely related males and females appear not to have been common.

#### 7.3.5.5 Male/male relatedness

Mean intra male band sharing was low (Table 7.2), but from only three pairwise comparisons the differences were not significant from either the population level of band sharing or the intra female level of band sharing. Nevertheless, intra male relatedness proved consistently low throughout the fingerprint analysis (Fig 7.1). Total mean band sharing for all the Billesdon colony males, tested in this study equaled 8.57% , SE= 2.25. This was also consistent with the Rutland Water male coefficient of band sharing.

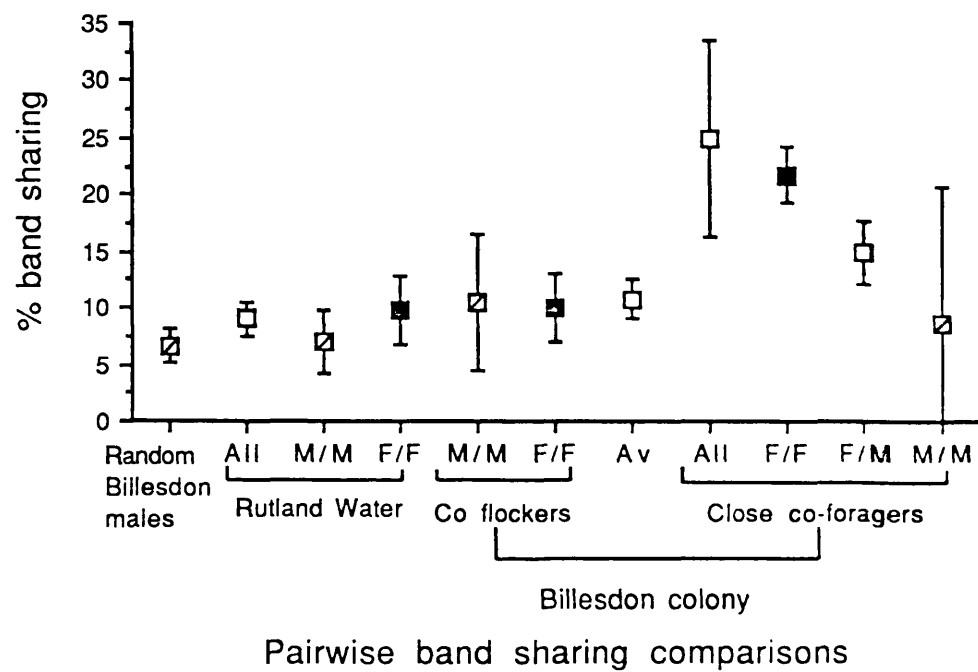
#### 7.4 Conclusions

Justification for drawing conclusions from the fingerprinting data was limited given the exclusion of rigorous segregation analysis. Nevertheless, four interesting points arose from the results.

1) There was no evidence of general inbreeding in either the Billesdon or Rutland water colonies. Co-migrating loci were rare.

2) On average band sharing was slightly higher in co-foraging individuals, and consistently so in females (Fig. 7.1).

3) On average band sharing was lower in males than females, and again consistently so throughout the analysis (Fig. 7.1).



**Figure 7.3** Summary of band sharing levels. Males (MM) . Females (FF) . (Error bars = 1x SE)

4) Close relatives were not often detected throughout the analysis.

Not only was intra colonial mean band sharing low, but co-migrating bands were rare in both colonial samples, that is, from Billesdon Coplow and Rutland Water, respectively. The dispersal in some quarter was substantial. However, within the Billesdon colony, co-migrating band frequency was more prevalent in co-foraging birds, and particularly so in co-foraging females. As, in general, high levels (close relatives, including offspring and siblings) of relatedness were not detected between co-foraging individuals, one suspects that interrelatedness was maintained, not directly through kin selection, but through asymmetric dispersal, biased in this study towards males. Male biased dispersal would be contrary to most avian dispersal systems studied so far (Greenwood 1980).

There were three possible sources from which artifacts may have arisen.

- 1) Close foraging jackdaw associations were incorrectly assigned
- 2) Sex determination was incorrect.
- 3) Band scoring was incorrect

If the first point was true then it was unlikely

that so much variation in band sharing would have accompanied the three different levels of group association (that is, the colony, flock foragers and close co-foragers). Close foraging groups were more likely, under the premise of this argument, to score low average levels of band sharing as detected in the colonial samples.

Correct sex determination was very important and the methods are describe at greater length in Chapter 9. However, on the basis of morphological characters, two demes arose from which birds could be identified as either males or females. I am confident of the sexing of individuals based on this analysis, of which the majority were, in any case, confirmed by behavioural observations.

Band scoring was indeed difficult to determine from the autoradiographs used here. Lambda calibration markers aided the process, and careful measurements between bands was otherwise required. Further qualitative support was derived from the consistency with which the methodology was conducted from one autoradiograph to the next. And ultimately an intuitive look at the band patterns tends to uphold the legitimacy of the technique.

## 7.5 Discussion

Given that five breeding females (sharing on average 20% of bands) were part of the core group analysed, one



could hypothesize that there are selective advantages to be gained from matrilineal accession to nest sites. The problem arises that arguments put forward to explain female philopatry can also explain the converse. For example, competition for nest sites (see following chapter) may explain dispersal in search of other sites or, as described here may promote selection for matrilineal accession, as the securing of sites may be assisted by nearby relatives (Greenwood 1980).

A great deal more information needs to be collected before conclusions can be formulated regarding this aspect of jackdaw ecology. Nevertheless, one apparently distinct feature of jackdaws (also requiring further investigation) was that males did not and are not capable of defending a resource (nest site) without the female's assistance (Röell 1978).

Female dispersal has been described in a variety of mating systems, from cooperative societies (Woolfenden and Fitzpatrick 1978) to communal nesters (Chabrzyk & Coulson 1976), leking systems (Lill 1974), and territorial hole nesting species (Greenwood et al 1978). In all cases males exercise a degree of resource holding potential, for which there is an advantage in patrilineal accession. However, in birds with known male biased dispersal, resource defence is lacking, and emphasis is placed instead on female acquisition. In these instances (eg lesser snow goose *Chen c. caerulescens* Cooke et al

1975 and the long-tailed duck *Clangula hyemalis*, Alison (1975) pair formation takes place away from the breeding grounds, and often on winter migration. Colonies mix, pairs form and the males return with the females to breed (Greenwood 1980). Male dispersal then reflects female breeding dispersion, while females remain strongly philopatric.

Jackdaw pairs are also established away from the nest, and normally well in advance of the breeding season (Coombs 1978). Thus it would seem that mate acquisition is a priority that benefits the males, at least by greatly improving their chances of defending a newly available nest site.

Nest site acquisition in jackdaws is highly competitive (in other colonial species, including rooks, nest sites are less often limiting and may be built or excavated, though naturally their final position may be critical) such that, one would expect high dispersal perhaps in both sexes. Are there any reasons why females should be less inclined to disperse, as juveniles, than males?

Male biased dispersal is normally recognised if,

a) female reproductive investment is high relative to the males (typical of polygynous systems), and,

b) where male resource defence is low. Males are therefore as likely to acquire breeding status elsewhere as locally (Again typical of polygynous mating systems).

Both of these points were relevant to jackdaws, where all incubation is completed by the female (Goodwin 1969; Coombs 1978), and males are unable to retain nest sites, without the efforts of both birds (Röell 1978 and pers. obs).

Röell (1978) reported that in his study colony 'non resident' birds were less successful at gaining access to nest sites than residents, due to interference from the latter. If this was true of all jackdaws colonies then males would surely benefit from seeking resident females elsewhere.

#### 7.5.1 Hypothesis

Amidst much speculation and circumstantial evidence, I have attempted to formulate an hypothesis to explain female biased philopatry in jackdaws. That is:

i) That nest sites are a limited resource (see following chapter).

ii) That there are benefits to females in remaining in the natal area, as this may facilitate nest site accession.

iii) That males require females to help defend nest sites.

iv) Thus males disperse in search of females, before the breeding season, rather than defend female breeding resources.

Alternatively (or in conjunction), winter foraging and the asymmetrical effects of hierarchy may modify or dictate sex biased dispersal. Females can improve their social status simply by pairing with high ranking males (Röell 1978). On average, male/ male competition is likely to be of greater intensity than male/female competition, thereby augmenting the dispersal of subordinate immature males. However, similar conditions are probably common to many birds, and while they may be instrumental in promoting winter dispersal (see Chapter 6) they cannot be construed as the prime factors maintaining asymmetric sex dispersal in breeding colonies.

In conclusion, much more information is required on each of the following points.

- 1) The defensibility of nest sites by males and the consequences of defeat. (Removal of females.)
- 2) A thorough analysis of relatedness in breeding males and females from traditionally established colonies.
- 3) A thorough analysis of ringing data for evidence of sex biased dispersal.

## **8 BREEDING BEHAVIOUR**

### **8.1 Introduction**

The Billesdon Coplow jackdaw colony was centered around an newly established nestbox colony in Tom Spinny, the main study rookery. This enabled me to study aspects of jackdaw breeding behaviour and develop a more complete picture of jackdaws social life. I concentrated my observations on identifying aspects of competitive behaviour and foraging ability, required for securing nest sites, feeding incubating females, rearing nestlings and guarding females from the sexual advances of other males. These competitive aspects are discussed with respect to information from previous chapters, in relation to the consequences on individual dispersion, dispersal and intercolonial relatedness.

### **8.2 Nestbox acquisition**

#### **8.2.1 Nestbox success**

The immediate success of the nestbox scheme was a surprise as nest site acquisition is normally thought to occur in September (Coombs 1978). All twenty nestboxes were built and erected during the second week of March 1987, and all except box 19 were utilised by jackdaws in that year (a nest was built in box 19 but was never used). In 1988 box 6 was commandeered by grey squirrels

*Scurius carolinensis*, otherwise jackdaws bred in all the remaining boxes. The nestbox entrance holes were too small to allow tawny owls *Strix aluco* access and otherwise only stock doves *Columba oenas* attempted to breed in them.

### 8.2.2 Nest site competition

Nestbox acquisition was characterised by much fighting between rival jackdaw pairs, indicating that competition for nest sites was intense (see also Röell 1978). On some occasions it was difficult to assess the true ownership of a box before incubation. For example, in 1988 much of the nest in box 11 was built by the female partner of RWRW, only to be used by GWRWo and female, while the former pair nested in box 17. Few animals other than grey squirrels seemed capable of competing with jackdaws for nest sites. Typical harassment of other nest site occupants, whether of the same species or not was further evidence of the pressure on jackdaws to secure breeding sites.

Nest site interference from other jackdaws in the colony was commonplace throughout the breeding season, including the post hatching period when the advantages of nest site competition and extra-pair mating were of no consequence. Nestbox 20 was subject to intensive three hour post dawn watches, on 10 consecutive days in late May and June 1988. Thirty-eight incidents were observed involving other jackdaws and the nest site or nest site pair.

The majority (23) of incidents involved three of four jackdaws contesting their position on top of the nestbox via the implementation of threat postures (Coombs 1978). However, on 11 occasions a jackdaw from outside of the recognised pair entered the nestbox to be immediately followed and displaced by the resident female. The local male (identifiable by a metal ring, and clearly contrasting nape) occasionally chased away intruding birds but never, to my knowledge, entered the nestbox. The most persistent infiltrators were two tagged females, one GWGY from box 18 (1988) which entered the box twice, and the second GWYW entered the box eight times and looked into the box on a further six occasions, before being pursued. The latter bird did not breed on the study site during 1988 but raised two chicks in box 2 in 1987.

I originally interpreted this interference as helping behaviour but on no occasion was I aware of food being carried by the interfering adults. Only once did a bird enter and emerge from a box, uninhibited, carrying an item (a feather), before being pursued by the resident female. I would tend now to interpret such behaviour as displacement activity rather than helping, as infiltrating birds were certainly not tolerated by the resident female, did not appear to contribute in any significant fashion to the welfare of the brood, but were persistent in their inquisitive attempts to gain access to the chicks. Both of the recognised, interfering females, were females that had failed to produce broods

that year. I can only speculate as to whether this was significant in their continued inquisitiveness towards a successful clutch. Neither intruding female was closely related to the resident female (from DNA fingerprint analysis). One could interpret the above account as an example of female-female aggression, interference and competition.

### **8.3 Colony composition**

The Tom Spinny nest box population must have comprised either:

i) Birds 1 year old, capable of breeding in their second summer though not normally doing so until one year later (Goodwin 1968; Coombs 1978).

ii) Breeding adults that colonised from elsewhere, leaving their previous sites to members of categories i) and iii).

iii) 38 potentially breeding adults that would normally have forgone breeding due to nest site shortage.

#### **8.3.1 Age structure**

##### **8.3.1.1 Identification**

Jackdaws can be aged up until their second full year of life on the basis of iris colour and plumage characteristics. Post nuptial juveniles acquire blue irides that change to brown by early winter. The brown



irides then give way to white, so that immature birds of approximately one years age (in May) display white irides with brown blotches. During the course of their second year the irides gradually change to pure white or silver/white or grey, characteristic of fully adult birds. Immature jackdaws also retain their original flight feathers (remiges and rectrices) until mid May of the first full year. A complete summer moult is then undertaken (Svensson 1985). The flight feathers of first year immature birds are blackish brown and worn, where as adult plumage, by contrast appears glossy black. Two year old adults begin their complete summer moult in mid June, approximately one month after one year old birds (Coombs 1978). Jackdaws can subsequently be aged with some confidence, both in the hand and by observation, if one can procure close enough views.

#### **8.3.1.2 Breeding age**

Over the two breeding seasons, 1987 and 1988, 48 (68%) of breeding birds, from 12 tagged birds and 36 observational records, all proved to be adults (at least two years old), providing no indication that the proportion of young, premature breeders was especially high in the population. Six locally ringed jackdaws, trapped together with those tagged above, (ringed as nestlings, Warrilow pers. comm.), provided useful confirmation of age characteristics. Five (of the six above) breeding jackdaws ringed as pulli at Billesdon

Coplow (from nine pairs each year) were fully mature birds.

### 8.3.2 Occupation of traditional nest sites

All known Billesdon Coplow sites (the closest to the study site), traditionally occupied by jackdaws, were again utilised in 1987 and 1988 (N= 21; Warrilow pers. comm., and per. obs.). The nestbox scheme did not apparently succeed in creating a surfeit of nest sites but merely provided breeding opportunities for a further 19 pairs.

### 8.3.3 Conclusions

Nest site competition was intensive between adult jackdaws, and much energy was spent on their procurement. From the evidence available age structure did not appear to have been significantly affected and other local sites were not vacated. The implication remains that adult jackdaws were therefore competing for a limited resource.

## 8.4 Breeding success

Fledging success was very poor in 1988 for reasons not properly understood (Table 8.1). Disturbance to the nests by my own presence was possibly a contributory factor, but I have no reason to suppose that disturbance

**Table 8.1** Jackdaw population breeding data for two seasons, 1987 and 1988. SE = standard error.

Season	1987	1988
<hr/>		
Egg		
total	78	79
Mean		
clutch size	3.9 (SE= 0.27)	4.16 (SE= 0.24)
Total		
hatchings	41	56
% hatchings	53%	71%
Fledged		
total	22	5
Chicks/pair	2.16	2.95
Chicks/ successful pair	1.47	2.95
% nest producing chicks	79.0	21.1
<hr/>		

was any greater in 1988 than it was in 1987.

Parental inexperience does not explain the discrepancy, as at least six of the breeding individuals from the first season bred in the second season, though only one was successful in raising any young (GWYW), compared with five in 1987 (Table 8.1).

Twenty-two chicks disappeared either as a result of predation or parent removal. The nestbox entrance holes were designed to prevent access to tawny owls *Strix aluco* and carrion crows *Corvus corone*, and grey squirrels were never common in the wood. Other potential predators include stoats and weasels but I have no reason to suspect that any of these predators were more effective in 1988 than 1987. The same argument applies to jackdaws themselves, which Coombs (1978) reports as having removed eggs and chicks from the nests of conspecifics. While some loss of jackdaw progeny may have been attributable to predation or intraspecific competition and removal, in 1988 I recovered 34 chick corpses from the nestbox population, implying 61% mortality due to causes other than predation.

I never observed any deleterious effects from claw clipping, and indeed many pulli had died in 1988, before I was able to remove blood. All 21 fledged nestlings from 1987 were bled by claw clipping, with no apparent side effects. All 21 had regrown the claws, some of which were indistinguishable from the non clipped claws.

Mean clutch size was marginally higher in 1988 than 1987, as was hatching success. The latter point preempts an explanation of high infertility due to either precocious breeding or poor female condition.

There was some indirect evidence of nestling starvation, as three large broods in boxes 3, 4 and 12 completely failed (total of 17 eggs and 16 pulli) though one chick respectively from boxes 3 and 12 survived up to one week to the point fledging, before vanishing prematurely. Eggs in box 4 all hatched within two days of each other and the chicks died within the following 24 hours, none having been predated. There is evidence that in asynchronous broods, runts die quickly, thereby increasing the chances of survival of the stronger chicks when food is limiting (Gibbons 1987). Asynchronous hatching may explain the longer survival time of progeny in boxes 3 and 12, but with so many failed broods, I had not enough comparative information to seriously investigate this effect.

With only five chicks fledging from 56 hatchlings, starvation and/or disease were the only feasible explanations for the chick failure. Most dead broods were cold, occasionally with the odd individual still barely alive. The parents never returned to these boxes to my knowledge, and because many of them were untagged I could not confirm their fate. However, of the tagged

birds that bred, at least five were observed alive the following autumn (§ 7.3.2.3). Jackdaws are often reported as having poor fledging success (e.g. Warrilow pers. comm.) but I have no explanation for the complete loss of broods experienced in 1988.

## **8.5 Male foraging ability**

### **8.5.1 Background**

In both jackdaws and rooks incubation is carried out by the female only, while the males supply virtually all food during this time (Coombs 1978; Goodwin 1968; Röell 1978; Røskft 1981; pers. obs.). The ability of the male to maintain an adequate supply of food to the female should therefore be a significant factor influencing female physiological and reproductive condition. It then follows that male foraging ability should be reflected in the females ability to produce eggs and/or for both parents to rear offspring.

