

COLONIALITY IN THE ROOK (CORVUS FRUGILEGUS L.)

by

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To Frug

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ABSTRACT

Results are presented for data collected during an 18 month period for a population of the Rook Corvus frugilegus L. centred at 55° 44' N, 2° 54' W in southern Scotland, together with some data collected from nearby populations during a previous 12 month period.

The home range of Rooks varied between seasons. During the winter, Rooks which shared a communal roost utilized the same general area in flocks which were heterogeneous with respect to breeding colony membership. During the breeding period (March-June), individuals from each colony were more closely associated with the area close to their colony, and flocks were correspondingly more homogeneous with respect to colony membership.

Radio telemetry revealed that breeding males rarely returned to a field on subsequent feeding trips, but on those occasions where this did occur, it was to a field known to give a high intake rate of high quality food, and where the sub-lingual pouch was quickly filled.

Rooks were strongly attracted to feeding conspecifics, an effect which increased with the number of birds in a flock and the spacing between individuals at higher flock sizes. Birds were thought to gain from joining flocks because they reflect high prey densities. Rooks arrived at one out of sight rich food source in a pattern predicted by a model involving one Rook following others on flights from the colony. Arrivals at other sources within or out of sight of the colony showed a pattern which could be explained by simple local

enhancement to a feeding flock.

Departures from the nesting colony and arrivals at a feeding field showed temporal clumping. One possible explanation for this is that birds in a colony may have followed others to locate good feeding sites.

It is speculated that, by utilizing predominantly sub-surface food, flock feeding became essential for the evolving Rook, and that colonial nesting may serve to amplify the advantages of feeding by local enhancement. The change in food distribution consequent upon the change in the feeding habit seems a likely explanation for coloniality in the Rook.

Cost efficient methods for catching live individuals were developed so that these could be marked for individual recognition in the field. Subsequent behavioural observations enabled sexing of some marked individuals, and using discriminant function analysis of body measures, a means of discriminating between the sexes of this monomorphic species is now possible. This is described in a substantial appendix.

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CHAPTER ONE

INTRODUCTION

RELATIONSHIP BETWEEN FOOD RESOURCES AND SOCIAL ORGANIZATION

1.1 INTRODUCTION

The social organization typical of an animal species is that pattern which emerges as a result of the social relationships between individuals. By associating with conspecifics in a way which is typical for that species, an individual is assumed to be gaining genetic advantage relative to any alternative relationship, through the process of natural selection (Alexander 1974). The social organization typical of a species may vary from defence of an exclusive area by an individual or pair, in which all activities are performed, through to closely co-operating kinship groups who share most resources. The Rook Corvus frugilegus L., a large (325-560g) European and Asiatic crow of the family Corvidae, which is the subject of this thesis, falls somewhere between these two extremes, sharing its range and resources with other individuals, defending only the minimum area required for reproduction, its nest site. The aim of this thesis is to gain some insight of the advantages gained from such behaviour.

Conspicuous features of the biology of the Rook include its habit of nesting in colonies, feeding in flocks and forming large communal winter roosts (Coombs 1978). Determinants of coloniality and flock feeding in birds derived by the comparative approach (Clutton-Brock and Harvey 1979) suggest two over-riding factors, the distribution and abundance of food, and predator pressure. It is impossible to determine the original determinants of a particular social organization, because this may have attracted new functions made possible or necessary by the original form (Triesman 1975). But studies on social organization can at least identify current features

which may be of advantage to individuals participating and therefore acting to maintain the status quo.

1.2 DETERMINANTS OF SOCIAL ORGANIZATION

1.2.1 Predators

1.2.1.1 Predators and Nesting

The individuals of some bird species have been shown to benefit from improved protection from nest predation by grouping their nests into a colony. These species include the White Pelican Pelecanus erythrorhynchus (Schaller 1964), the Black Headed Gull Larus ridibundus (Patterson 1965) and the Bank Swallow Riparia riparia (Hoogland and Sherman 1976). In the Rook, there is no evidence of this occurring. In the former species, individuals appear to gain as a result of group attacks upon the potential predators, a feature lacking in Rooks (Roskaft 1980). Another potential advantage of nest groups derives from the arguments of Hamilton (1971) on the principle of the selfish herd, where each individual may gain advantage by decreasing the probability of itself being eaten by a predator (Foster and Treherne 1981). However, the sympatric, congeneric Carrion Crow Corvus corone, a bird essentially similar to the Rook and subject to similar predation pressures, defends an all-purpose nesting and feeding territory (Type A, Hinde 1955). The occurrence of widely spaced

individual nests in the Carrion Crow may be indicative of the relative unimportance of predator pressure on birds of this size in maintaining colonial tree nesting in the Rook.