Assuming that food resources were equally available to all males in the colony, I looked for variation in the ability of males to return food to the females. I subsequently chose periods when simultaneous demands on a variety of males were of a similar intensity. That was, when females were brooding eggs, but were near to or on the point of hatching. As females were still fully incubating (whether on one egg or more) and had been so

for some 16 to 18 days, the continuous demands of the females for the attention of the males should have represented a point of high physical stress for the males, and as such have been an appropriate time to test the males capacity to support the female.

#### **8.5.2 Hypothesis**

After detecting heterogeneity within foraging rooks (Chapter 6) and with hierarchies having been identified in jackdaws (Röell 1978), I expected to find significant heterogeneity amongst the foraging abilities of male jackdaws. Foraging ability might then be reflected in fledging success, as males help to rear chicks. The same argument was less likely to apply to clutch size, as the females reproductive condition, prior to egg laying, was influenced more by her own feeding ability than that of her partner.

#### **8.5.3 Procedure**

I repeatedly recorded the times taken for male jackdaws to return to the nest with food, following their departure from the nestbox. Observations began at dawn (~ 0330-0345 GMT) and continued for approximately four hours. These hours were the most uniform in temperature, before the suns warmth took effect and the most active in terms of jackdaw behaviour. From around 0800 GMT (0900 British summer time) onwards males began to loaf by the

nestboxes rather than search for food.

I only managed to test seven males in total, as I could only cover small sections of the wood at any one time and many nests were at similar stages of incubation. I subsequently positioned a hide to view, a) boxes 12 and 13 from the 12th May to the 14th inclusive, and b) boxes 20 and 19 from 15th to the 17th May inclusive. I observed boxes 8 (18th May), 2 and 5 (19th May) from the adjacent field on the north side of the wood (Fig. 1.2 and 1.5).

#### 8.5.5 Results

From the results presented in Table 8.2 (and Table 2 Appendix H) it was clear that there were significant differences between males in their return times (Fig. 8.1). However, on the basis of these seven cases, neither clutch size nor fledgling success significantly correlated with male return times. Alternatively, male return times may not necessarily reflect male feeding ability, as males may return infrequently but with large loads. Nevertheless, at this stage in the breeding season, with newly hatched young, an infrequent food supply may well have been fatal for weak nestlings and runts. This aspect of male foraging ability requires further investigation as with such small sample size the results were largely inconclusive.

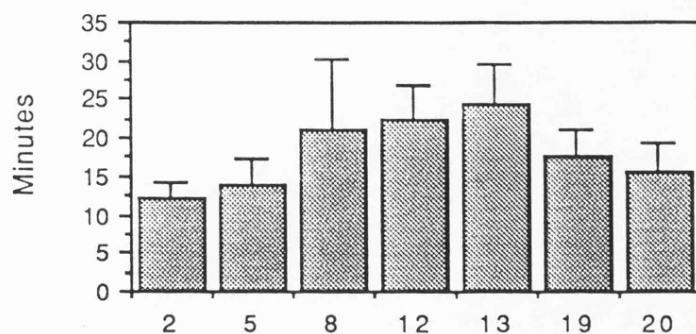


**Table 8.2** Mean return rates (in minutes) and the corresponding clutch success of seven male jackdaws. (1988 season).

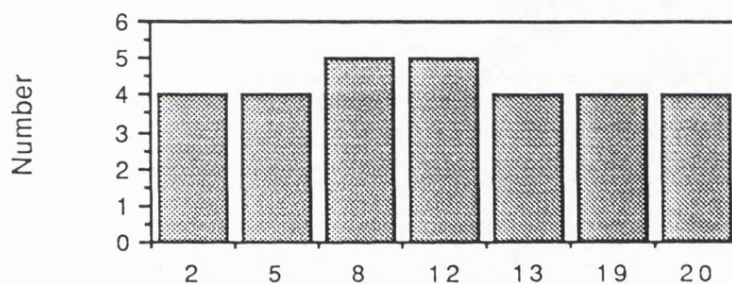
<b>Nestbox</b>	<b>2</b>	<b>5</b>	<b>8</b>	<b>12</b>	<b>13</b>	<b>19</b>	<b>20</b>
<hr/>							
<b>Mean</b>	12.3	13.9	21.0	22.5	24.6	17.7	15.5
<b>SE</b>	1.0	1.7	4.6	2.1	2.5	3.3	1.9
<b>N</b>	10	13	14	25	28	8	38
<hr/>							
<b>Clutch</b>	4	4	5	5	4	4	4
<b>Hatch</b>	4	2	4	5	4	4	4
<b>Fledge</b>	0	1	0	0	1	1	2
<hr/>							

**Figure 8.1** Male foraging return times (a) with the corresponding clutch (b), hatching (c) and fledging successes.

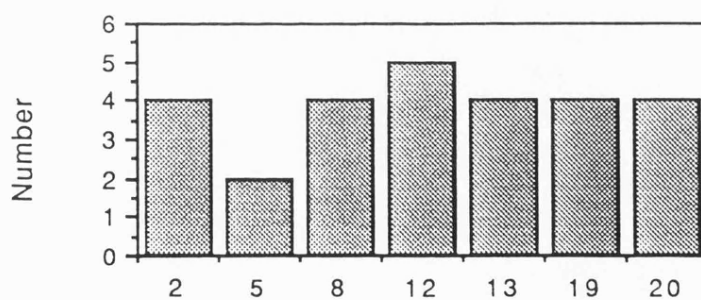
a) Return times (SE)



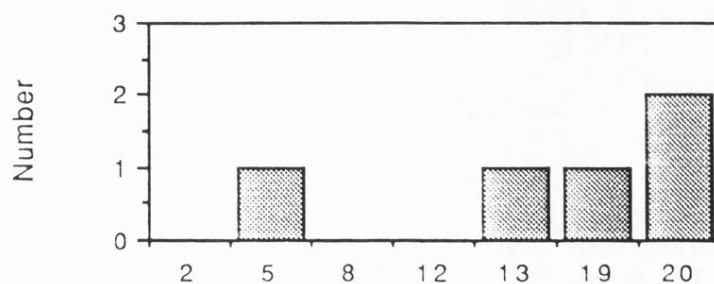
b) Clutch size



c) Hatching success



d) Fledging success



Nestbox

## 8.6 Mate guarding

### 8.6.1 Background

In mate guarding, the male protects the female from the sexual intentions of other males by shadowing her and challenging the intruders (Birkhead 1979; Grafen and Ridley 1983; McKinney 1986; Møller 1986). Mate guarding is especially likely to occur in males that are monogamous and invest heavily in their offspring. As monogamous males invest virtually all their annual reproductive effort in one female they should consequently ensure their paternity by remaining in attendance with the female. The same should also be true of males that invest in parental care (but see the mallard *Anas platyrhynchos*, Goodburn 1984).

As jackdaws fell into the last two categories I also expected to see mate guarding in this species.

### 8.6.2 Procedure

I tentatively tested for mate guarding by measuring the distance between the two individuals of three pairs of jackdaws, at three different points in time. These times represented moments before, during and after the females most receptive period and therefore mate guarding should have been most intensive during the second phase. The three sample dates were:

a) 30th March, approximately one month prior to egg laying.

b) 28th April, between three days before and one day into the predicted egg laying period (as it turned out).

c) 20th April, when hatchlings had hatched and the benefits of extra-pair copulations (EPCs) had ceased.

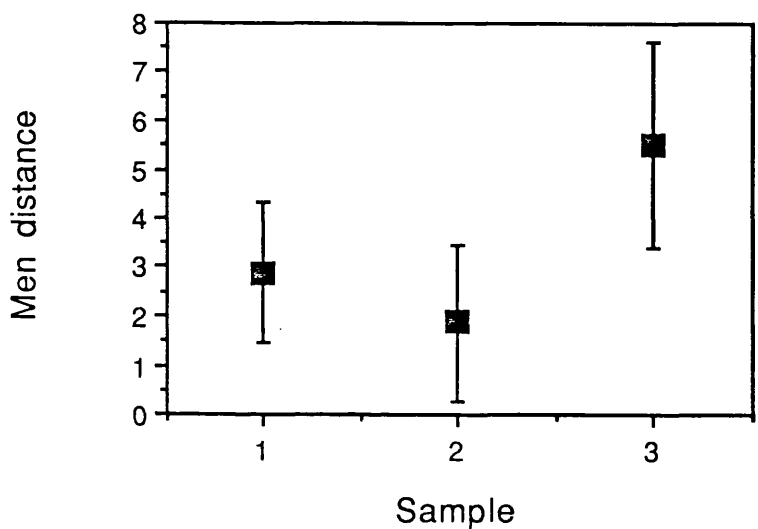
The distances between paired individuals were estimated by placing them into the classes 0 (touching) 0.1, 0.2, 0.3, 0.4, 0.5, 1.0, 2.0, 3.0, 4.0, 5.0, 10, 20 metres. Every time the two birds of a pair appeared together I recorded the distance between them, and continued to do so every five minutes for which both birds were in view (Table 3 Appendix H).

### 8.6.3 Results

There were no significant differences between the mean intra-pair distances for the three jackdaw pairs under observation, data were pooled (Table 3, Appendix H). I therefore arrived at three mean values for intra-pair distance for the three sampling dates. These are given in Fig. 8.2.

Although the intra-pair distance was smaller during the second phase the differences were not significant (z-test). Thus the result was indicative of the intensification of mate guarding towards the females most fertile period, but several explanations arise. However,

**Figure 8.2** Mean distance between male and female jackdaws on three days, before, during and after the females 'receptive' period. Error bars =  $\pm$  SE.



during the third phase, both parents were beginning to feed nestlings and therefore, the distance between them was necessarily much more variable. Thus, the first and second phases provided a better comparison as the male was in both situations free to escort the female. And indeed the male may have intensified mate guarding, but it was more interesting to note that while free from the constraints of parental duties, and despite being one month away from egg laying, male and female remained in close association. As male jackdaws therefore remained close to the females throughout the year (Coombs 1978, and pers. obs.), mate guarding was more difficult to assess.

In retrospect, as distance may not be perceived by jackdaws in such precise terms as those measured above, data may have been more informative had I have quantified whether the males followed females more often than vice versa (Hunter pers. comm.).

However, these results served to emphasise the importance of the pair bond in the jackdaw breeding colonies, though a functional explanation for this pattern of behaviour was not obvious.

## 8.7 General discussion

In mate guarding terms, males that continue to escort females, might obscure the true fertile period and thus prevent its advertisement to other males. However, this argument has little appeal because other behavioural cues, such as nest building or courtship feeding, may

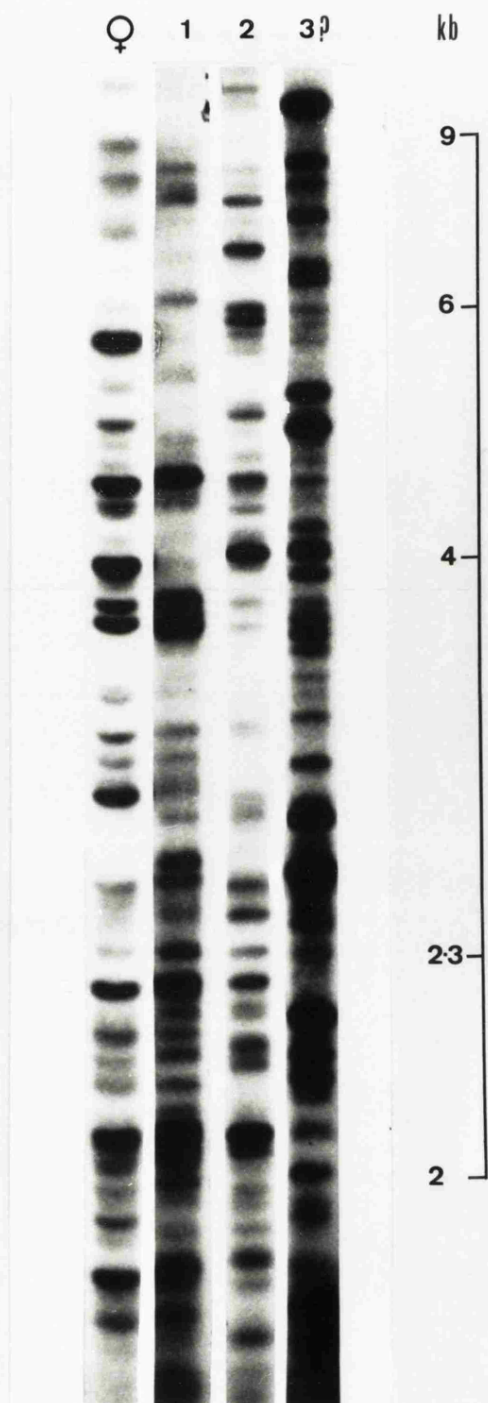
also be reliable indicators of the females receptiveness.

I only ever witnessed one mating and one attempted extra-pair mating in two full seasons of observations. The first took place on top of a nestbox, uninterrupted (Coombs 1978, states that mating occurs within the nest hole, and indeed I regularly witnessed much unseen but audible activity within nestboxes for the first hour after dawn).

The second incident involved an intruding male dashing in between the resident male and female, attempting to mount the female, but being very much resisted by her until they parted with the intruder being pursued by the resident male. The attempted extra-pair copulation took place on the 22nd April 1988 approximately one week before egg laying, though the resident pair had been nest building for five or six days. It was interesting however, that the female forcefully resisted the copulation attempt (though as in rooks this intolerance may increase with age, Røskoft 1983). This again, implied that a faithful pair was an important property of jackdaw reproductive success and that females resisted males that were unlikely to contribute to the raising of her offspring.

Some males do possibly succeed in successfully fertilizing females outside the pair (Plate 8.1; Table 1 Appendix I) though I have no quantitative evaluation of the rate of successful extra-pair copulations (EPCs) within the colony. But questions arise such as,

**Plate 8.1** DNA fingerprint of a female and three offspring for which the third offspring shares relatively few bands with the sibship.





are successful males a) already paired and perform EPC's as a form of insurance policy, or b) unpaired subdominant males that would not otherwise breed?

I can only hypothesise that the second case was more likely in jackdaws, as there were advantages in male-female pairs remaining faithful. Thus:

1) The male has no resource holding potential on his own, hence the male and female are required to secure a nest site (Röell 1978).

2) Nestling survival requires investment from both sexes (Coombs 1978).

3) Male investment required to ensure nestling survival implies that males should, as far as possible, ensure their paternity.

4) Intra-pair and nestling investment decreases the likelihood of males completing EPCs, especially as males would be unable to invest much time in supporting potentially sired offspring in other broods (c.f. dunnocks *Prunella modularis* Burke et al 1989).

It may then be that the long term partnership established during the winter months is important for familiarising each male and female with their partner, assessing foraging ability and therefore establishing a secure relationship.

## 9 SEXING JACKDAWS

### 9.1 Introduction

This chapter discusses the features on which jackdaws were sexed, the accuracy of which was crucial to Chapters 7 and 8 particularly, and ultimately to the whole of the thesis as much discussion is based on the role of the sexes in maintaining flock structure.

### 9.2 Discriminating features

Jackdaws were sexed on the following criteria:

1) Male cloacal protuberance. In sexually active males, before the females have laid eggs, the cloaca may protrude abruptly from the body. This feature is never so prominent in females.

2) Diagnostic behavioural activities of male jackdaws include,

- i) dominance within the pair,
- ii) reluctance to help build the nest though continuously attentive,
- iii) courtship feeding, where the male feeds the female at intervals prior to egg laying.
- iv) feeding of the incubating female, but rarely incubating themselves.

3) Physically, males generally look larger than the associating females, and the grey nape tends to contrast more sharply with the rest of the body (pers. obs. see below).

4) Female brood patch. In preparation for incubation a sexually active female loses feathers from much of her belly, exposing an large area of highly vascularised skin. Males occasionally develop such a patch, but never so large and extensive as in the females.

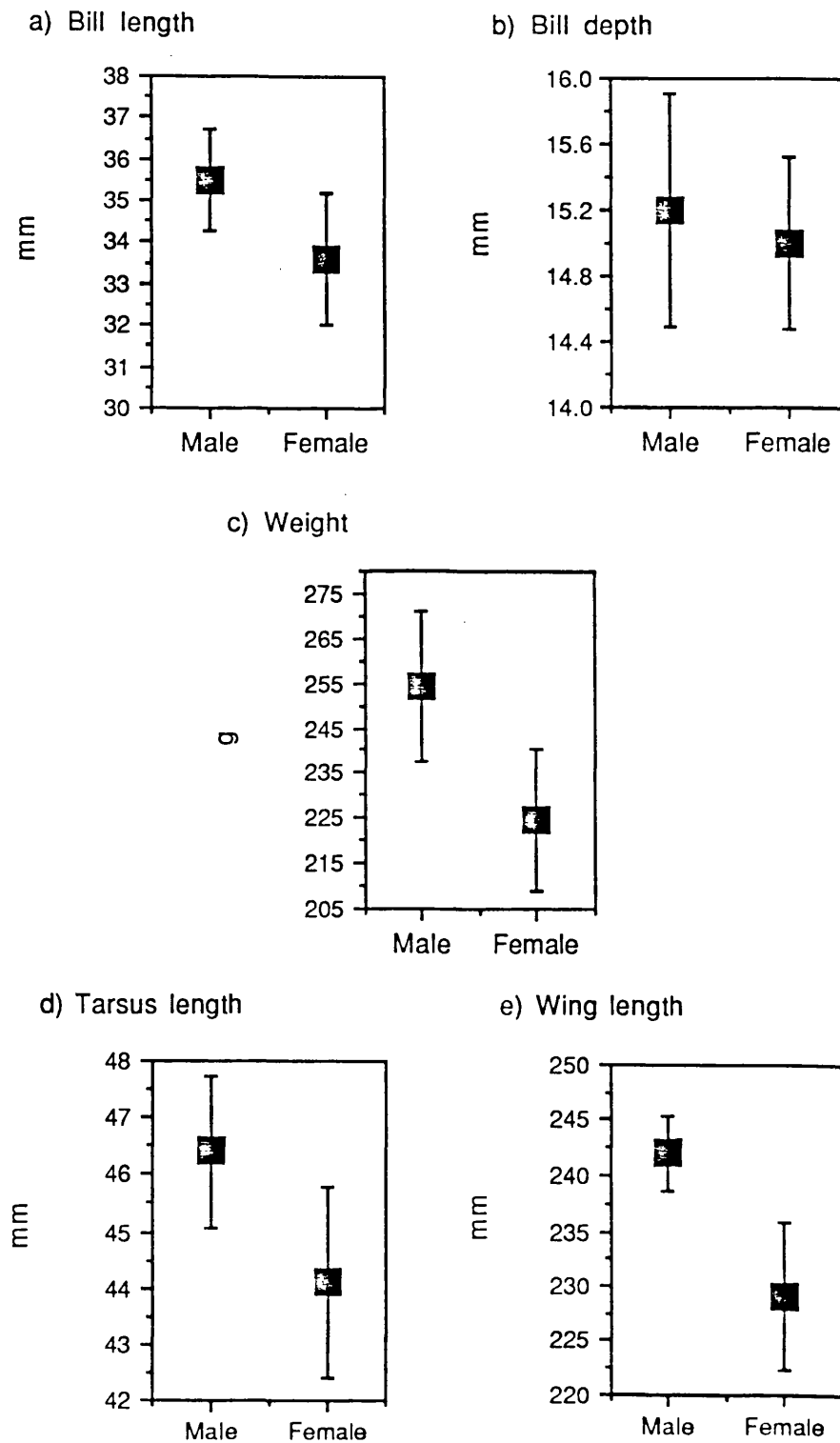
5) Female incubates the eggs.

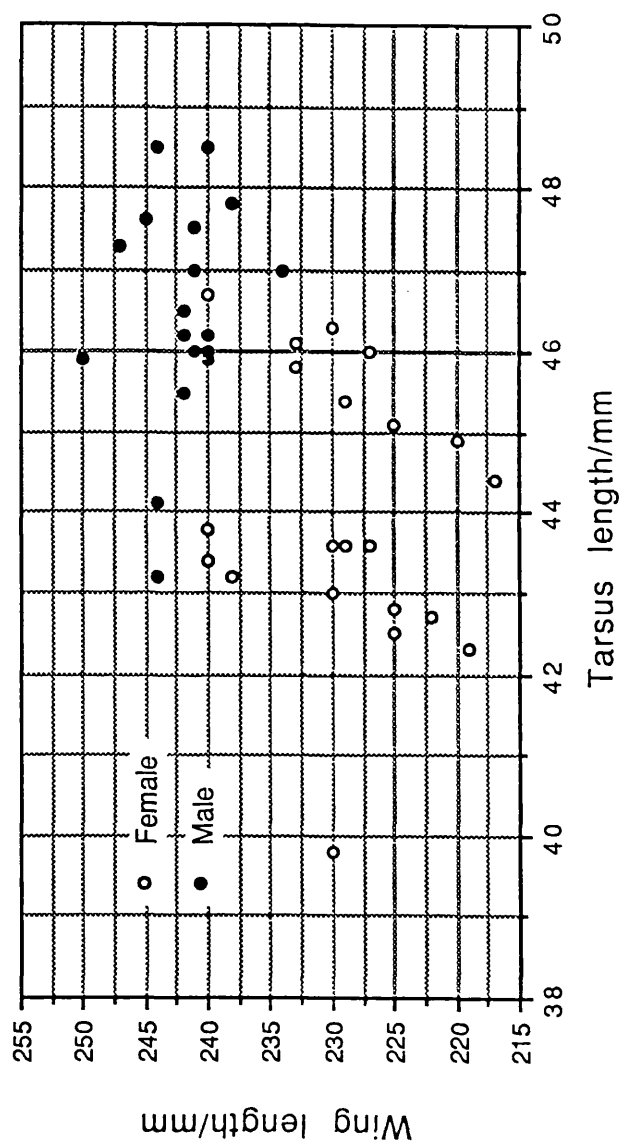
6) Females solicit courtship feeding by calling and shimmering the wings and tail (similar to that shown by juveniles when begging for food).

### 9.3 Biometrics

On 21 males and 20 females I analysed biometric data (Table 2, Appendix I) for discriminant features. In all of the following parameters: weight, wing length, tarsus length, bill length and bill depth (see section 1.2.1) there was overlap between males and females though the latter were generally smaller (Fig. 9.1). However, when all features were considered together simultaneously the margin of overlap was considerably narrowed, and reduced to only 4.8% of the total number of birds. For practical

**Figure 9.1** The comparison of male and female jackdaws for five biometric parameters (Error bars =  $\pm$  SE).





**Figure 9.2** The discriminant analysis of male and female jackdaws on the basis of wing length and tarsus length.

field purposes, the two most reliable criteria were wing length (wl) and tarsus length (tl). A plot wl on tl produced two demes with little overlap (7.6% error, Fig. 9.2). If border line cases were then further compared with weight and bill dimensions, few unresolved individuals remained. However, only adult birds (>1 year old, see section 8.2.1) could be confidently sexed on these biometric criteria. In immature birds, extreme measures erring on the large side would have identified males, but small values could have been characteristic of either sex.

## 10 SUMMARY

This study set out to investigate social and genetic aspects of flocking behaviour in two sympatric corvid species the rook *Corvus frugilegus* and the jackdaw *C. monedula*. The aim of the study was to identify individual heterogeneity in foraging ability, and to look for genetic ties that may have served to maintain close associations within flocks.

Genetic relatedness was obviously not a significant component of mixed species flock foraging. Mixed-species flocks were a very common and regular part of both species activities, so much so that other than when breeding, many activities, throughout the year were simultaneously carried out by rooks and jackdaws alike (Chapter 3). The annual roosting and foraging patterns were for example, common to both species.

The importance of food distribution and co-occurrence was emphasised as being the most significant contributory factor responsible for the observed interspecific association. Rooks and jackdaws were not randomly placed within the foraging flocks but were concentrated into species specific groups, inferring that the fine tuning of food location was more species specific than interspecific. The importance of the latter point was as follows. That although each species could quickly locate a potential food patch by following the other species, other than grain, the main species specific food items

were different and the advantages of interspecific social facilitation reduced. Intraspecific social facilitation would still be of great benefit for specific resource location and result in species specific aggregations.

Apart from different food resources, species specific clumping also reduced interspecific contact and interference. As a consequence, rates of interspecific aggression were very low on grassland and only when food was concentrated, such as in food troughs, were rates of aggression especially high. But the question remained as to whether species specific aggregations were a consequence of resource location, or kin selection in rooks and jackdaws respectively, which conveniently preadapted the two species to exist together. Whatever the cause, the association between rooks and jackdaws could have been described as convenient, for the advantages of flock foraging, those of improve location of patchy and unpredictable food resources, improved overall vigilance and reduced per capita vigilance were realised, while interspecific competition and interference was much reduced.

The question was then directed towards intraspecific groups within flocks and their social structure (Chapters 6 & 7). Was there variation in individual competitive ability as suggested for rooks by Swingland (1977) and in oystercatchers by Goss-Custard and Durrell (1981), and if so did competition affect species dispersion?



Or was kin selection responsible for maintaining species specific groups?

There was good reason to suspect that the latter point might have been significant, as kin groups have been identified in many avian societies, even when some individuals did not initially appear to benefit. There are many recognised cases of parental facilitation (Brown and Brown 1984) where offspring remaining in their natal area eventually obtain parental status (for example, acorn woodpecker, Macroberts and Macroberts 1976; Mexican jay, Brown and Brown 1984). Individuals may forgo immediate benefits to secure longer term payoffs, in the form of eventual territorial (florida scrub jay, Woolfenden and Fitzpatrick 1984) and/or nest site (superb blue wren, Rowley 1965) acquisition. Thus it was possible that the family group of rooks that formed in the summer were maintained on a long term basis.

Kin related foraging groups may be a consequence of kin selection having evolved in breeding systems or alternatively, the result of real selective advantages for relatedness in foraging groups. The latter point is easily envisaged as a simple manifestations of parental care at the nest. Thus, parents and offspring move location to a foraging area, and parents continue to spend time and energy feeding their offspring, or allowing them access to discovered resources.

Natural selection will favour parents that tolerate

their close relatives over other individuals, as those offspring are then more likely to survive, reproduce and so continue the trait for "tolerance towards close kin". The offspring of universally intolerant parents will expend more energy acquiring food, and thus be less likely to survive and reproduce. Universally tolerant parents would not only benefit the offspring of 'close kin' tolerant parents but also remove the exclusive access to discovered resources that their offspring would otherwise have. This latter strategy would not be expected to exist at high frequency in a population of close kin tolerant parent (Dawkins 1978).

However, the likelihood of kin selection evolving in foraging groups depends on the necessity for altruistic behaviour. Thus, where food is difficult to find and the chances of offspring survival without parental help low, then for birds with low mean clutches, such as rooks and jackdaws, parental help and the development of group kinship may prove advantageous. But because there are costs associated with high levels of population relatedness (Greenwood 1980, Shields 1982), if the demands for food acquisition were never too great, then selection for parental or sibling altruism would be weak beyond the stage where offspring were able to acquire food for themselves.

There is evidence that the demands on rooks and jackdaws to locate food is not great and that in mild and temperate climates birds maintain their body weight easily, with major difficulties, for rooks at least,

being associated conversely, with summer time (Feare et al 1974). Thus the advantages of becoming familiar with an area (one possible reason for low dispersal and higher levels of relatedness) are not important, as food resources though unpredictably placed are invariably plentiful. In this respect there would be no demands on rooks or jackdaws to maintain high levels of group relatedness.

Unlike mixed species flocks, individuals of single species flocks invariably compete for exactly the same food resource. If the resource is spatially and/or temporarily unpredictable, then, as discussed in the general introduction there will be an advantage to flock foraging, as food distributed in this way is harvested more efficiently by groups rather than individuals. However, once food patches are located, all individuals then exploit a common resource. If the resource is immediately or eventually limiting then this would lead to competition, with some individuals benefiting more than others. The balance between the benefits of locating food and the costs of competing for food influences the size and distribution of the groups observed.

In large flocks, subordinate birds such as immature rooks, are inevitable exposed to interference from dominant individuals. This is true whether kin selection exists or not. Ideally, immatures require the experience of their parents without exposure to the

attentions of other adults and hence seek smaller flocks with higher immature adult ratios. This observation was made in Chapter 6. However, if food was not scarce, but simply unpredictably distributed, then individuals would not gain from foraging in groups of related individuals. They would merely require any group of individuals to initially help locate the food patches, thereafter each individual would forage adequately on its own. Again subordinates, would be forced either to the periphery of a flock or to forage elsewhere, and again flocks comprising relatively high subordinate to dominant ratios would be preferred.

In rooks, immature birds did not forage as efficiently as adults in large flocks, but fed less and wandered more. It was suggested in Chapter 6 that the observed immature distribution, (biased towards smaller flocks) was a function of adult interference particularly in larger flocks. Predicted optimal flock sizes were calculated to include flocks in which immatures were seeking to maximise their net gains, that is, between the costs of interference in large flocks and the cost of poor food location in small flocks. Most immature were found in medium sized flocks between 10 and 40 strong and foraging efficiency improved also in these flocks.

On the information so far examined there was little evidence for kin selection within foraging groups of rooks, as on the contrary, it was implied that adult/immature interactions promoted the dispersal of

immatures (as recognised by Patterson and Grace, 1984). Furthermore, strong interspecific affiliations were shown to be largely a function of food distribution. Could the same not be true of intraspecific associations?

I was not able to investigate intragroup relatedness in rooks, but in jackdaws, members of co-foraging groups were not on average closely related. Nevertheless, closely foraging individuals were generally more closely related than the average level for the colony. Two colonies tested were outbred, with randomly selected individuals showing very low levels of relatedness. Only closely co-foraging females were significantly more related than average, though females were also consistently more closely related to each other than males.

Because co-foraging individuals were not consistently closely related (that is, not offspring or siblings) the implication was that the slightly higher levels of relatedness detected were a consequence of relatively low dispersal rather than selection for kinship. As described above, selection for kin related groups would have increasingly intensified the level of relatedness (see also General introduction, pp 7). But low dispersal, would eventually have resulted in only averagely higher levels of relatedness, as was found in female jackdaws.

So colonies were outbred and dispersal probably high, yet intra-female relatedness was higher than average. This encompassed the following two points.

i) that dispersal was probably immature biased as adults showed a high degree of site fidelity (information from tagged birds), and immature dispersal was also consistent with the information on young rooks taken both from this and previous studies (Patterson and Grace 1984).

ii) that immature dispersal was lower in females than in males.

In most birds, female biased dispersal is recognised as the norm, yet there is no strong argument to suggest that this should be the case in jackdaws. Furthermore, those species of bird that have been demonstrated to have higher levels of male biased dispersal have features in common with jackdaws. Thus in the Anatidae two species in particular, the Lesser snow goose and long-tailed duck have high male biased dispersal associated with low male resource holding potential, as was true of jackdaws.

Jackdaws normally form pairs in autumn, with males unable to exercise successful resource defence on their own (that is without the females, Röell 1978). This is probably a consequence of severe nest site shortages, resulting in very intense competition for those available (Chapter 8). Subordinate males cannot secure nest sites without female assistance, though females may do so by pairing with locally dominant males. This second point

also meant that females could modify their status by pairing with dominant males (Röell 1978), thereby resulting in more intense male/male competition (in foraging flocks for instance) than female/female competition; again promoting male biased dispersal.

Lower female dispersal may have resulted, either because there was advantage in female accession to nest sites, or that females were simply tolerated more than males at nest sites as they posed less of a threat to the paternity of the offspring. If young females were allowed to approach the nest sites, then familiarity with the sites may have facilitated acquisition later in life. In this sense related females (to the nesting females) may have fared better than unrelated individuals, so that in consequence, the average level of female/female relatedness in nest colonies is increased.

There are many interesting questions to be answered regarding male and female dispersal in jackdaws and in this respect rooks and jackdaws may not be alike, as rook nest sites are unlikely to be as limiting as suitable nest holes or ledges are to jackdaws. Ringing studies of sex biased dispersal would provide useful information, as would quantitative studies of the maternity of jackdaw offspring, as brood parasitism, if rife may be contrary to the hypothesis of female/female nestsite tolerance above. And indeed in Chapter 8, there was very little evidence of nest site tolerance towards non resident individuals.

To reiterate, two main points arose from the kinship analysis.

Firstly, and of relevance to the main theme of the thesis, there was no evidence of direct selection for relatedness within foraging groups of jackdaws, though close foragers may have shared slightly higher levels of relatedness than average. Thus, relatedness did not emerge as a significant component of jackdaw foraging groups.

Secondly, kinship analysis suggested that higher than average levels of relatedness, within foraging groups, was largely due to higher inter-female relatedness.

In conclusion, the following points were made in the study.

- 1) Competitive heterogeneity was present within foraging groups.

- 2) Competitive interference probably effected immature (subordinate) distribution, as dispersion of the latter was biased towards smaller flocks than those preferred by adults.

- 3) A direct genetic component to flocking was not detected in flocking jackdaws.

- 4) Commonly co-occurring food resources were discussed as the most likely factors promoting mixed species associations, and therefore possibly responsible for intraspecific aggregations too.



## APPENDICES

### Appendix A. (Chapter 1)

#### Tagging practicalities

##### i) Bird welfare

Some concern has been shown over the potential damage to birds caused by tagging, and Hart (1987) elaborated over a method originally described by Anderson (1963) and subsequently modified by Hart to reduce wing abraison. Anderson (op. cit.) fitted "Darvic" patagial tags using alloy wing pins. However, this method was reported by Hart to cause callouses to form around the retaining washers. Hart (1987) added a second pin to prevent rotation of the tag and was successful in reducing wing abraison. I 'recaptured' (one dead) 21 tagged individuals 9 from the previous years trapping. Some feather abrasion was evident on the underwing of ten individuals, but callouses were not apparent on any individual. Nor, on fitting the tags, was I aware of bleeding from the pin hole, though Hart (op. cit.) reported slight bleeding from a number of his birds. On the latter point, I feel that bleeding need not occur if the position of the pin is carefully selected so as to avoid blood vessels. Blood vessels can be located with the fingers, and an adjacent 'thin' area of patagium selected instead.

## ii) Practicalities

Forty-one of the first 45 adult jackdaws tagged in 1987 were identified between late January and early April 1988. Only one individual was observed with a lost tag. Identification of original tagged jackdaws was still good during the winter of 1988. The tags were therefore durable, and not prone to the problems of scratching and paint removal that accompanies 'Darvic' tags.

## iii) Selection for or against tags

1) There was no detectable difference between the rate of encounters suffered by tagged birds in comparison with untagged birds ( $t = 1.08$ , N.S,  $df = 21$ ).

2) Southern and Southern (1985) demonstrated that in ring-billed gulls *Larus delawarensis* patagial tags significantly affected female acquisition of mates. My data provides no evidence of discrimination against tagged jackdaws whether male or female (Table 8.1) though the sample sizes were small. One female, tagged GWRY lost her mate GWBR early in the 1988 season but continued to breed with a second male. In 1987, eight breeding birds were tagged, with apparently no obvious effects on their continued breeding season. Of these eight tagged birds, six re-nested the following year, with a further two tagged birds from 1987 also acquiring 1988

nest sites. The eight re-nesting tagged birds represented 20% of the breeding population, and thereby reflected the proportion of tagged birds in the population as a whole (see Appendix H).

Appendix B (Chapter 2)

Table 1 The pairwise band sharing coefficients  $x$  of one parent and three offspring.

		Sibship		
	Male	$S_1$	$S_2$	$S_3$
No. of bands $N$	40	40	42	32
Male $n$		28	25	15
$x$		0.70	0.61	0.42
$S_1$			27	18
			0.66	0.51
$S_2$				18
				0.43

### Appendix C (Chapter 3)

**Table 1** Daily activity (N= 26). SE= standard error.

	Foraging	Flying	Resting/ preening	Roosting
	334	90	171	845
	359	86	165	830
	314	85	192	849
	340	64	182	854
	312	93	193	867
	348	111	114	867
	186	154	186	914
	361	105	154	820
	363	123	103	851
	371	155	89	825
	423	116	46	855
	249	122	203	866
	391	94	117	839
	216	92	261	871
	381	81	159	819
	332	88	189	831
	376	106	122	836
	262	91	282	805
	320	67	217	836
	359	104	188	789
	341	95	197	807
	356	76	189	819
	243	83	285	829
	350	82	199	809
	332	81	152	875
	364	62	170	844
Mean =	330	96	174	841
SE =	10.6	10.8	4.6	5.3

# Appendix C (continued)

**Table 2** Early morning, and evening (pre roost) corvid assemblies (N=21). Loc.=Location (field). For.= did flock forage at place of assembly., RK= rookery.