1.2.1.2 Predators and Flock Feeding

Individuals are thought to gain advantage from joining with others when feeding by decreasing the chance of being eaten by a predator through one of several mechanisms. These include the greater combined vigilance of the group (Kenward 1978, Hoogland 1981), joint threat by group members (Kruuk 1972), decreasing the probability of being singled out from the group (Hamilton 1971, Foster and Treherne 1981) and by visual confusion of the predator (Neil and Cullen 1974, Foster and Treherne 1981). These factors apply also to colonial nesting.

Research has shown that birds in flocks detect predators faster (Powell 1974, Siegfried and Underhill 1975, Kenward 1978, Lazarus 1979, Bertram 1980) than solitary birds, and that this effect increases with the number of birds in the flock. These effects have been shown to be important in small wintering sandpipers, which when feeding alone are 3.2 times more likely to be eaten by a Merlin Falco columbarius than if in a flock (Page and Whitaker 1975). Whether Rook flocks offer a similar advantage is not clear, but it is quite common to see solitary Rooks feeding.

1.2.2 Food.

1.2.2.1 Food and Nesting Patterns

The effect of food dispersion pattern upon the nesting behaviour of a species could in theory act through the amplification of local enhancement. Local enhancement is a type of social learning which increases the likelihood of an individual responding to part of its environment as a consequence of the response of another to it (Hinde 1970). This would be important where birds exploit a food resource having a scattered mosaic distribution pattern of unpredictable, high density patches, occurring in a low density background (Fisher 1954). Location of the good patches may be costly in terms of time and energy used in search, some of which could be obviated by following individuals from the colony who had located food. Such a system could also apply to communal roosts (Ward 1965).

There is no field evidence which shows that nesting colonies or communal roosts act in this way, although there are several studies which produce evidence which is congruent with the hypothesis (Ward 1965, Krebs 1974). De Groot's (1980) study presents laboratory data which proves that the mechanism can actually work. Several studies setting out to test the idea in the field have produced negative results (Loman and Tamm 1980, Fleming 1981, Andersson et al 1981, Mock in press), but do not disprove the hypothesis. There are important problems with proving the hypothesis, and they are discussed further in Chapter Six.

1.2.2.2 Food and Flocking

Feeding flocks occur where the food utilized does not represent a defensible resource, in terms of the benefits accrued from the costs involved in its defence (Brown 1964). Sometimes where food dispersion patterns fluctuate, parallel fluctuations in territorial defence and flocking can be observed in many species (Snow 1956, Davies and Snow 1965, Walsberg 1968, Zahavi 1971, Davies 1977).

Within these constraints, individuals joining a flock may gain a positive feeding advantage in at least two ways. Firstly, as birds flying over a feeding flock are very likely to land either in or close by it, and the length of stay is longer on a food patch of high density, flocks will build up on better food areas (Krebs 1974, Barnard 1980, Waite 1981). Thus by landing with a flock, a bird stands a better chance of finding a good food source. This is local enhancement operating at the intermediate of three levels, the other two being attraction to a good general area in the home range, and to small patches within the flock area.

Local enhancement on the finest scale operates by concentrating attention on small patches within the flock area. When feeding on temporally and spatially unpredictable, clumped and cryptic prey, homing in on areas where others are being successful is the most cost-effective way of feeding. Studies supporting this view include those which involve computer simulations of feeding flocks (Thompson, Vertinsky and Krebs 1974, Chantrey in press), and those using real animals in the lab, controlling food dispersion (Krebs et al 1972, Krebs 1973, Smith and Sweatman 1974). Local enhancement operating at

the coarsest level is discussed further in Chapter 4.

1.2.3 Other causes for grouping.

Animals may associate for reasons other than food and predators. They may gather at a scarce resource, such as animals at a waterhole. Where a scarce resource is actually limiting, groups may form to acquire and defend that resource against other groups, as hypothesised for primates (Wrangham 1979a & b, 1980), lions (Bygott et al 1979, Koenig 1981a) and in birds (Koenig 1981b). Smaller mutualistic groups may form when a territorial individual may permit another individual onto its territory. This may be because the costs of decreased food abundance are outweighed by benefits derived from sharing territorial defence (Charles 1972, Davies and Houston 1981).

1.3 RELEVANT GENERAL BIOLOGY OF ROOKS.

It is unlikely that Rooks group together to defend a scarce resource from others. No inter-group encounters occur, and Rooks from neighbouring colonies overlap extensively in feeding range (Chapter Two) and are often seen in each others' colonies.

As predation acts are so rare, it would be difficult to quantify the effects of predation upon the nesting and feeding habits of Rooks. For this reason, the study reported here concerns the food finding advantages which could occur from flock feeding and colonial nesting. This section contains a review of those aspects of Rook

biology relevant to the results presented in later chapters.

1.3.1 Asynchronous hatching.

By commencing incubation before completion of the clutch, the female Rook produces a brood with a staggered hatching period. By the time all the eggs have hatched, a size hierarchy is apparent in the young, the first hatched being the largest (Lockie 1955). When feeding the young, the parents feed the most active first, giving food to the smaller, less insistent hatchlings only when the older ones are sated. In times of food shortage, the smaller nestlings die, and so the brood is reduced to a number which the parents can feed. In situations where nestling food has an unpredictable and fluctuating nature, and availability cannot be predicted at the time of laying, this behavioural mechanism has the effect of maximising individual fitness. The last laid eggs may therefore be viewed as opportunistic: if the food supplies are good, they may be successfully raised, but in most years they will not. It is possible that the cost of laying an extra egg is small compared with the increase in relative fitness of successfully fledging extra young.

Artificial manipulation of hunger in a brood of Jackdaws by Lockie (1955) showed that older nestlings received significantly more food than younger ones, whilst provisioning with extra food by Hamadani (1978) resulted in improved survival of the last hatched young. In Rooks, 90% of nestling deaths by starvation occurred in last hatched young (Lockie 1959). As a result, natural selection will favour those parents who can supply food to their nestlings at a faster rate, for

this will result in greater relative reproductive output.

1.3.2 The food of nestling Rooks.

By restricting the oesophagus of nestling Rooks with a tight fitting collar, swallowing of food is prevented and food given by the parents can be analysed. Earthworms (Lumbricidae) were shown to form most (up to 80% by volume) of the diet of Rooks in Oxfordshire, with the proportion of leatherjackets (larvae of Tipula spp.) increasing throughout the nestling period (Lockie 1954). Other animal food included lepidopteran larvae, beetles, weevils and lycosid spiders (i.e. the general surface invertebrates of grassland). In one year, which was cold and dry, earthworms were less available (see section 1.3.3) and where possible were replaced by other invertebrates. Much of the shortfall still remaining was made up with grain, which resulted in an increase in nestling mortality, probably because of the lower protein content of the food (Owen 1959).

The components of the diet are confirmed by Feare et al (1974) in N.E. Scotland, who shot 7 breeding males returning to their nests with full sub-lingual pouches. Preliminary studies by collaring nestlings in Staffordshire have revealed a nestling diet of earthworms and leatherjackets (Waite pers. comm.).

1.3.3 Patterns of earthworm availability

In order for the advantages of local enhancement for food finding in Rooks to be shown, it is necessary to demonstrate that their principal prey is cryptic, and occurs in unpredictable, high quality patches. As earthworms are the principal component, aspects of their availability are reviewed here.