Date	Duration (mins)	AM		Temp °C	% Cloud (% cover)	PM	
		Loc. (field)	For.			Loc.	For.
090186	31.2	3	no	4.0	50	3	n
220186	15.0	5	yes	3.7	30	21	n
110286	21.7	17	yes	4.0	50	19	y
130286	23.2	18	no	4.0	50	RK	n
101186	20.8	3	no	3.5	25	RK	n
231186	14.7	3	yes	6.0	70	Z	n
021286	18.3	RK	no	5.2	50	3	n
061286	9.6	21	no	1.0	10	17	n
091286	16.5	3	yes	1.5	00	22	n
121286	18.1	3	yes	1.0	10	RK	n
050187	29.3	19	no	5.5	100	RK	n
170187	12.9	1	yes	4.0	75	Z	n
140287	29.1	RK	no	0.0	00	Z	n
170287	22.6	1	yes	2.0	40	3	y
031187	22.8	2	no	5.6	70	22	n
111187	22.6	3/1	yes	6.3	50	21	n
221187	13.6	3	yes	4.5	20	19	n
301187	14.8	3	yes	6.0	50	RK	n
041287	22.6	D	yes	4.5	50	16	n
121287	20.1	5	no	1.0	10	21	n
161287	24.1	18	yes	2.5	10	38	n

Mean= 20.17mins

# Appendix D (Chapter 4)

**Table 1** Earthworm dry weight/gx100. L= length mm

L <20mm	21-30	31-40	41-50	51-60	61-70	71-80	>90
10.0(13)	23.0(5)	60.0(15)	79.0(2)	92.0(2)	222	248	555
10.3	32.0(4)	34.0(3)	45.0	120	178	621	631
10.2	49.0(6)	44.6	41.0	80.0	240	480	787
10.3	44.0	85.0	65.0(2)	90.0	232	476	734
10.4	46.0(6)	26.0	64.0(3)	78.0	231	269	766
09.0(8)	18.0	31.0	66.0(3)	140	199	329	621
17.0(12)	35.0	44.0(4)	67.0(6)	141	198(2)	381	
18.0(4)	42.0	62.0(24)	62.0(2)	112	210(2)		
16.0(4)	43.0(4)	80.0(2)	61.0(6)	110 (2)	241		
17.5	27.0(2)	56.0	70.0(2)	200	246		
19.0(2)	26.0(3)	42.0	68.0(7)	164	230		
20.0	38.0(2)	61.0(3)	72.0	111	257		
13.0	24.0(2)	69.0(2)	71.0	101	244		
08.0(2)	49.1(3)	48.0(2)		99.0			
11.0	46.6	64.0(2)		97.0			
	29.0(2)	41.0		109			
	30.0	70.0(3)		108			
	39.9(2)	81.0(4)		100 (2)			
	21.0	79.0(4)		89.9			
	61.0(3)	35.0		96.7			
	41.0	47.0	.	109	.	.	
	48.0(3)	65.0					
	49.3(2)	68.0					
	41.1	76.0					
	48.1	89.0					
	39.6						
	28.0						
	20.7						
	31.0						
<hr/> X 13.0	<hr/> 39.0	<hr/> 64.0	<hr/> 65.0	<hr/> 110	<hr/> 222	<hr/> 401	<hr/> 682
SE 1.1	1.0	1.0	1.2	5.0	6.0	50.0	38
N 54	64	89	37	27	15	7	6

# Appendix D (continued)

Table 2 Handling times (seconds)

Earthworm length (1=1 bill ~5cm)	<½l	½l	1l	1½l	>2l
	1.37	1.00	3.05	6.27	10.42
	1.27	1.19	3.77	6.30	8.80
	0.88	1.21	2.08	6.80	13.60
	0.45	2.01	3.21	4.23	7.10
	2.01	1.24	2.47	7.10	11.10
	0.71	1.32	1.53	7.90	9.60
	0.75	1.43	2.81	6.30	9.72
	0.95(4)	2.08	3.09	4.90	8.40
	0.75	1.13	2.32	5.80	10.11
	1.38	0.81	2.16	7.20	9.91
	1.00	1.32	1.12	6.14	
	0.59	1.07	4.08	4.10	
	0.59	1.10	0.99	8.60	
	1.24	1.00	4.51	11.13	
	0.59	1.03	1.99		
	1.42	1.22			
	0.92(3)	1.00			
	1.15	0.95			
	0.93(2)	0.81			
	0.96(2)	1.58(3)			
	0.68	1.00			
	1.01	0.67			
	0.84(2)	0.96			
	0.91	0.89			
	0.81				
	0.76				
	0.71				
	0.56				
	0.62				
Mean=	0.93	1.19	2.61	6.63	9.80
SE=	0.05	0.07	0.27	0.49	0.57
N=	37	26	15	14	10

# Appendix D (continued)

**Table 3** Invertebrate biomass (wet weight)/m<sup>2</sup> from soil samples.

	Immatures	Adults	Other	Flock size
	51.76	54.12	41.32	80
	38.95	37.23	36.05	60
	22.59	36.05	30.23	32
	69.50	46.48	30.99	140
	53.35	38.30	31.20	72
	23.78	55.09	38.74	89
	37.12	56.38	16.03	200
	52.72	34.00	36.70	24
	49.93	32.16	41.10	92
	41.96	39.50	33.25	41
	32.50	45.84	44.22	40
	15.28	55.31	26.47	28
	<hr/>	<hr/>	<hr/>	
Mean=	41.12	44.19	33.86	
SE=	4.61	2.64	2.22	



# Appendix D (continued)

**Table 4** Soil sampling data.

ID	TN	TWEI	TEN	EN	TFL	RK	JK	RAT	IWEI	NO	TEMP	RAIN
01	13	0.689	146.6	410.2	221	111	110	1.00	0.110	12	08.5	0.0
02	24	1.222	125.1	262.3	052	028	024	1.25	0.149	19	04.0	2.0
03	17	0.663	111.9	199.7	038	013	025	0.50	0.007	01	09.5	0.0
04	14	0.910	095.4	095.4	017	014	003	5.00	0.152	08	11.5	0.0
05	08	0.422	176.7	176.7	073	040	033	1.20	0.002	01	10.0	1.5
06	26	1.690	291.9	390.7	200	100	100	1.00	0.106	09	06.0	4.5
07	07	0.410	081.0	195.7	034	027	007	3.86	0.146	10	07.5	5.5
08	28	1.432	278.7	402.6	200	100	100	1.00	0.299	21	08.5	2.5
09	16	0.601	171.3	345.2	100	056	044	1.27	0.125	09	12.5	3.0
10	07	0.243	098.2	182.1	018	009	009	1.00	0.091	08	09.0	1.5
11	04	0.127	008.9	041.7	007	002	005	0.40	0.005	01	11.0	0.0
12	19	0.548	112.2	112.2	038	022	016	1.38	0.044	32	11.0	0.0
13	15	0.522	120.9	189.7	058	023	035	0.03	0.112	13	07.5	3.5
14	21	0.255	067.9	067.9	018	010	008	1.25	0.002	01	09.0	2.5
15	23	0.966	356.1	513.0	240	120	120	1.00	0.830	24	10.5	3.0
16	17	0.804	189.6	194.3	072	040	032	1.20	0.166	22	10.0	1.5
17	10	0.412	133.3	167.1	081	041	040	1.00	0.009	04	09.0	3.5
18	24	1.065	145.2	246.1	042	031	011	2.82	0.041	07	06.0	2.5
19	12	0.666	121.6	121.6	043	019	024	0.79	0.020	02	11.0	4.0

## Abbreviations:

ID= sample number, TN= top 2cm abundance, TWEI= top 2cm biomass, TEN= top 2cm energy, EN= total energy, TFL= total flock size, RK= rook numbers, JK= jackdaw numbers, RAT= ratio rooks:jackdaws, IWE= invertebrate biomass (excluding earthworms) NO= invertebrate number (excluding earthworms), TEMP= ambient temperature. RAIN= rainfall (mm).

# Appendix E (Chapter 5)

**Table 1** Winter foraging niche overlap of rooks (RK) and jackdaws (JD) for November to February inclusive (diets from Holyoak 1968).  $p$  = proportion of total dietary repertoire allocated to each resource type.

Resource	Proportion			Rearranged $C_o$
	JD( $p_i$ )	RK( $p_j$ )	$ p_i - p_j $	
Acorns	0.006	0.039	0.033	0.349
Grain	0.39	0.536	0.146	0.512
Farm produce	0.092	0.098	0.006	0.303
Weedseeds	0.172	0.045	0.127	0.309
Fruit	0.01	0.000	0.01	0.300
Carrion	0.014	0.011	0.003	0.282
Gastropods	0.068	0.025	0.043	0.385
Oligochaetes	0.006	0.027	0.021	0.518
Curculionids	0.088	0.069	0.019	0.304
Coleoptera immagines	0.01	0.003	0.007	0.213
Coleoptera larvae	0.008	0.000	0.008	0.202
Diptera imagines	0.01	0.011	0.001	0.279
Diptera larvae & pupae	0.00	0.017	0.017	0.453
Lepidoptera larvae	0.053	0.111	0.058	0.751
$\Sigma$ 0.478				
$\times \frac{1}{2}$ 0.239				
$C_o = 1 - 0.761$				$C_{cf} = 0.369$

# Appendix E (continued)

Table 2 Jackdaw time budget data.

ID	T	D	NN	TFL	RFL	JFL	WK	PK	LU	SER	FE	EN	LURT
001	10.5	10	10	002	000	002	57.0	05.8	30.9	00.0	02.9	00	-9.
001	10.5	10	10	004	000	004	61.1	08.2	20.2	04.5	03.0	00	19.4
002	10.5	05	05	020	000	020	48.7	36.7	15.5	00.0	00.0	00	04.7
003	10.5	10	10	012	006	006	00.6	57.6	13.6	27.5	00.0	00	04.3
004	10.5	10	03	011	008	003	02.4	62.7	21.4	12.6	03.3	01	05.7
005	10.5	10	03	011	008	003	11.7	73.0	07.2	02.6	00.0	00	07.6
006	10.0	05	05	076	001	075	14.5	70.7	04.0	06.9	03.1	00	01.9
007	10.5	00	00	025	000	025	00.0	00.0	00.0	00.0	00.0	00	10.2
008	10.5	10	10	015	008	007	00.0	00.0	00.0	00.0	00.0	00	18.6
009	10.5	05	05	034	013	031	00.0	00.0	00.0	00.0	00.0	00	19.0
010	09.0	15	07	040	030	010	35.7	46.7	10.8	02.7	03.0	00	03.2
011	09.0	15	07	040	030	010	45.8	27.5	09.5	12.7	00.0	00	04.0
011	09.0	15	05	043	031	012	30.6	40.1	10.2	09.9	05.3	02	03.8
012	09.0	10	10	004	002	002	31.5	27.0	22.3	18.7	00.0	00	11.0
013	09.0	20	20	004	002	002	59.5	14.6	22.7	00.0	00.0	00	07.8
014	09.0	90	90	008	007	001	85.2	00.0	07.0	00.0	05.7	00	06.7
015	09.0	30	10	009	006	003	49.3	21.0	25.3	00.0	00.0	00	12.9
016	09.0	10	10	002	000	002	15.1	13.4	65.5	00.0	00.0	00	18.3
017	09.0	05	50	006	003	003	60.2	03.4	30.2	03.7	00.0	00	15.4
018	09.0	05	05	075	000	075	04.0	60.8	02.8	27.4	04.2	00	02.0
019	11.0	10	10	004	002	002	73.4	02.6	20.6	01.9	00.0	00	21.2
020	11.0	10	10	004	002	002	22.8	26.9	28.2	21.6	00.0	00	18.5
021	11.0	05	05	040	030	010	40.5	41.8	12.3	02.1	01.6	00	05.4
022	11.0	05	05	040	030	010	43.7	28.5	10.0	13.9	00.0	00	05.4
023	11.0	05	13	040	030	010	36.5	24.4	16.4	22.2	00.0	00	10.0
024	11.0	10	10	008	007	001	79.5	00.0	11.8	00.0	05.9	00	08.9
025	11.0	10	20	040	030	010	53.9	14.3	24.3	00.0	00.0	00	04.4
026	11.0	40	40	003	000	003	46.7	17.2	35.2	00.0	00.0	00	19.6
027	11.0	10	10	002	000	002	29.2	13.7	55.8	00.0	00.0	00	30.2
028	10.5	20	20	002	002	002	72.6	14.6	11.8	00.0	00.0	00	07.5
029	10.5	08	08	010	004	004	07.2	60.9	29.3	01.3	00.0	00	09.7
030	10.5	05	05	026	013	013	00.0	41.3	45.8	11.5	00.0	00	21.0
031	----	10	10	002	000	002	58.1	20.7	12.3	02.5	05.5	00	05.7

# Appendix E Table 2 (continued)

032	05.0	10	10	081	060	021	43.4	38.1	00.8	14.9	01.9	00
033	05.0	10	10	081	060	021	48.3	41.9	01.2	07.4	01.0	00
034	05.0	10	10	081	060	021	39.6	50.6	00.9	06.7	01.6	00
035	05.0	08	05	168	058	110	01.6	90.0	02.4	01.7	03.8	00
036	05.0	08	05	168	058	110	00.0	76.8	00.9	16.9	02.5	00
037	05.0	05	02	168	058	110	03.3	82.1	02.8	08.7	01.7	04
038	05.0	05	03	168	058	110	01.5	83.1	00.7	10.9	01.9	01
039	05.0	05	03	169	058	110	00.4	10.3	03.2	03.4	00.2	02
040	05.0	05	03	168	058	110	04.1	85.0	02.5	05.9	01.9	00
041	05.0	05	03	169	059	110	03.6	82.9	02.8	05.3	03.5	01
042	05.0	05	03	062	036	026	18.1	51.5	06.4	15.5	02.8	01
043	05.0	10	20	084	064	020	42.7	36.8	01.0	16.1	03.3	00

## Abbreviations:

ID= samle number, T= temperature, D= density, NN= nearest neighbour, TFL= total flock size, RFL= rook numbers, JFL= jackdaw numbers, WK= walking, PK= pecking, LU= looking up, SER= searching, FE= feeding, EN= encounter rate, LURT= look up rate.

## Appendix F (Chapter 6)

**Table 1** Adult time budget data.

ID	T	RK	TFK	D	NN	SIT	WK	PK	LU	SER	FE	EN	FERT	SU	LURT	RATIO
006	-9.0	50	059	10	10	00.0	13.7	65.1	18.1	00.6	02.4	01	01.1	15	02.0	0.020
007	-9.0	20	020	10	10	01.6	29.2	47.8	16.4	01.3	01.3	00	00.6	04	04.9	0.000
008	-9.0	01	001	--	--	06.6	21.3	25.9	22.3	22.4	00.7		01.1	11	05.4	0.000
009	-9.0	12	012	10	15	00.0	41.4	26.6	18.5	03.5	04.5	02	01.1	13	03.4	0.167
010	-9.0	20	020	10	10	00.0	25.1	54.2	10.7	01.6	00.0	03	00.0	00	02.4	0.150
011	-9.0	12	012	10	20	00.0	15.6	30.9	26.3	00.0	26.2	00	07.1	63	04.3	0.000
012	-9.0	12	012	10	03	03.1	26.1	32.7	29.0	00.0	08.1	00	01.5	13	06.4	0.000
013	-9.0	20	020	05	01	00.0	57.4	21.0	00.0	01.6	17.2	01	03.3	44	00.0	0.050
014	-9.0	20	020	05	02	16.6	32.5	09.4	34.2	01.4	05.6	00	01.6	43	05.3	0.000
015	-9.0	70	081	05	03	00.0	18.8	49.0	16.7	04.4	19.9	08	04.6	23	04.6	0.114
016	-9.0	70	080	05	05	00.0	03.4	76.7	06.1	00.0	12.5	01	08.8	26	03.7	0.014
017	10.5	02	002	07	07	00.0	00.6	74.0	09.0	00.0	03.0	00	00.0	00	-9.	0.000
018	10.5	01	001	--	--	00.0	24.6	06.1	29.2	06.2	01.4	00	00.8	25	-9.	0.000
019	10.5	01	001	--	--	00.0	45.7	05.0	24.0	01.1	09.1	00	04.0	47	-9.	0.000
020	11.0	13	034	08	08	00.0	03.4	73.0	06.2	00.0	11.0	01	05.6	13	03.6	0.029
021	11.0	24	048	05	04	00.0	04.5	77.0	09.0	00.0	08.9	00	06.4	12	03.9	0.000
022	10.5	03	003	23	23	00.0	72.5	15.0	08.0	06.0	00.0	00	00.0	00	-9.	0.000
023	10.5	02	002	02	02	00.0	03.2	59.0	20.0	19.0	03.0	00	01.3	06	-9.	0.000
024	10.5	02	002	02	02	00.0	08.7	25.0	39.0	19.0	05.0	00	04.7	14	-9.	0.000
025	10.5	03	003	30	30	00.0	73.7	16.9	04.9	03.1	00.0	00	00.0	00	07.1	0.000
026	10.5	02	002	02	02	00.0	01.5	54.4	24.1	16.2	03.3	00	05.5	04	01.2	0.000
027	10.5	02	002	02	02	00.0	12.5	25.1	38.5	20.4	01.9	00	04.2	16	04.7	0.000
028	10.5	01	001	--	--	03.1	09.3	30.8	31.6	23.6	04.9	00	00.8	03	10.8	0.000
029	10.5	05	005	05	04	00.0	11.1	76.4	07.1	03.0	01.4	00	00.8	02	03.9	0.000
030	10.5	01	001	--	--	00.0	14.4	17.6	44.5	22.3	00.9	01	00.8	08	06.0	1.000
031	10.5	04	004	14	20	05.0	31.4	10.2	44.9	07.0	00.9	00	00.7	14	08.8	0.000
032	10.5	02	002	30	30	04.8	35.6	28.7	25.6	11.0	02.1	00	02.4	21	08.9	0.000
033	10.5	02	002	45	45	01.8	26.1	33.7	26.9	09.3	01.8	00	01.2	06	04.7	0.000
034	11.0	01	001	--	--	04.4	09.5	37.5	38.2	05.7	05.0	00	01.0	03	-9.	0.000
035	11.0	-9	015	10	07	00.0	18.5	62.7	02.2	14.9	01.7	00	00.8	03	-9.	0.000
036	11.0	04	004	10	10	00.0	08.0	81.8	05.8	01.7	01.9	00	00.8	03	-9.	0.000
037	11.0	01	001	--	--	00.0	05.4	49.6	35.7	02.1	01.9	01	20.6	32	-9.	1.000