Earthworms account for over half the biomass of the soil fauna (Satchell 1955), but their density and distribution are extremely variable. The largest influence on earthworm numbers is soil type (Evans 1948), which is modified by such factors as topography and agricultural practice. The effects on population size and structure appear to be mediated through pH (Bodenheimer 1939, Guild 1951a, 1951b, Satchell 1955), moisture (Heimburger 1924, Bodenheimer 1939, Gerard 1967) and organic content (Satchell 1955, Svendsen 1957a, Boyd 1958). Land use also has an effect on population size, with permanent pasture supporting the largest numbers and biomass (Reynoldson 1955, Reynoldson, O'Connor and Kelly 1955), which may be six times the size of populations supported by disturbed soils (Atlavinyte 1964). Earthworm populations increase rapidly under a grass ley so long as the land use remains unchanged, in the first year populations double in size to levels approximately one third those found under permanent pasture (Reynoldson 1966). Thereafter, populations continue to increase at least until 6 years after seeding with grass (Heppleston 1971). Subsequent use of the permanent pasture can also affect numbers. Grazing and addition of fertilizer increases population size (Heath 1962), sheep grazing having little effect when compared to cattle grazing (Satchell 1955, Houston 1977a).

So on a coarse scale, great variations occur between fields in the numbers and biomass of earthworms in the soil. However, even within fields densities vary greatly, for instance cow pats attract earthworms such that populations beneath them may be at twice the background level (Svendsen 1957a, Boyd 1958). Variations of earthworm density within a field may approach 50% either side of the mean (Evans and Guild 1948), so by selectively using only permanent pasture fields, Rooks can only increase the likelihood of finding a very good patch, but not guarantee it. Guild (1951b) after his finding of a five to six fold difference in population densities within an upland field in Scotland, ^{concluded} that each field should be regarded as containing a series of earthworm populations. He also concluded, apart from pH, moisture and temperature that soil depth, texture, food supply, herbage cover, basal mat and exposure can effect population densities within a field (Guild 1952a, 1952b). Atlavinyte (1964) also found four fold differences in the same sloping field depending on which level on a slope was sampled.

Within these general constraints of earthworm population densities, a number of factors may temporarily affect the availability of earthworms to Rooks, i.e. the depth at which they are found. These involve the drying influences of wind (its direction, temperature, relative humidity) sunshine (morning or afternoon), and those features which will increase availability, such as rain showers and manure spreading. Earthworms are very mobile, migrating horizontally and vertically when conditions become unfavourable (Heimbürger 1924, Guild 1952a), and vertical downward migration due to the drying effects of the wind or sun will make earthworms unavailable to Rooks. Because of the many variables, locations of very good patches will be constantly