Appendix F Table 1 (continued)

ID	T	RK	TFK	D	NN	SIT	WK	PK	LU	SER	FE	EN	FERT	SU	LURT	RATIO
038	11.0	01	001	--	--	00.0	11.1	17.9	24.3	45.6	01.1	01	00.9	09	-9.	1.000
039	09.0	30	030	15	08	00.0	43.1	28.7	07.6	11.6	08.6	00	01.6	10	05.1	0.000
040	09.0	15	015	10	10	29.1	00.0	07.8	53.4	08.5	00.0	00	00.0	00	02.3	0.000
041	09.0	09	009	35	35	00.0	14.4	25.2	35.3	19.1	07.4	00	01.8	15	05.8	0.000
042	09.0	14	014	50	50	40.3	09.0	11.2	21.1	14.9	03.2	00	00.8	14	03.9	0.000
043	10.5	10	040	15	15	02.8	18.8	27.0	33.0	11.8	05.1	00	02.3	13	07.9	0.000
044	10.5	11	086	10	02	00.0	11.3	68.6	05.8	06.7	07.2	01	03.5	11	04.0	0.000
045	10.5	12	087	15	50	14.4	30.6	15.8	14.6	18.3	06.0	00	02.1	24	03.7	0.000
046	10.5	01	076	10	10	00.0	07.8	54.7	14.1	16.9	06.1	00	02.9	10	04.6	0.000
047	10.5	07	008	20	10	00.0	19.9	23.5	33.2	18.6	01.7	00	01.9	12	06.0	0.000
048	11.0	30	040	15	05	00.0	33.5	28.4	19.2	09.5	09.2	01	01.9	15	06.1	0.033
049	11.0	07	008	20	10	00.0	12.1	47.1	31.5	04.7	02.1	00	00.9	05	08.3	0.000
050	04.0	80	080	04	05	00.0	17.8	53.6	08.9	08.4	21.0	05	05.8	09	04.5	0.063
051	04.0	80	080	04	05	00.0	12.9	60.2	05.4	11.2	11.5	01	03.1	07	03.7	0.013
052	04.0	01	001	--	--	00.0	06.7	32.6	46.3	05.2	08.9	00	04.2	08	06.9	0.000
053	04.0	40	040	08	08	00.0	49.8	26.8	07.8	12.6	12.6	00	01.1	08	13.7	0.000
054	04.0	40	040	08	10	40.1	13.8	21.5	12.9	03.1	11.5	01	01.1	11	05.3	0.025
055	04.0	40	040	08	20	00.0	24.0	39.4	03.5	19.5	05.4	00	01.2	05	03.7	0.000
056	04.0	45	045	05	03	00.0	03.9	68.5	06.6	10.4	10.3	00	04.5	10	02.1	0.000
057	04.0	45	045	05	05	00.0	08.8	75.9	07.9	02.9	03.4	00	02.6	06	01.3	0.000
058	04.0	80	080	03	08	01.5	19.8	48.6	12.5	02.3	19.9	03	03.7	11	03.1	0.036
059	04.0	29	029	05	02	00.0	12.8	56.1	15.0	12.1	03.5	00	01.6	06	04.2	0.000
060	04.0	50	067	12	30	26.2	34.9	21.6	11.0	08.9	00.0	01	00.0	00	05.4	0.020
061	08.0	78	078	05	05	06.0	38.5	28.9	07.9	15.7	02.6	04	02.3	18	04.2	0.050
062	08.0	78	078	05	05	02.4	17.4	45.3	07.8	12.0	13.7	01	02.7	12	02.2	0.013
063	08.0	09	009	08	08	00.0	26.0	28.8	14.5	03.0	07.0	00	02.1	08	03.4	0.000
064	08.0	13	013	06	06	00.0	03.4	74.7	09.2	03.1	09.4	00	08.1	14	06.5	0.000
065	08.0	21	021	08	12	00.0	16.1	49.5	17.3	09.4	03.7	00	02.5	05	05.6	0.000
066	08.0	21	021	08	05	00.0	20.7	64.1	10.3	08.9	02.2	00	01.4	03	04.1	0.000
067	08.0	99	250	08	08	00.0	24.3	41.8	06.6	13.5	13.3	11	04.6	15	03.4	0.044
068	08.0	99	250	05	05	00.0	04.3	46.2	01.8	21.5	25.9	06	02.8	11	00.7	0.024
069	08.0	99	250	05	03	00.0	37.1	31.0	00.4	18.6	09.8	03	01.3	09	00.4	0.012
070	08.0	30	030	02	02	14.3	00.5	39.5	05.3	19.5	18.9	00	06.5	26	01.7	0.000
071	08.0	99	150	05	05	00.0	22.6	35.1	00.6	36.9	04.3	07	04.2	20	00.5	0.047
072	08.0	06	006	05	10	00.0	48.2	19.8	26.6	05.4	01.6	00	00.9	05	00.9	0.000

Appendix F Table 1 (continued)

ID	T	RK	TFK	D	NN	SIT	WK	PK	LU	SER	FE	EN	FERT	SU	LURT	RATIO
073	08.0	52	052	00	05	00.0	37.0	22.4	14.1	23.8	02.1	02	01.7	18	01.7	0.039
074	08.0	99	200	05	04	00.2	13.9	48.9	02.8	29.6	04.1	01	03.3	15	01.1	0.000
075	08.0	99	200	05	07	00.0	39.6	31.0	06.9	13.2	12.0	00	01.7	29	01.7	0.000
076	08.0	60	080	00	15	00.0	28.2	33.6	14.9	21.1	01.9	04	00.6	04	04.1	0.050
077	16.0	50	050	00	50	05.4	25.3	16.1	06.1	42.8	04.1	08	01.8	38	02.5	0.160
078	16.0	50	050	00	15	03.4	09.8	10.3	12.9	61.1	02.0	09	00.8	23	03.4	0.180
079	16.0	99	150	05	05	00.0	00.0	56.3	06.1	35.7	01.5		00.8	04	02.1	0.087
080	16.0	99	150	08	08	00.0	00.0	46.9	01.3	50.8	00.7		00.5	03	00.5	0.013
081	16.0	99	150	05	09	01.0	00.0	75.1	04.6	17.4	01.5	11	01.0	04	02.1	0.073
082	16.0	99	150	05	20	11.4	00.0	56.4	16.2	13.3	11.4	06	00.4	02	01.2	0.040
083	16.0	90	140	08	08	29.1	00.9	46.2	10.2	12.7	00.8	01	00.5	03	03.1	0.007
084	16.0	50	060	10	10	09.9	08.3	34.3	25.2	21.2	00.0	01	00.0	00	04.2	0.017
085	16.0	02	004	30	30	04.7	33.0	35.8	20.8	04.4	01.0	00	00.4	02	05.9	0.000
086	11.0	-9	400	03	09	01.8	22.3	64.9	01.2	05.2	14.0	01	01.3	05	00.6	0.003
087	11.0	-9	400	03	18	00.4	60.0	19.6	08.5	08.6	12.8	00	02.8	14	01.6	0.000
088	08.0	99	350	05	04	00.0	07.3	76.0	01.2	05.5	06.8	01	04.7	15	00.7	0.003
089	08.0	99	350	05	20	00.0	50.0	31.6	02.1	13.7	19.4	00	01.3	07	01.3	0.000
090	08.0	99	350	05	20	00.0	68.5	21.5	00.6	07.2	01.9	11	00.9	00	00.9	0.031
091	04.5	99	350	10	50	00.0	59.7	07.1	09.3	22.1	07.6	00	01.0	19	06.7	0.000
092	11.5	52	053	10	05	00.0	23.4	27.2	18.5	29.6	06.1	01	00.8	07	03.6	0.019
093	11.5	36	042	10	06	00.0	42.1	28.8	02.1	23.7	03.2	02	01.2	10	01.5	0.048
094	11.5	50	055	10	06	01.3	29.5	36.6	01.8	28.9	01.5	00	00.9	06	01.3	0.000
095	11.5	51	061	08	10	00.0	23.1	34.0	14.3	26.2	02.2	02	01.0	07	03.3	0.033
096	11.5	48	060	10	16	01.9	45.5	23.4	02.8	23.0	02.9	00	01.2	19	01.2	0.000
097	08.5	25	030	02	02	07.3	35.4	30.6	02.1	18.3	09.1	00	05.8	43	01.3	0.000
098	08.5	99	150	05	05	00.0	27.2	43.3	00.3	17.1	03.0	08	02.0	11	00.5	0.053
099	08.5	06	006	05	10	00.0	32.6	23.9	07.4	33.4	02.3	00	01.5	16	01.5	0.000
100	-9.0	20	020	05	01	10.2	44.7	24.7	00.9	03.7	15.5	00	02.4	27	00.4	0.000
101	-9.0	20	020	05	05	11.1	23.5	21.1	25.4	01.6	17.0	00	04.7	-9	02.6	0.000
102	08.5	06	012	10	05	00.0	37.9	29.2	22.5	03.3	04.9	02	01.8	14	05.0	0.167
103	-9.0	01	001	--	--	07.0	22.3	23.9	21.8	22.9	01.7	00	01.0	08	03.7	0.000
104	-9.0	20	020	10	10	05.5	24.4	52.6	11.6	02.1	02.1	04	00.2	03	02.7	0.200
105	-9.0	10	012	10	20	00.0	16.4	47.2	17.7	00.4	17.7	00	06.2	33	01.9	0.000
106	-9.0	12	012	10	03	04.1	22.7	28.8	21.0	10.7	12.3	00	03.0	35	02.8	0.000

Appendix F Table 1 (continued)

ID	T	RK	TFK	D	NN	SIT	WK	PK	LU	SER	FE	EN	FERT	SU	LURT	RATIO
107	-9.0	10	020	05	03	00.0	27.8	23.9	28.7	01.9	17.3	00	04.6	41	04.4	0.000
108	-9.0	64	070	05	03	01.0	17.1	52.3	10.7	06.2	09.6	08	05.8	47	01.8	0.110
109	05.0	40	040	08	08	00.0	44.9	24.2	06.8	12.3	11.6	00	05.0	31	00.6	0.000
110	05.0	40	040	08	10	09.0	29.8	28.6	12.2	12.8	06.3	01	02.1	19	02.1	0.025
111	05.0	40	040	08	20	01.1	23.0	30.6	09.2	27.6	08.2	00	02.8	21	01.2	0.000
112	08.0	21	024	08	12	00.0	19.1	43.5	19.5	14.3	02.4	00	01.3	07	03.5	0.000
113	08.0	21	023	08	05	00.0	19.0	51.6	08.4	18.3	01.9	00	01.4	05	01.9	0.000
114	05.0	45	045	05	03	00.0	22.1	45.2	04.1	20.0	08.1	00	02.0	08	02.0	0.000
115	05.0	45	045	05	05	00.0	18.3	44.4	08.4	15.7	10.3	03	03.9	16	02.8	0.067
116	07.5	80	080	03	08	00.0	13.5	55.1	08.4	15.7	10.3	04	04.1	16	02.2	0.050
117	07.5	13	013	06	06	00.0	02.4	59.9	06.6	23.8	06.8	00	03.0	11	02.5	0.000
118	07.5	29	029	05	03	08.7	21.6	39.3	10.3	13.7	06.1	00	01.3	07	03.4	0.000
119	07.5	50	067	12	30	17.4	22.9	15.6	08.1	32.3	01.5	01	00.8	20	02.4	0.015
120	08.0	09	009	08	08	06.9	34.8	21.2	18.5	12.0	05.3	00	02.2	19	02.2	0.000
121	08.0	99	250	08	08	00.0	23.7	43.6	04.7	10.3	07.4	11	03.3	13	02.5	0.044
122	08.0	99	250	05	03	02.0	35.4	30.3	02.0	18.3	09.1	04	02.0	18	00.8	0.016
123	08.0	99	250	05	05	00.0	03.1	63.4	01.1	16.3	11.1	06	03.5	10	00.9	0.024
124	08.0	78	078	05	05	03.6	33.2	28.5	15.3	09.6	05.8	04	01.3	12	04.1	0.071
125	08.0	78	078	05	05	01.5	17.9	43.2	05.1	21.7	09.2	01	03.6	13	01.2	0.013

Abbreviations:

ID = identification, T= temperature, R= rook numbers, TFLK = total flock size, D= density, NNR= nearest neighbour, ST= sitting, WK= walking, PK = pecking, LU= looking up, SER= searching, FE= feeding, EN= encounter rate, FERT= feeding rate, SU= success, LURT= look up rate, RATIO= Ratio of immatures to adults. (-9= missing data.)



# Appendix F (continued)

Table 2 Immature time budget data.

ID	T	FLK	D	NR	ST	WK	PK	LU	SE	FE	EN	FERT	SU	LURT	NI	RAT
001	10.5	003	10	10	00.0	11.7	58.0	07.0	08.0	07.0	00	02.6	11	02.0	01	0.00
002	10.5	2 004	10	10	00.0	10.7	60.0	06.8	09.1	07.2	00	03.1	12	03.0	01	0.00
003	10.5	2 003	99	99	00.0	13.0	26.3	26.0	05.9	09.6	00	02.6	16	02.0	01	0.00
004	10.5	2 017	10	10	00.0	17.6	39.0	12.2	15.1	02.3	00	01.2	07	03.0	06	0.00
005	10.5	2 002	20	20	00.0	18.5	11.0	18.6	22.5	27.2	00	03.2	56	00.0	02	0.00
006	10.5	1 003	05	05	00.0	05.1	70.4	12.2	02.0	08.7	00	04.5	15	02.0	01	0.00
007	10.5	1 012	05	05	00.0	03.2	66.7	17.5	10.5	02.0	00	01.5	05	11.0	01	0.00
008	10.5	2 002	05	05	01.1	20.1	40.2	29.7	05.2	03.2	00	00.5	06	01.0	01	0.00
009	10.5	1 013	05	05	00.0	00.2	61.5	11.3	21.8	04.7	00	02.5	04	12.0	01	0.00
010	10.5	1 021	05	05	00.0	01.7	67.1	12.0	13.4	05.4	00	03.0	11	11.0	02	0.00
011	10.5	2 002	50	50	00.0	04.3	54.4	30.7	07.9	02.3	00	01.5	06	01.0	01	0.00
012	10.5	1 005	05	05	05.1	04.5	63.7	12.9	03.2	02.1	03	01.3	05	04.0	01	0.60
013	10.5	1 004	05	03	02.8	27.8	55.4	05.3	04.5	01.2	01	00.6	04	03.0	01	0.25
014	10.0	2 002	10	10	04.0	05.5	59.6	23.8	11.1	00.9	00	00.1	01	01.0	01	0.00
015	10.0	1 005	07	07	00.0	32.6	38.6	02.6	19.9	04.3	00	01.7	15	01.7	03	0.00
016	10.0	1 002	05	05	00.0	31.2	20.6	06.6	36.9	00.0	00	00.0	00	01.0	01	0.00
017	11.0	1 006	04	04	00.0	06.5	60.0	27.9	04.2	02.1	03	01.8	04	02.0	03	0.50
018	11.0	2 003	05	05	00.0	04.9	51.5	20.0	15.9	07.8	00	03.6	10	02.0	01	0.00
019	11.0	2 004	10	10	00.0	06.1	56.1	07.2	06.6	06.9	00	03.3	11	03.0	01	0.00
020	11.0	1 004	10	06	00.0	25.8	59.6	09.2	04.1	01.8	01	01.3	04	03.0	01	0.25
021	11.0	1 002	10	10	00.0	01.3	39.7	31.5	13.2	11.7	01	-9.	14	01.0	01	0.25
022	11.0	1 012	10	08	00.0	30.1	31.0	28.8	02.3	07.2	00	-9.	22	11.0	01	0.00
023	11.0	1 009	08	08	00.0	06.5	36.8	15.6	35.0	05.9	00	-9.	15	08.0	01	0.00
024	11.5	2 003	15	15	00.0	00.4	28.9	27.0	19.7	10.6	01	04.3	13	02.0	01	0.33
025	10.0	1 050	02	02	07.1	03.2	20.7	59.5	09.5	04.1	01	-9.	00	50.0	01	0.02
026	10.0	2 050	02	35	00.7	49.9	20.8	09.3	12.7	03.3	02	03.8	24	50.0	01	0.04
027	10.5	2 004	20	30	00.0	44.7	27.9	08.1	14.2	03.8	00	01.1	17	03.0	01	0.00
028	10.5	2 004	20	10	00.0	31.5	21.2	10.0	40.4	00.0	00	00.0	00	03.0	01	0.00
029	10.5	2 004	20	20	09.4	41.3	13.4	12.9	21.7	00.5	00	04.8	10	03.0	01	0.00

Appendix F Table 2 (continued)