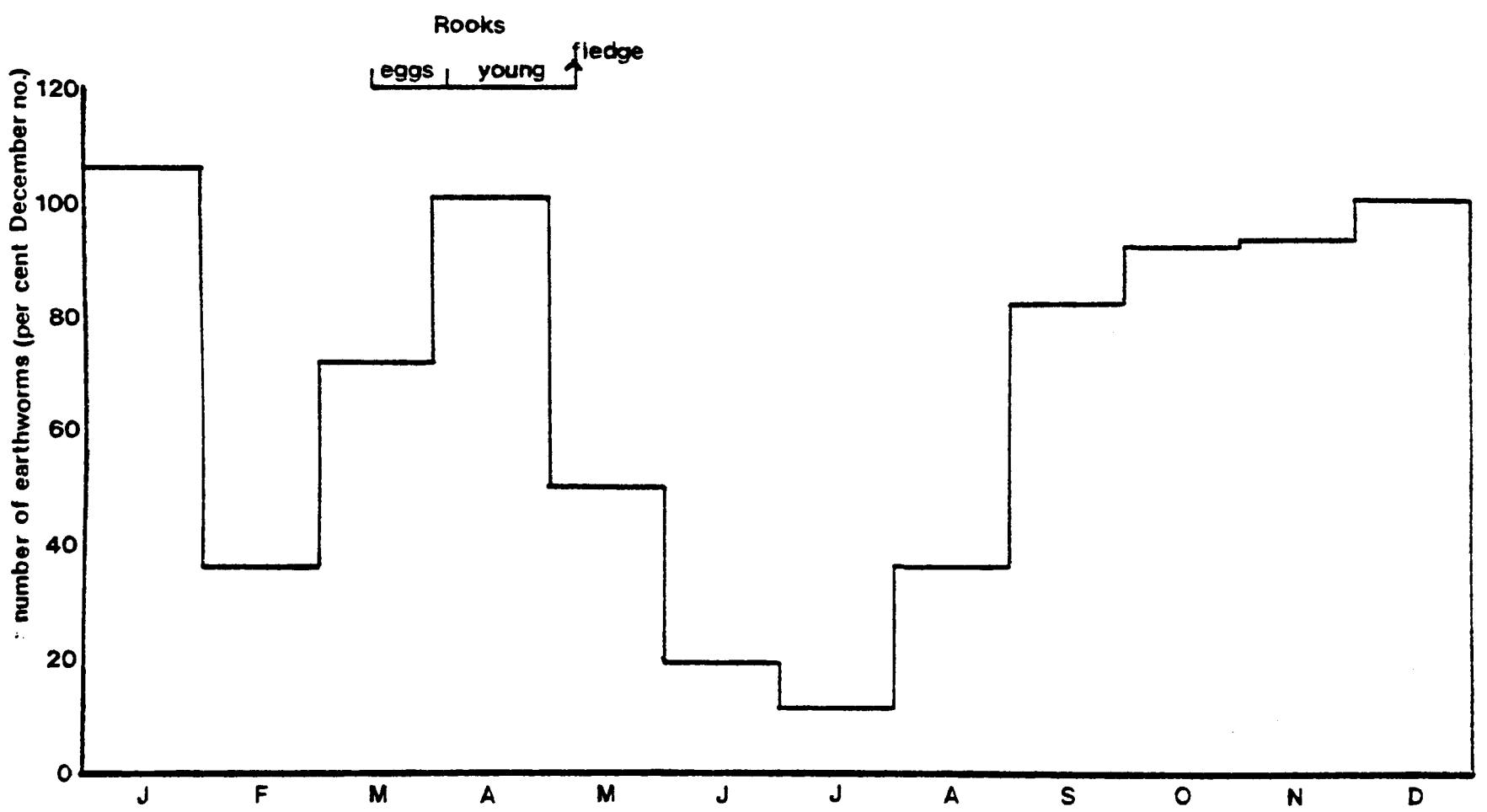
shifting. Evidence of the time scale of shifts of densities is limited to differences between months ⁱⁿ particular fields (Feare et al 1974, Waite 1981), and no sampling programme has been able to demonstrate shifts of densities on an hourly basis. However, further evidence of significant clumping within and between fields, and changes over time are presented by Waite (1981).

Figure 1-1 shows a generalised availability histogram of earthworms throughout the year, ^(top 3" soil) calculated from the data of several authors, together with the first onset of the various breeding stages of the Rook, and reveals the coincidence of breeding with springtime peaks of earthworms. The earthworm numbers were calculated expressing each monthly figure as a percentage of the December figure in an attempt to standardise for habitat and sampling technique differences. All information published about the availability of earthworms shows a cycle with peaks in December and April, a major trough from late May until September and another in February (Evans and Guild 1948A, Boyd 1958, Davies and Snow 1965, Reynoldson 1966, Gerard 1967, Dunnet and Patterson 1968, Heppleston 1971). The summer trough is caused by the low rainfall and high temperature, that of February due to low soil temperatures. In the summer worms may aestivate at depth, and become unavailable to Rooks.

Predation upon worms can also affect their numbers. By preventing Golden Plovers Pluvialis apricaria feeding on a field for 22 days, Bengtson et al (1976) demonstrated that when the birds were taking only 5-6 worms each per day, the earthworm density was halved, from 238 to 107/m². Rooks exert a much greater predation rate; during the breeding season males made on average 52.6 visits a day to the nest

Figure 1-1

Seasonal cycle of earthworm availability with first onset of breeding stages in the Rook. Figures for earthworm numbers from various sources detailed in text, expressed as percentage of December figure.



with approximately 11.8g food on each trip (Feare et al 1974). This is approximately 610g per Rook pair per day and may be an important factor in modifying numbers available.

Less is known about the distribution of leatherjackets, but they also to have a highly clumped distribution (Tinbergen 1976, 1981). Leatherjackets are extremely susceptible to drought and in the final instar to parasites (Barnes 1941). As with earthworms, they are sensitive to changes in the moisture level of the soil and will migrate to damper patches, where they occur in densities ranging from 20 to 50/m² (Barnes 1949) and from 6 to 69/ m² (Tinbergen 1981).