ID	T	FLK	D	NR	ST	WK	PK	LU	SE	FE	EN	FERT	SU	LURT	NI	RAT
030	10.5	2	006	10	10	00.0	23.5	16.2	15.2	31.9	12.9	00	01.1	20	05.0	01 0.00
031	10.5	2	020	10	10	00.6	20.1	42.6	17.0	10.4	11.1	01	00.7	06	05.0	04 0.05
032	12.0	2	018	15	12	00.0	19.9	30.8	09.7	32.9	00.0	00	00.0	00	06.0	03 0.00
033	12.0	1	005	20	05	00.0	15.3	11.3	05.2	67.8	00.0	00	00.0	00	04.0	0.00
034	12.0	2	001	99	99	00.0	05.3	11.3	45.2	37.8	00.0	00	00.0	00	00.0	01 0.00
035	15.0	1	014	08	09	00.0	05.5	61.0	20.9	06.7	05.5	00	03.7	18	03.5	04 0.00
036	15.0	1	014	05	05	00.0	03.3	79.6	02.5	00.6	05.0	03	03.6	14	03.5	04 0.21
037	15.0	1	021	10	07	00.0	15.6	57.5	07.8	13.8	03.9	01	02.6	15	04.2	05 0.05
038	15.0	1	021	10	05	01.1	10.7	49.5	13.9	22.2	05.2	00	00.6	04	04.2	05 0.00
039	15.0	1	022	05	05	00.0	46.6	26.7	10.9	05.4	08.0	00	05.1	32	03.6	06 0.00
040	15.0	2	004	15	15	00.0	24.3	26.6	37.1	00.7	00.7	01	00.6	04	03.0	01 0.25
041	15.0	2	004	05	05	00.0	15.4	34.7	23.6	18.6	02.6	03	01.3	10	03.0	01 0.75
042	15.0	2	007	20	30	00.0	38.2	36.3	11.9	09.5	03.8	00	02.1	10	06.0	01 0.00
043	15.0	2	007	20	30	00.0	57.3	17.9	12.0	09.9	02.4	00	01.3	11	06.0	01 0.00
044	15.0	2	007	20	30	00.0	30.3	48.5	07.9	07.7	05.2	00	03.1	11	06.0	01 0.00
045	15.0	2	007	30	35	00.0	57.8	24.2	10.6	02.9	04.1	00	02.6	18	06.0	01 0.00
046	15.0	2	007	15	10	08.4	69.1	14.7	07.4	06.3	02.0	00	01.8	16	06.0	01 0.00
047	15.0	2	007	15	10	00.3	72.7	12.3	05.8	06.7	01.9	00	02.0	19	06.0	01 0.00
048	15.0	2	007	15	10	00.0	54.2	20.4	07.9	16.5	00.4	00	00.7	05	06.0	01 0.00
049	15.0	2	007	15	10	00.0	63.2	25.1	05.7	03.1	02.1	00	02.5	18	06.0	01 0.00
050	15.0	2	008	15	10	00.2	67.7	16.7	06.7	05.6	02.7	00	02.1	19	07.0	01 0.00
051	11.5	1	034	10	10	00.4	06.3	47.3	09.7	32.2	09.2	01	00.5	05	33.0	01 0.03
052	11.5	1	018	10	05	00.0	11.0	45.7	16.5	20.8	08.5	01	00.0	00	09.0	02 0.06
053	11.5	1	025	10	05	00.6	20.9	44.6	04.8	17.9	03.2	02	00.9	05	11.3	02 0.08
054	03.5	2	079	08	05	00.0	15.3	67.4	00.6	10.2	00.9	02	00.0	00	15.8	05 0.01
055	03.5	2	080	05	05	00.0	16.2	74.2	03.7	04.9	00.8	00	01.3	06	16.0	05 0.06
056	03.5	1	080	05	04	00.0	21.1	55.5	04.1	13.5	01.9	05	00.0	00	16.0	05 0.05
057	03.5	1	055	08	05	00.0	54.8	37.3	00.3	06.0	03.2	03	00.3	02	14.8	04 0.00
058	10.5	2	006	10	10	00.0	23.5	16.2	15.2	31.9	12.9	00	01.1	20	05.0	01 0.00
059	10.0	2	002	10	10	04.0	05.5	39.6	33.8	11.1	00.9	00	00.1	01	01.0	01 0.05
060	10.5	2	020	10	10	00.8	22.1	34.6	12.0	20.4	05.1	01	00.7	04	05.0	04 0.05
061	10.5	1	004	05	03	02.8	27.8	55.4	05.3	04.5	01.2	01	00.6	02	03.0	01 0.25
062	12.0	1	005	20	05	00.0	14.3	21.3	05.2	57.8	03.4	00	00.9	08	04.0	01 0.00
063	15.0	1	014	08	09	00.0	05.5	61.0	20.9	06.7	05.5	00	03.7	18	03.5	04 0.00

Appendix F Table 2 (continued)

ID	T	FLK	D	NR	ST	WK	PK	LU	SE	FE	EN	FERT	SU	LURT	NI	RAT
064	12.0	2	001	99	99	00.0	15.3	11.3	05.2	67.8	00.0	00	00.0	00	00.0	01 0.00
065	10.0	1	002	05	05	05.0	32.2	25.6	06.8	39.7	00.0	00	00.0	00	01.0	01 0.00
066	15.0	1	021	10	07	00.0	15.6	57.5	07.8	11.8	08.9	01	02.6	17	04.2	05 0.05
067	15.0	1	014	05	05	00.0	26.3	69.6	03.4	00.6	07.8	03	04.1	13	03.5	04 0.21
068	10.0	1	005	07	07	03.9	33.6	25.8	03.1	29.8	00.0	00	02.3	16	01.7	03 0.00
069	12.0	2	018	15	12	00.0	17.9	07.8	07.7	64.9	05.5	00	00.0	00	06.0	03 0.00
070	08.5	2	007	15	10	00.3	74.5	11.3	06.1	08.7	01.9	02	02.1	18	06.0	01 0.29
071	08.0	2	110	05	05	00.0	37.7	34.2	11.8	29.5	02.1	00	02.1	09	21.0	05 0.00
072	08.5	2	111	05	03	00.0	37.4	36.8	12.2	11.9	01.4	04	01.5	04	21.2	05 0.04
073	08.0	2	006	10	10	00.0	30.3	51.5	08.9	06.9	02.3	00	02.9	10	05.0	01 0.00
074	09.0	2	008	10	15	00.0	56.8	26.2	10.9	03.1	04.2	00	02.7	18	03.0	02 0.00
075	09.5	2	006	15	10	08.5	70.1	15.8	07.4	05.3	02.0	00	01.8	16	05.0	01 0.00
076	09.5	2	008	20	30	00.0	30.3	38.5	07.9	17.7	05.2	00	04.1	12	03.0	02 0.00
077	06.5	2	005	30	35	00.0	26.8	37.2	10.7	22.9	04.1	00	02.6	18	04.0	01 0.00
078	05.0	2	106	05	10	00.3	71.7	13.3	06.2	08.2	01.9	00	01.9	09	20.2	05 0.00
079	05.0	2	115	05	05	07.8	58.2	13.7	09.2	06.3	01.2	03	01.8	09	18.2	06 0.03
080	05.0	2	126	05	08	00.0	38.2	39.2	19.8	10.5	04.1	02	02.2	00	30.5	04 0.02
081	05.0	2	125	05	04	00.0	27.3	47.9	13.1	09.9	00.4	04	01.9	00	24.0	05 0.03

Abbreviations:

ID = identification, T= temperature, R= rook numbers, TFLK = total flock size, D= density, NNR= nearest neighbour, ST= sitting, WK= walking, PK = pecking, LU= looking up, SER= searching, FE= feeding, EN= encounter rate, PKRT= peck rate, FERT= feeding rate, SU= success, LURT= look up rate, RAT= ratio of adults to immatures.

Table 1. Sand sharing data for Plate 1a.

Rutland Water															Hillesdon Coplow												
Track	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18									
band No.	21	21	15	24	21	11	22	25	22	23	21	29	27	20	22	23	19	22									
1 n	3	3	4	3	1	3	3	1	3	3	1	2	2	2	3	1	6	2									
x	0.140	0.160	0.170	0.140	0.060	0.140	0.130	0.046	0.140	0.128	0.047	0.088	0.090	0.140	0.045	0.267	0.086										
2	2	1	2	3	2	3	1	3	1	3	1	3	3	2	1	0	3	1									
	0.130	0.045	0.095	0.187	0.090	0.130	0.147	0.140	0.044	0.146	0.140	0.090	0.470	0.000	0.140	0.045											
3	1	1	1	2	2	1	0	0	1	2	3	1	1	0	0												
	0.050	0.053	0.068	0.104	0.097	0.052	0.000	0.000	0.130	0.060	0.160	0.052	0.051	0.000	0.000												
4	1	1	1	2	3	3	2	1	3	0	2	2	0	2													
	0.045	0.059	0.044	0.080	0.128	0.128	0.082	0.046	0.128	0.000	0.086	0.085	0.000	0.083													
5	0	1	1	1	3	1	3	1	2	2	2	1	3	1	3												
	0.000	0.047	0.044	0.047	0.014	0.128	0.077	0.090	0.090	0.047	0.140	0.045	0.134														
6	1	1	3	0	1	0	1	0	1	0	0	0	0	0	2	1											
	0.051	0.058	0.134	0.000	0.054	0.000	0.037	0.000	0.000	0.000	0.000	0.120	0.059														
7	2	3	1	2	1	1	1	0	2	2	1																
	0.085	0.140	0.044	0.085	0.044	0.044	0.044	0.000	0.053	0.087	0.037	0.044															
8	2	1	0	2	4	3	0	0	3	0	0	3	1														
	0.045	0.041	0.000	0.034	0.140	0.126	0.000	0.000	0.122	0.040																	
9	0	0	2	0	1	1	1	4	1																		
	0.000	0.000	0.035	0.000	0.047	0.044	0.044	0.044	0.173	0.004																	

Appendix G table 1 (continued)

10	0	1	1	1	0	2	0	2
	0.000	0.032	0.044	0.044	0.000	0.086	0.000	0.085
11	1	1	0	2	2	3	2	
	0.045	0.042	0.000	0.035	0.035	0.125	0.082	
12	1	2	2	1	1	3		
	0.047	0.095	0.095	0.047	0.047	0.140		
13	1	4	1	2	1			
	0.045	0.178	0.045	0.086	0.043			
14	1	3	0	2				
	0.046	0.140	0.000	0.086				
15	1	1	2					
	0.044	0.044	0.086					
16	1	2						
	0.044	0.170						
17	1							
	0.043							

\* SE Males Females  
 Portland 0.03 0.008 0.07 0.039

Willasdon 0.066 0.008 all male.

## Appendix G (continued)

Table 2 Tag record matrix of close co-foragers. 1987 April/June adult tags (45) recorded during the follow winters - Dec/Jan 87/88.

[illegible]

Appendix G (continued) Table 2

G	3	2	R G Y R
R I Y I B I R I R I W I B I W I G I W I G I Y I Y I W I B I G I R I R I R I R I W I B I G I Y I Y I G I W I G I G I R I B I Y I R I Y I B I R I G I W I W I B I Y I W I R I B I			
1 Y I B I B I W I B I B I B I B I G I Y I G I H I Y I G I B I W I Y I H I W I B I B I B I G I G I Y I Y I B I B I G I Y I H I Y I R I B I B I B I G I B I Y I G I B I G I W I B I			
BWRYI	. . . . .	X . . . . .	. . . . .
BWRBI	. . . . .	X . . . . .	. . . . .
BWRWI	. 3 . 6 . . . . .	4 . . . . .	X 10 9 . . . . .
BWRI	. 5 . 5 . 6 . 6 . . . . .	. 10 5 12 5 . 7 . 5 . 5 . . . . .	1 . 5 1 . . . . . 6 . 1 .
BWBW124	. 10 . 4 . 4 . . . . .	5 . 7 6 7 . . . . .	9 12 X . . 4 . 7 . 1 . . . . . 5 . 12 5 . . . . . 5 . 1 .
BWGW1	. . . . .	. . . . .	5 . 2 . . . . .
BWYGI	. . . . .	. . . . .	X . . . . .
BWYGI	. 5 4 . 5 . . 7 . . . . .	6 7 . . . . .	7 4 . . 3 . . . . .
BWGYI	. . . . .	. . . . .	1 . . . . .
BWWYI	. 6 . 3 . . . . .	5 . . . . .	5 7 . . . . . X . . . . .
BWG8I	. . . . .	. . . . .	X . . . . .
BWGR1	. 12 . 7 . . . . .	. . . . .	5 1 . . . . . X . . . . .
BWRG113	. 10 1 5 11 . . 5 . . . . .	4 . . . . .	. . . . . 2 . . . . . 1 . . . . . 1 . 1 . . .
BWBYI	. . . . .	. . . . .	X . . . . .
BWYBI	. . . . .	. . . . .	X . . . . .
RWRYI	. 6 . 7 . . . . .	6 . . . . .	1 5 . . . . . X . . . . .
RWYRI	. . . . .	. . . . .	X . . . . .
RWBR1	. . . . .	. . . . .	X . . . . .
RWRW110	. 12 1 5 7 2 . 5 . 4 . 1 9 1 . . . . .	1 5 12 . . 1 . 1 . 1 1 . . 1 . . 1 1 . . 1 . 2 . 1 .	. . . . .
RWGW1	. 9 . 5 . . . . .	5 . . . . .	1 5 . . . . . X . . . . . 1 . . . .
RWWGI	. . . . .	. . . . .	X . . . . .
RWWBI	. 6 . 1 . . . . .	. . . . .	X . . . . .
RWWYI	4 . 6 . . 6 . . 5 . . . . .	. . . . .	1 . . . . . 1 . . . . . 4 . 1 . . .
RWBG1	. . . . .	. . . . .	. . . . . 1 . . . . .
RBYRI	4 . 11 . 3 5 . . 8 . . . . 11 . . . . .	6 5 . . . . .	1 . . . . . 1 1 . . 1 . 3 . . .
GYWGI	. 4 . . . . .	4 . . . . .	. . . . . X . . . . .
YBRW1	. . . 4 . . . . .	6 . . . . .	1 1 . . . . . X . . . . .
RYBRI	. . . . .	. . . . .	. . . . . 1 . . . . .
G	3	2	R G Y R
R I Y I B I R I R I W I B I W I G I W I G I Y I Y I W I B I G I R I R I R I R I W I B I G I Y I Y I G I W I G I G I R I B I Y I R I Y I B I R I G I W I W I B I Y I W I R I B I			
1 Y I B I B I W I B I B I B I B I G I Y I G I H I Y I G I B I W I Y I H I W I B I B I B I G I G I Y I Y I B I B I G I Y I H I Y I R I B I B I B I G I B I Y I G I B I G I W I B I			

# Appendix G (continued)

Table 3 Mean intra colony band sharing, plate 1b.

Sex	o	o	o	o	o	o	o	o	o	o	o	o	o
Track	1	2	3	4	5	6	7	8	9	10	12	15	17
Band No.	25	30	24	28	20	27	19	19	19	13	13	17	27
1	n	3	4	4	6	7	3	4	4	1	2	3	3
	x	0.11	0.16	0.14	0.27	0.26	0.14	0.18	0.18	0.058	0.12	0.14	0.11
		3	2	2	5	4	1	4	2	2	2	2	3
		0.11	0.07	0.09	0.18	0.17	0.04	0.17	0.11	0.11	0.09	0.116	
3			3	1	4	1	3	1	2	4	3	3	
			0.12	0.045	0.15	0.05	0.14	0.047	0.12	0.237	0.15	0.12	
4				4	0	3	6	3	2	1	2	2	
				0.17	0.00	0.13	0.20	0.13	0.11	0.056	0.09	0.073	
5					2	2	0	3	0	1	1		
					0.087	0.10	0.00	0.15	0.00	0.06	0.05		
6						0	3	10	2	0	2	4	
						0.00	0.17	0.45	0.11	0.00	0.09	0.15	
7							1	2	2	1	2	1	
							0.05	0.11	0.13	0.065	0.10	0.045	
8								1	1	1	1	1	
								0.05	0.065	0.065	0.05	0.045	
9									0	0	1	4	
									0.00	0.00	0.056	0.13	
10										0	3	1	
										0.00	0.20	0.06	
11											2	2	
											0.136	0.11	
12												3	
													0.144

Total Mean  $\bar{x}$  = 0.1085 SE = 0.0035



# Appendix G (continued)

Table 4 Plate 2 close co-foragers (tracks 12,13 and 15 failed).

Nestbox	7	2					3			5	13	
	0	0	0	0	0	0	0	0	0	0	0	0
Track	1	2	3	4	5	6	7	8	9	10	11	14
band No.	23	21	9	37	21	27	43	33	38	32	39	31
1	n	5	1	7	6	12	9	3	9	7	8	7
	x	0.19	0.07	0.20	0.23	0.40	0.24	0.09	0.25	0.22	0.23	0.22
2			2	5	1	3	5	2	6	3	5	2
			0.15	0.187	0.048	0.127	0.177	0.078	0.22	0.12	0.185	0.08
3				4	0	0	2	1	3	2	3	1
				0.32	0.0	0.00	0.13	0.07	0.206	0.14	0.206	0.072
4					2	4	11	6	9	3	7	11
					0.075	0.128	0.23	0.17	0.24	0.233	0.197	0.326
5						2	6	5	5	5	4	4
						0.07	0.22	0.008	0.185	0.197	0.14	0.159
6							7	6	8	6	8	6
							0.24	0.126	0.25	0.21	0.253	0.21
7								4	3	5	7	6
								0.17	0.20	0.16	0.17	0.167
8									7	11	7	3
									0.20	0.338	0.20	0.094
9										12	15	4
										0.345	0.395	0.117
10											9	4
											0.26	0.127
11												6
												0.176
	x	SE	N									
Females	0.213	0.013	35									
Males	0.087	0.06	3									
M/F	0.149	0.014	25									

# Appendix H (Chapter 8)

**Table A** Breeding success at Tom Spinny for two consecutive seasons.

Nest box	1987				1988			
	Occupied by	Eggs	Hatch	Fledge	Occupied by	Eggs	Hatch	Fledge
1	GWY <sup>♀</sup>	4	3	2	YES	3	3	0
2	GWY <sup>♀</sup>	4	3	2	BYWR <sup>♂</sup>	4	4	0
3	GWB/RY	1	1	1	YES	6	5	0
4	YES	4	3	0	YES	6	6	0
5	GWY <sup>♀</sup>	6	5	1	GWY <sup>♀</sup>	4	2	1
6	YES	4	2	1	Squirrel	-	-	-
7	GWY <sup>♀</sup>	5	4	2	GWB <sup>♀</sup>	4	2	0
8	YES	4	4	0	YES	5	4	0
9	YES	6	4	1	YES	4	2	0
10	GWR <sup>♂</sup>	4	4	2	YES	4	2	0
11	YES	6	1	1	GWR <sup>♂</sup>	4	2	0
12	YES	1	1	0	TAG?	5	5	0
13	YES	4	2	2	YES	4	4	1
14	YES	4	3	1	YES	4	3	0
15	YES	5	1	1	YES	5	4	0
16	YES	4	1	1	YES	4	0	0
17	RWG	4	2	2	RWR <sup>♂</sup>	4	2	0
18	RWB <sup>♀</sup>	4	3	0	GWY <sup>♀</sup>	1	0	0
19	NIL	-	-	-	YES	4	4	1
20	YES	4	4	2	GWY <sup>♀</sup>	4	4	2

# Appendix H (continued)

**Table 2** Male jackdaw return times to nestboxes when feeding incubating females (minutes).

Nestbox	12	13	20	8	2	5	19
	13.0	40.1	5.2	34.0	15.1	24.0	13.0
	21.0	33.0	55.3	6.0	14.5	4.3	14.0
	9.1	23.3	9.3	8.5	11.5	14.1	36.3
	43.1	11.0	10.0	15.1	8.0	14.4	19.1
	24.1	3.1	5.5	11.2	16.2	6.3	23.0
	29.1	24.1	4.5	15.1	10.1	19.3	8.5
	10.1	63.0	5.5	14.5	9.1	22.0	7.2
	16.0	32.0	6.0	11.1	8.2	13.1	20.1
	19.2	33.1	15.2	22.0	15.1	8.3	
	22.2	39.2	13.1	18.3	15.0	17.0	
	26.3	22.0	26.3	15.2		10.2	
	18.4	24.0	19.2	11.2		9.1	
	42.0	39.0	16.3	69.3		20.1	
	19.1	41.2	14.4	43.1			
	19.0	36.0	20.0				
	28.0	20.3	7.0				
	36.1	19.1	8.2				
	3.5	28.3	9.3				
	43.0	16.0	5.5				
	22.1	15.0	13.5				
	31.1	15.3	27.0				
	19.4	15.0	19.2				
	17.1	22.0	12.1				
	14.0	22.4	21.2				
	15.4	29.1	43.4				
		10.4	16.2				
		9.4	18.3				
		4.2	12.1				
			36.2				
			43.1				
			10.3				
			11.5				
			7.1				
			8.1				
			7.3				
			6.0				
			13.2				
			9.3				
Mean	22.5	24.6	15.5	21.0	12.3	13.9	17.7
SE	2.1	2.5	1.9	4.6	1.0	1.7	3.3

# Appendix H (continued)

**Table 3** Male/female distance (nestbox) in metres at 10 minute intervals.

1. 30-3-88 (X=2.88, SE=0.17).

2. 27-4-88 (X=1.87, SE=0.81).

3. 18-4-88 (X=5.52, SE=1.06).

(7)			(18)			(20)		
1	2	3	1	2	3	1	2	3
0.5	0.5	20	0.5	0.5	15	0.1	0.5	
20								
0.2	0.2	3	0	0.6	20	0.6	0.1	0
1	3	1	2	1	10	1	0.1	6
1	2	40	0.5	1.5	0.1	10	0.2	5
0.5	0.5	0.5	0.5	0.5	0.5	0.2	2	0.2
1	0	0.2	1	1	0.5	0.2	4	10
1	1	0.1	20	5	0.5	1	1	0.2
2	1	20	20	10	0.5	0.5	0	0.5
3	1	1	0.2	0	0.5	4	0.2	40
0	0	10	0.2	0.2	0.5	1	0	6
4	2	10	0.5	0.2	10	0.5	0.2	5
10	4	10	10	0.1	1	1	0.7	0
0	1	1	0.2	0.4	1	4	0.5	0.1
20	0.5	0.5	0	0.5	0.2	20	2	0.4
0	0.5	1	0.1	1	5	0	0.5	0.2
0.2	0.5	3	0	0.5	1	0	4	0
0.5	0.1	0.1	0.1			0.1	1	0.2
0.2	0.1	0.1	0.5			0.1	0.5	20
30	0	0.5				20	40	40
0.1	0	10				0	0.5	10
0.5	0.1	0.2				0	0.5	5
0.5	0.3	10				0.1	4	1
0.5	0	0.5				6	6	5
	0.1	0.5				6	0.1	2
	10	0.1				0.5	0.5	2
	0.2	5				6	0.2	4
		2				4	1	3
						1	5	1
						0.5		4
						0.2		0.2
								2

## Appendix I (Chapters 8 and 9)

**Table 1** Band sharing analysis for plate 8.1.

	0	1	2	3
b	28	22	27	33
x		0.48	0.44	0.36
n		12	12	11
			0.53	0.26
			13	7
				0.26
				8

Siblings 1 and 2 share only 26% of bands with 3, possibly implying different paternity for 3.

---

**Table 2** Tagged jackdaw biometrics.

ID	BL	BD	WNG	WEI	TAR	C	A	S	DATE
Females:									
001	31.2	16.5	229	250	43.6	3	3	2	100587
002	31.5	15.5	217	225	44.4	3	3	2	130587
003	35.1	14.7	240	205	43.8	2	3	2	220587
004	33.6	15.0	240	235	46.7	1	3	2	290587
005	34.9	14.5	230	230	46.3	2	3	2	290587
006	34.7	15.2	233	220	45.8	2	3	2	290587
007	35.1	14.4	230	230	43.0	1	3	2	010687
008	32.3	14.6	225	219	42.5	1	3	2	010687
009	35.8	15.4	220	215	44.9	1	3	2	220687
010	35.6	15.2	225	240	45.1	2	3	2	220687
011	32.8	14.7	240	205	43.4	2	3	2	220687
012	32.4	15.0	227	200	43.6	1	3	2	220687
013	33.5	15.0	225	228	42.8	2	3	2	070488
014	33.7	14.7	230	205	43.6	2	3	2	020588
015	-9.0	-9.0	238	236	43.2	2	3	2	140588
016	-9.0	-9.0	230	216	39.8	2	3	2	140588
017	-9.0	-9.0	227	225	46.0	1	3	2	220588

Appendix I (Table 2) continued

018	-9.0	-9.0	233	255	46.1	1	2	2	220588
019	-9.0	-9.0	222	223	42.7	2	2	2	220588
020	-9.0	-9.0	219	209	42.3	2	2	2	250588

Males:

021	31.6	15.2	229	245	45.4	2	3	1	210587
022	33.6	16.9	238	270	47.8	2	2	1	120587
023	34.4	15.1	244	295	48.5	4	3	1	210587
024	34.2	15.9	242	269	45.5	3	3	1	210587
025	34.6	15.3	245	265	47.6	3	3	1	220587
026	36.8	15.3	242	264	45.5	3	2	1	220587
027	34.5	15.0	244	250	44.1	3	3	2	220587
028	35.8	15.6	240	262	46.0	3	3	1	260587
029	35.6	15.6	240	250	48.5	2	3	1	290587
030	35.9	14.5	250	240	45.9	2	3	1	220687
031	37.3	15.2	247	250	47.3	2	3	1	220687
032	37.0	15.0	240	255	46.2	2	3	1	220687
033	35.6	14.3	241	230	47.0	3	3	1	220687
034	34.3	14.0	242	220	46.2	1	3	1	220687
035	37.0	15.4	242	235	46.5	2	3	1	220687
036	----	----	242	253	45.5	2	3	1	140588
037	----	----	240	250	45.9	2	3	1	140488
038	----	----	241	270	46.0	3	3	1	140488
039	----	----	244	256	43.2	3	3	1	140488
040	----	----	241	240	47.5	2	3	1	220588
041	----	----	234	260	47.0	2	3	1	220588

Unconfirmed sex:

000	31.7	15.2	229	245	45.4	2	2	1	210587
000	----	----	240	250	45.9	2	3	1	140488
000	----	----	244	250	----	-	-	-	140488
000	----	----	248	251	----	-	-	-	140488
000	----	----	250	275	----	-	-	-	140488
000	31.0	14.3	221	225	44.8	2	3	2	210587
000	32.5	14.4	216	212	44.5	2	2	2	030687
000	34.2	14.8	225	200	43.8	1	3	2	220587
000	38.2	15.0	206	210	45.2	1	3	1	220687

000 36.1 14.7 240 250 43.8 3 3 1 220587

Abbreviations: ID= Identification number, BL= bill length, BD= Bill depth, WNG= wing length, WEI= weight, TAR= tarsus, C= physical condition (1 poor, 4 good), A= age (1 juvenile, 2 immature, 3 adult), S= sex (1 male, 2 female), DATE= capture date.

## REFERENCES

- Alison R.M. 1975. Breeding biology and behaviour of the Oldsquaw (*Clangula hyemalis* L.) Ornithol. Monogr., 18: 1-52.
- Anderson A. 1963. Patagial tags for water fowl. *Journal of Wildlife Management*, 27: 370-389.
- Andersson M., Götmark F. and Wiklund C. 1981. Food information in the black-headed gull *Larus ridibundus*. *Behav. Ecol Sociobiol.*, 9: 195-200.
- Barnard C.J. 1978. Aspects of winter flocking and food-fighting in the house sparrow *Passer domesticus* L.) D.Phil. thesis, University of Oxford.
- Barnard C.J. 1980. Equilibrium flock size and factors affecting arrival and departure in feeding house sparrows. *Anim. Behav.*, 28: 503-511.
- Barnard C.J. & Stephens H. 1983. Costs and benefits of single and mixed species flocking in fieldfares (*Turdus pilaris*) and redwings (*T. illacus*). *Behaviour* 84: 91-123.
- Barnard C.J. Thompson D.B.A. 1985. *Gulls and Plovers*: Croom Helm. London.



- Bayer R.D. 1982. How important are bird colonies as information centres? *Auk* 78: 63-71.
- Begon M., Harper J.L & Townshend C.R. 1986. *Ecology: organisms, populations and communities*. Oxford: Blackwell.
- Bell G.I., Selby M.J. & Rutter W.J. 1982. The highly polymorphic region near the insulin gene is composed of tandemly repeating sequences. *Nature*, 295: 31-35.
- Berger M. & Hart J.S. 1972. In: King J.R. 1974. *Publications of the Nuttall Ornithological Club* 15: 4-55.
- Bernstein M.H. et al 1972. In: King J.R. 1974. *Publications of the Nuttall Ornithological Club* 15: 4-55.
- Bertram B.C.R. 1980. Vigilance and group size in ostriches. *Anim. Behav.*, 28: 278-286.
- Birkhead T.R. 1974. Utilization of guillemot (*Uria aalge*) colonies by jackdaws (*Corvus monedula*). *Ornis Scand.* 5: 71-81.
- Birkhead T.R. 1979. Mate guarding in the magpie *Pica pica*. *Anim. Behav.*, 27: 866-874.

- Bishop O.N. 1966. Statistics for Biology. Longman. Harlow.
- Bolton P.J. and Phillipson J. 1976. Energy equivalents of their egesta and a mineral soil. *Pedobiologia*, 16: 443-450.
- British Trust for Ornithology. 1984. The ringers manual. British Trust for Ornithology. Tring.
- Brockmann H.J & Barnard C.J. 1979. Kleptoparasitism in birds. *Anim. Behav.*, 27: 487-514.
- Brown J.L and Brown E.R. 1984. Parental facilitation: parent offspring relations in communally breeding birds. *Behav. Ecol. Sociobiol.* 14: 203-209.
- Burke T. & Bruford M.W. 1987. DNA fingerprinting in wild birds. *Nature*, 327: 149-152.
- Burke T.B., Davies N.B., Bruford M.B., & Hatchwell B.J. 1989. Parental care and mating behaviour of polyandrous dunnocks *Prunella modularis* related to paternity by DNA fingerprinting. *Nature*, 338: 249-251.
- Burkitt J.P. 1935. Notes on the rook. *British birds*, 28: 322-326.

- Busse V.K. 1977. Statistisches Prüfefahren des Untermischungsgrades von im Watt rastenden Flußseeschwalben-und Küstenseeschwalben-Schwärmen (*Sterna hirundo* L. und *S. paradisaea* Pont.). Z. Tierpsychol., 43: 295-303.
- Busse P. 1969. Results of ringing of European Corvidae. *Acta Ornithologica*, 11: 263-315.
- Caraco T. 1979. Time budgeting and group size: a theory. *Ecology*, 60(3): 611-617.
- Caraco T. 1981. Risk sensitivity and foraging groups. *Ecology*. 62: 527-531.
- Caraco T., Martindale S. & Pulliam H.R. 1980. Avian flocking in the presence of a predator. *Nature* 285: 400-401.
- Caraco T. & Pulliam H.R. 1980. Time budgets and flocking dynamics. Proc. XVII Int, Ornith. Cong. Berlin, Germany.
- Chabrzyk G & Coulson J.C. 1976. Survival and recruitment in the herring gull *Larus argentatus* J. *Animal Ecol.*, 45: 187-203.
- Charnov E. 1986. Group selection revisited. *Nature*, 321: 23-24.

- Cody M.L. 1971. Finch flocks in the Mohave Desert. *Theoretical Population Biology* 2: 142-158.
- Cooke F., MacInnes C.D. and Prevett J.P. 1975. Gene flow between populations of the lesser snow goose. *Auk*, 92: 493-510. In: Greenwood P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- Coombs F.C. 1978. *The Crows: A study of the corvids of Europe*. Batsford, London.
- Crook J.H. 1965. The adaptive significance of avian social organisations. *Symp. Zool. Soc. London*, 14: 181-218.
- Darwin C.R. 1889. *The Origin of the Species by means of Natural Selection*. London. Murray.
- Davies N.B. 1985. Cooperation and conflict among dunnocks, *Prunella modularis*, in a variable mating system. *Anim. Behav.*, 33: 628-648.
- Davies N.B. 1978. Parental meanness and offspring independence: an experiment with hand-reared great tits *Parus major*. *Ibis*, 120: 509-515.
- Dawkins R. 1979. Twelve misunderstandings of Kin selection. *Z. Tierpsychol.*, 51: 184-200

- De Groot. P. 1980. Information transfer in a socially roosting weaver bird (*Quelea quelea*; Ploceinae): an experimental study. *Anim. behav.*, 28: 1249-1254.
- Dunn E.K. 1973. Robbing behaviour of roseate terns. *Auk* 90: 641-651.
- Dunnet G.M. & Patterson I.J. 1968. The rook problem in North-east Scotland. The problems of birds as pests (Eds. Murton R.K & Wright E.N.) pp 119-139. Academic Press London.
- Dunnet G.M., Fordham R.A., Patterson I.J. 1969. Ecological studies of the rook *Corvus frugilegus* L., in North East Scotland. Proportion and distribution of young rooks (*Corvus frugilegus*). *J. App. Ecol.*, 6: 459-473.
- Edwards C.A. & Lofty J.R. 1977. The biology of the earthworm. Chapman & Hill. London.
- Elgar M. & Harvey P. 1987. Colonial Information centres. *Trends in Evolution and Ecology*, 2(2): 34.
- Elgar M.A. & Catterall C.P. 1981. Flocking and predator surveillance in house sparrows. *Anim. Behav.*, 29: 868-872.
- Elliott J.M. 1977. Some methods for the statistical

analysis of benthic invertebrates. Freshwater Biological Association. Kendal.

Ewald P.W. & Rohwer S. 1982. Effects of supplemental feeding on timing of breeding, clutch size, and polygamy in red winged blackbirds *Agelaius phoeniceus*. *J Anim. Ecol.*, 51. 429-450.

Feare C.J., Dunnet G.M., Patterson I.J. 1974. Ecological studies of the rook *Corvus frugilegus* L., in North East Scotland. Food intake and behaviour in the rook (*Corvus frugilegus*). *J. App. Ecol.* 11: 867-896.

Fowler J., and Cohen L. *Statistics for Ornithologists*. British Trust for Ornithology. Tring.

Fretwell S.D. 1972. *Populations in a seasonal environment*. Princeton University Press. Princeton, NJ.

Fuchs E. 1977. Kleptoparasitism of sandwich terns *Sterna sandvicensis* and black-headed gulls *Larus ridibundus*. *Ibis*, 119: 183-190.

- Gerard B.M. 1964. A synopsis of British Fauna: No. 6, Lumbricidae, with keys and descriptions. Linnaen Society of London.
- Gibbons D.W. 1987. Hatching asynchrony reduces parental investment in jackdaws. *J. Anim. Ecol.*, 56: 403-414.
- Giban J. 1947. Donnees fournier parle baguage sur le biologie de Feux (*Corvus frugilegus*) en France et sur le migratin de l'espece en Europe Occidentale. *Annales des Epiphytes*, Paris, 13: 20-41.
- Goodburn S.F. 1984. Mate guarding in the Mallard *Anas platyrhynchos*. *Ornis. Scand.* 15: 261-265.
- Goodwin D. 1976. *Crows of the World*. Comstock. Cornell Press.
- Goss-Custard J.D. 1976. Variation in the dipersion of redshank *Tringa totanus* on their winter feeding grounds. *Ibis*, 118: 257-263.
- Goss-Custard J.D. 1985. In: Sibly R.M. and Smith R.H. 1985. *Behavioural Ecology*. eds. Blackwell Scientific publications. Oxford.

- Goss-Custard J.D., Durell S.E.A. le V dit. 1981.  
Individual age differences in the feeding ecology of  
oystercatchers *Haematopus ostralegus*. *Ibis*. 125:  
155-171
- Goss-Custard J.D., Durell S.E.A. le V dit & Ens J.V.  
1983a. Individuals differences in aggressiveness and  
food stealing among wintering oystercatchers *Haematopus*  
*ostralegus*. *J. Anim. Ecol.*, 30: 917-28.
- Goss-Custard J.D., Durell S., McGrorty S & Reading C.J.  
1983b. Use of mussel beds *Mytilus edulis* L. by  
oystercatchers *Haematopus ostralegus* L. according to  
age and population size. *J. Anim. Ecol.* 51: 543-54.
- Gould S.J. & Lewontin R.C. 1979. The spandrels of San  
Marco and the Panglossian Paradigm: a critique of the  
adaptionist programme. *Proc. R. Soc. Lond. B.* 205:  
581-598.
- Grafen A. 1979. The hawk-dove game played between  
relatives. *Anim. Behav.*, 27(3): 905-907.
- Grafen A. & Ridley M. 1983. A model of mate guarding. *J.*  
*theor. Biol.*, 102: 549-567.
- Grant P.R 1971. Interactive behaviour of puffins  
(*Fratercula arctica* L.) and skuas (*Stercorarius*  
*parasiticus* L.). *Behaviour*, 40: 263-281.



- Green P.T. 1982a. Coloniality in the rook. Ph.D thesis, Edinburgh University.
- Green P.T. 1982b. Bigamy in the rook *Corvus frugilegus*. *Ibis*, 124: 320-325.
- Greene E. 1987. Individuals in an osprey colony discriminate between high and low quality information. *Nature*, 329: 239-241.
- Greenwood P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.
- Greenwood P.J., Harvey P.H. & Perrins C.M. 1978. Inbreeding and dispersal in the great tit. *Nature*, Lond. 271: 52-54
- Greenwood P.J. & Harvey P.H. 1982. The natal and breeding dispersal of birds. *Ann. Rev. Syst.*, 13: 1-21.
- Hamilton W.D. 1964. The genetic evolution of social behaviour. *J. theor. Biol.*, 7: 1-16.
- Hamilton W.D. 1971. Geometry for the selfish herd. *J. theor. Biol.*, 31: 295-311.
- Harper D.G.C. 1982. Competitive foraging in mallards:

- 'ideal free' ducks. *Anim. Behav.* 30: 575-584.
- Hart A.D.M. 1987. Patagial tags for Herring Gulls: improved durability. *Ring. & Migr.* 8: 19-26.
- Henderson I.G. In press. The exploitation of tits *Parus* spp., long-tailed tits *Aegathos caudatus* and goldcrests *Regulus regulus* by treecreepers *Certhia familiaris*: a behavioural approach. *Bird Study*.
- Höglund J. 1985. Foraging success of rooks *Corvus frugilegus* in mixed-species flocks of different sizes. *Ornis. Fennica*, 62: 19-22.
- Högstedt G. 1980. Resource partitioning in the magpie *Pica pica* and the jackdaw *Corvus monedula* during the breeding season. *Ornis Scand.*, 11: 110-115.
- Holyoak D. 1968. A comparative study of the food of some British Corvidae. *Bird Study*, 15: 147-153.
- Holyoak D. 1971 Movements and mortality of Corvidae. *Bird Study*, 18: 97-106
- Hoogland K.N 1979. In: Greenwood P.J., 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav.* 28: 1140-1162.

- Inglis I.R & Lazarus J. 1981. Vigilance and flock size in brent geese: the edge effect. *Z. Tierpsychol.* 57: 193-200.
- Jeffreys A.J. & Morton D.B. 1987. DNA fingerprints of dogs and cats. *Animal Genetics*, 18: 1-15.
- Jeffreys A.J., Wilson V. & Thein S.L. 1985a. "minisatellite" fingerprints in DNA. *Nature*, 314: 67-73.
- Jeffreys A.J., Wilson V. & Thein S.L. 1985b. Individual-specific 'fingerprints' of human DNA. *Nature*. 316: 76-79.
- Jeffreys A.J., Wilson V. & Thein S.L., Weatherall D.J. & Ponder B.A.J. 1986. DNA "Fingerprints and Segregation Analysis of Multiple Markers in Human Pedigrees. *Am. J. Human Genetics*, 39: 11-24.
- Jennings T. & Evans S.M. 1980, Influence of position in the flock and flock size on vigilance in the starling *Sturnus vulgaris*. *Anim. Behav.*, 28: 634-635.
- Kendeigh S.G. 1970. Energy requirements for existence in relation to size of bird. *The Condor*, 72: 60-65.

- Kenward R.E. 1978. Hawks and doves: attack success and selection in goshawk flights at wood pigeons. *J. Anim. Ecol.*, 47: 449-460.
- King J.R. 1974. Seasonal allocation of time and energy resources in birds. In: R.A. Paynter (ed) *Avian Energetics*, 4-85. Cambridge, M.A.: Publications of the Nuttall Ornithological Club No. 15.
- Krebs J.R. 1973. Social learning and the significance of mixed-species flocks of chickadees (*Parus spp.*). *Can. J. Zool.*, 51; 1275-1288
- Krebs J.R. 1974. Colonial nesting and social feeding as strategies for exploiting food resources in the great blue heron (*Ardea herodias*). *Behaviour*, 51: 99-131.
- Krebs J.R. & Davies N.B. 1978. *Behavioural Ecology: An Evolutionary Approach*. Blackwell Scientific Press. Oxford.
- Krebs J.R., MacRobert M.H. & Cullen J.M. 1972. Flocking and feeding in the great tit *Parus major* - an experimental study. *Ibis*, 114: 507-530.
- Lack P. 1986. *The Atlas of wintering birds in Britain and Ireland*. Poyser, Staffordshire.
- Lazarus J. 1979. The early warning function of flocking

- in birds: an experiential study with captive quelea. *Anim. Behav.*, 27: 855-865.
- Lehner P.N. 1979. *The Handbook of Ecological Methods*. S.T.P.M. Press. New York.
- Leitch A. 1972. Roosting patterns of Corvidae in Aberdeenshire. M.Sc. (Ecol.) Thesis. University of Aberdeen. In: McKilligan N.G. 1980. The winter exodus of the rook from a Scottish Highland valley. *Bird study*, 27: 93-100.
- Lewin B.L. 1983. *Genes II*. (2nd ed.). Wiley. USA.
- Lill A. 1974. Sexual behaviour of the lek-forming white-bearded manakin (*Manacus manacus trinitatis* Hartert) *Z. Tierpsychol.* 36: 1-36.
- Lincoln F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. *U.S. Dept. Agrig. Circ.*, 118, 1-4.
- Lincoln G.A., Racey P.A., Sharp P.J. & Klandorf H. 1980. Endocrine changes associated with spring and autumn sexuality of the rook *Corvus frugilegus*. *J. Zool. Lond.*, 190: 137-153.
- Linton L.R., Ronald W.D. & Wrona F.J. 1981. Resource utilization indices: an assessment. *J. Anim. Ecol* 50:

283-292.

Lockie J.D. 1955. The breeding and feeding of jackdaws and rooks with notes on the carrion crow and other Corvidae. *Ibis*, 97: 341-369.

Lockie J.D. 1956a. The food and feeding behaviour of the jackdaw, rook and carrion crow. *J. Anim. Ecol.*, 25: 421-428.

Lockie J.D. 1956b. Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. *Bird Study* 3: 180-190.

Loman J. 1980. Habitat distribution and feeding strategies of four Swedish corvid species during winter. *Ekologia Polska*, 28: 95-109.

Lorenz K. 1931. Beiträge zur Ethologie sozialer Corviden. *J. Orn.*, 75: 511-519. In: Coombs C.J.F 1978. *The Crows*. Batsford, London.

Lorenz K. 1932. Betrachtungen über das Erkennen der art eigenen Triebhandlungen der Vögel. *J. Orn.*, 79: 67-127. In: Coombs C.J.F 1978. *The Crows*. Batesford, London.

Lorenz K.Z. 1952. *King Solomon's Ring*. Methuen, London.

- Lovari S. 1979, Aspects of rank order in a flock of captive jackdaws. *Biology of Behaviour*, 4: 311-326.
- Macdonald R.A. & Whelan J. 1986. Seasonal variations in the feeding range and flock structure of the rook *Corvus frugilegus* in eastern Ireland. *Ibis*, 128: 540-557.
- MacRoberts M.H. & MacRoberts B.R. 1976. Social organisation and behavior of the acorn woodpecker in central coastal California. *Ornithol. Monogr.* no. 21: 115.
- Marshall A.J. & Coombs C.J.F. 1957. The interaction of enviromental, internal and behavioural factors in the rook *Corvus f. frugilegus* Linnaeus. *Proc. Zool. Soc. Lond.* 128: 545-589.
- Maynard Smith J. 1974. The theory of games and the evolution of animal conflicts. *J. theor Biol.* 47: 209-221.
- Maniatis T, Fritsch E.F. & Sambrook J. 1982. Molecular cloning, a laboratory manual. Cold Spring Harbor, New York.
- McCracken G.F. & Bradbury J.W. 1981. Social organisation and kinship in the poygynous bat *Phyllostomus hastatus*. *Behav. Ecol. Sociobiol.*, 8: 11-34.

- McKilligan N.G. 1980. The winter exodus of the rook from a Scottish Highland valley. *Bird study*, 27: 93-100.
- McKinney F. 1986. Mate guarding and the confidence of paternity. 19th International Ornithological Congress.
- Milinski M. 1984. Competitive resource sharing: an experimental test of a learning rule for ESSs. *Anim. Behav.* 32, 233-242.
- Møller A.P. 1986. Mate guarding in the swallow *Hirundo rustica*. *Behav. Ecol. Sociobiol.*, 21: 119-123.
- Mock D.W., Lamey T.C. & Thompson D.B.A. 1988. Falsifiability and the information centre hypothesis. *Ornis. Scand.*, 19: 231-248.
- Morse D. H. 1978. Structure and foraging patterns of flocks of tits and associated species in an English woodland during the winter. *Ibis.*, 120: 298-312.
- Murton R.K. 1971. Why do some bird species feed in flocks? *Ibis*, 113: 534-536.
- Orians G.H. 1961. King J.R. 1974. Seasonal allocation of time and energy resources in birds. In: R.A. Paynter (ed) *Avian Energetics*, 4-85. Cambridge, M.A.: Publications of the Nuttall Ornithological Club No. 15.
- Olsson H. & Persson O. 1979. Varför lever kråkfåglar i



blandflockar vintertid? (Why do corvids form mixed flocks in winter?) Anser, 18: 19-24.

Patterson I.J. 1978. Tags and other distant recognition markers for birds. *Animal Marking. Recognition Marking of Animals Research* (Ed. Stonehouse B.), pp 54-62. Macmillan. London

Patterson I.J., Dunnet G.M and Fordham R.A. 1971. Ecological studies of the rook *Corvus frugilegus* L., in North East Scotland. *Dispersion. J. App. Ecol.*, 8: 815-833.

Patterson I.J., Dunnet G.M. & Goodbody S.R. 1988. Body weight and juvenile mortality in the rook *Corvus frugilegus*. *J. Anim. Ecol.*, 57: 1041-1052.

Patterson I.J. & Grace E.S. 1984. Recruitment of young rooks *Corvus frugilegus* into breeding populations. *J. Anim Ecol.*, 53: 559-572.

Perrins C.M. 1979. *British tits*. London Collins.

Phillipson W.R. 1933. The rook roosts of south Northumberland and the boundary between their feeding territories. *British Birds*, 27: 66-71.

Powell G.V.N. 1974. Experimental analysis of the social value of flocking by starlings (*Sturnus vulgaris*) in

- relation to predation and foraging. *Anim. Behav.* 22: 501-505.
- Pulliam H.R. 1973. On the advantages of flocking. *J. theor. Biol.*, 38: 419-422.
- Pulliam H.R. & Caraco T. 1984. Living in groups: In Krebs J.R. and Davies N.B. (eds). *Behavioural Ecology*. Blackwell. Oxford.
- Purchas T.P.G. 1980. Feeding ecology of rooks (*Corvus frugilegus*) on the Heretaunga Plains, Hawkes Bay, New Zealand. *New Zealand Journal of Zoology*, 7: 557-578.
- Richards P.R. 1975. Pair formation and pair bond in captive rooks. *Bird Study*, 23: 207-211
- Richardson S.C., Patterson I.J. & Dunnet G.M. 1979. Fluctuations in colony size in the rook, *Corvus frugilegus*. *J. Anim. Ecol.*, 48: 103-110.
- Röell A. 1978. Social behaviour of the jackdaw *Corvus monedula* in relation to its niche. *Behaviour*, 64: 1-124.
- Rohwer S. & Ewald P.W. 1981. The cost of dominance and the advantage of subordination in a badge signalling system. *Evolution*, 35: 441-454.

- Røskaft E. 1981. The daily activity pattern of the rook *Corvus frugilegus* during the breeding season. *Fauna norv. Ser. C. Cinclus*, 4: 76-81.
- Røskaft E. 1983a. The relationship between fledgling weights of captive rooks and the position in the dominance hierarchy one year later. *Fauna norv. Ser. C. Cinclus*, 6: 78-80.
- Røskaft E. 1983b. Male promiscuity and female adultery by the rook *Corvus frugilegus*. *Ornis Scand.*, 14: 175-179.
- Rothschild M. & Clay T. 1952. *Fleas, flukes and cuckoos*. Collins. London.
- Rowley I. 1965. The life history of the superb blue wren *Malurus cyaneus*. *Emu*, 64: 251-297.
- Rubenstein D.I., Barnett R.J., Ridgley R.S and Kopfer P.H. 1977. Adaptive advantages of mixed species feeding flocks among seed-eating finches in Costa Rica. *Ibis*, 119: 10-21.
- Sale P.F. 1974. Overlap in resource use and interspecific competition. *Oecologia (Berl.)*, 17: 245-256.
- Schartz R.L & Zimmerman J.L. 1971. The time and energy budget of the male dickcissel (*Spiza americana*), *Condor* 73: 65-76

- Schoener T.W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, 49: 704-726.
- Seel D.C. 1976. Molt in five species of Corvidae in Britain. *Ibis*, 118: 491-527.
- Shields W.M 1982. Philopatry, inbreeding and the evolution of sex. State University of New York. Albany.
- Sibley C.G and Ahlquist J. 1982. The phylogeny and classification of the passerine birds, based on comparisons of the genetic material, DNA. pp 83-121 in Proc. 18th Intl. Ornithol. Congr. Moscow. Ilyichev V.D., & Gavrilov V.M. (Eds) Nauka Publ. Moscow.
- Sibley C.G and Ahlquist J. 1986. Reconstructing bird phylogeny by comparing DNA's. *Sci. Amer.*, 254: 68-78.
- Siegel S. 1957. Non parametric statistics for behavioural sciences. Magraw-Hill, New York.
- Sillman A.J. 1972. Avian vision, in: Farner D.S, King J.R., Parkes K.C. *Avian Biology Vol III*. Academic Press.
- Sokal R.R & Rolf F.J 1969. *Biometry* (2nd ed.). Freeman. San Francisco.

- Southern E.M. 1975. Detection of specific sequences among DNA fragments by gel electrophoresis. *J. Mol. Biol.*, 98: 503.
- Southern L.K & Southern W.E. 1985. Some effects of wing tags on breeding ring-billed gulls. *Auk*, 102: 38-42.
- Southwood T.R.E. 1978. *Ecological methods: with particular referenc to insect populations*. Chapman and Hall. London.
- Studd M., Montgomerie R.D. & Robertson R.J. 1983. Group size and predator surveillance in foraging house sparrows (*Passer domestica*). *Can. J. Zool.*, 61: 226-231.
- Stewart W. 1911. The movements of young rooks. *British Birds*, 5: 30.
- Sutherland W.J. & Koene P. Field estimates of the strengths of interference between oystercatchers *Haemotopus ostralegus*. *Oecologia*, 55: 108-109.
- Svensson L. 1984. *Identification guide to European passerines*. Stockholm.
- Swingland R. 1977. The social and spacial organisation of winter communal roosting in rooks (*Corvus frugilegus*). *J. Zoo London*, 182: 509-528.

- Tamm S. 1977. Social dominance in captive jackdaws (*Corvus monedula*). Behavioural processes, 2: 293-299
- Thorpe W.H. 1963. Learning and Instinct in Animals (p.120). Methuen. London.
- Trivers R.L. 1974. Parent offspring conflict. Amer. Zool., 14: 249-264.
- Ulfstrand S. 1979. Age and plumage associated differences of behaviour among blackheaded gulls *Larus ridibundus*: foraging success, conflict victoriousness and reaction to disturbance. *Oikos*, 33: 160-166.
- Vines G. 1980. Spatial consequences of aggressive behaviour in flocks of oystercatchers, *Haemotopus ostralegus* L. *Anim. Behav.*, 28: 1175-1183.
- Waite R.K. 1981. Local enhancement for food finding by rooks (*Corvus frugilegus*) Z. Tierpsychol, 5: 15-36.
- Waite R.K 1984a. Sympatric Corvids. Effects of social behaviour, aggression and avoidance on feeding. *Behav. Ecol. Sociobiology*, 53: 55-59.
- Waite R.K. 1984b. Winter habitat selection and foraging behaviour in sympatric corvids. *Ornis. Scandinavica*, 15: 55-62.

- Ward P. 1965. Feeding ecology of the Black-faced Dioch  
Quela quela in Nigeria. *Ibis*, 107: 173-214.
- Ward P. & Zahavi A. 1973. The importance of certain  
assemblages of birds as Information Centres for food  
finding. *Ibis*, 115: 517-534.
- White G. 1789. *The Natural History and Antiques of  
Selbourne*. London.
- Woolfenden G.E. & Fitzpatrick J.W. 1984. *The florida  
scrub jay: Demography of a cooperative-breeding bird*.  
Princeton University Press, Princeton. N.J.
- Wyman A. & White R. 1980. *Proc. natn. Acad. Sci. USA*, 77:  
6754-6758. In: Jeffreys A.J., Wilson V. & Thein S.L.  
1985a. "minisatellite" fingerprints in DNA. *Nature*,  
314: 67-73.
- Wynne-Edwards V.C. 1962. *Animal Dispersion in Relation to  
Social Behaviour*. Oliver & Boyd, Edinburgh and London.
- Yapp W.B. 1951. The population of rooks (*Corvus  
frugilegus*) in west Gloucestershire. II. *J. Anim.  
Ecol.*, 20: 169-172.
- Yarrell W. 1845 *A History of British Birds*. London. In:  
Coombs C.J.F 1978. *The Crows*. Batesford, London.

Zahavi A. 1971. the function of pre-roost gatherings and communal roosts. *Ibis*, 113: 106-109

Zimmermann D. 1951. Zur Brutbiologie der Dohle, *Coloeus monedula* (L). *Orn. Beobachter*, 48: 73-111. In: Coombs C.J.F 1978. *The Crows*. Batesford, London.





Frontispiece Cartoon from *Punch*, December 6th, 1881

## ABSTRACT

A thesis submitted for the degree of  
Doctor of Philosophy

On the social and genetic composition  
of rook *Corvus frugilegus*  
and jackdaw *C. monedula* flocks.

Ian G. Henderson

From December 1985 to December 1988, an study was made of the functional significance of rook and jackdaw flocks with a view to identifying reasons for intra and interspecific flock cohesiveness.

Flocks of rooks were investigated by way of behavioural observation for competitive heterogeneity and the impact of such on the dispersion of individual members. Thus, immature and adult birds were compared for their respective abilities to compete within foraging flocks.

Evidence for kin selection in foraging flocks was investigated in jackdaws by way of behavioural observation of individually marked (wing tagged) birds and using DNA fingerprinting to ascertain the degree of relatedness between associating individuals.

Interspecific associations were studied a) to identify the similarities and differences between foraging rooks and jackdaws and b) to provide hypotheses for functional flocking without cause for genetically related explanations.

Immature rooks did not forage as efficiently as adults in larger flocks, and thus selected smaller flocks, with higher immature:adult ratios. Adult interference was a possible cause of immature dispersion.

Kin selection was not found to be a significant component of co-foraging groups, though female jackdaws had higher than average levels of relatedness, possibly due to lower female than male dispersal.

The daily behaviour of rooks and jackdaws was remarkably similar and 80% of foraging flocks contained both species. Commonly co-occurring food resources, low direct resource competition and subsequent low levels of interspecific aggression were thought responsible for this association.

In conclusion, competitive heterogeneity was found in rooks that effected individual dispersion, discouraging young birds rather than encouraging them, to remain within the colony. Likewise little evidence of kin selection was found in foraging jackdaws. Rooks and jackdaws associated together frequently, on the basis, it was suggested, of where one species was feeding, the other was also likely to forage successfully.