1.4 SAMPLING BEHAVIOUR

The best food patches are unpredictable in location, the food is cryptic, and inability to find sufficient can cause sequential death of nestlings. Food finding is therefore likely to affect the relative fitness of males. It is on the male that the full burden of feeding young occurs, for he feeds the female on the nest whilst she incubates, and must supply all the food for the young in the first three weeks of life, making on average 52.6 visits per day, bringing a daily total of around 610g of food (Feare et al 1974).

Nothing ^{was} ~~is~~ known about foraging patterns of individual Rooks, and Chapter Three presents results for the first radio tracking study on this species, and gives some idea of the sampling range of two adult males. The results suggest that memory of previous intake rate is an important feature in the decision of where to go to feed. However,

the results presented in Chapter Four suggest that there are other factors which might influence the future foraging location. Since the density of the food collected for young Rooks (whether sub-surface or in herbage) and exploitable densities cannot be detected from the air, any other visible manifestations of high prey densities are likely to be detected by an aerial Rook. The presence of other Rooks feeding is probably the best indication of food, and the reasons for this are also discussed in Chapter Four.

Chapter Two reveals that the range of breeding male Rooks is extensive, and so searching its entire home range for feeding flocks is a time and energy consuming process. A way of obviating extensive search is to utilize the predominant flight lines of Rooks from the colony, thus using the 'group knowledge' of the best food locations. This has been briefly mentioned in section 1.2.2.1 under the topic of local enhancement on the coarse scale, and will be considered in relation to results presented in Chapters 4 and 5, and the ideas presented in Chapter 6.

1.5 THE ROOK IN CONTEXT.

It is often enlightening to compare similar species utilizing different resources, and ^{observing} the reaction of different species to similar ecological conditions, in order to see the effects of environmental factors on social organization. For instance, Phainopepla nitens, a small (24g) frugivorous and insectivorous bird, defends an exclusive territory when feeding on defensible clumps of mistletoe berries, but when it breeds again later in the year in a

different habitat utilizing a series of unpredictable and quickly depleted food sources, the birds feed peaceably together and defend only small nesting territories (Walsberg 1968). With the Rook being one of two exceptions in its genus, through not defending an all purpose nesting and feeding territory, it is intriguing to speculate why this is so from a comparison with the other groups of Corvus species occurring around the world. The results of such a speculation are presented in Chapter Six.

1.6 SUMMARY

1. Social organization can be determined or maintained by a number of factors. These include predators, food distribution and competition for limiting resources.
2. This study concentrates on the food finding advantages of flocking and colonial nesting.
3. General features of the Rook's biology - serial brood reduction, and a food supply which is cryptic and of unpredictable location - suggest that improved food finding abilities would be of advantage.
4. The thesis therefore investigates how the social organization may improve food finding abilities of individuals in the context of its food distribution, and includes a comparative review of how other species react to different food dispersion patterns.

CHAPTER TWO

THE USE OF SPACE

2.1 INTRODUCTION

In this chapter I describe the ranging behaviour of a population of Rooks, and those factors which appear to structure such movements. One of the main aims of this study was to investigate how Rooks locate good sources of food, and the results reported in this chapter reveal how individuals of known breeding location utilize the environment throughout the year. In later experiments involving members of different rookeries, it was important to have an understanding of how members from different rookeries utilized the study area. The chapter begins by describing the pattern of daily movements shown by Rooks as described by past workers, and how my study population fits into this picture. This is followed by a description of how individuals of known breeding locations utilize the environment,

2.2 THE DETERMINANTS OF THE HOME RANGE OF ROOKS

The daily movement patterns of Rooks in Britain are ^{constrained} by two factors. One is the nesting colony, or rookery, to which an individual is attached if breeding, and the other is the communal roost used by that colony. The relative effect of these varies much with season but it is very pervasive and results in a highly structured pattern. For clarity, I will start by describing the effect of the nesting colony.

2.2.1 The rookery

The rookery is a group of 3 to 3500 nests in the tops of a group of trees (Patterson et al 1971). Although the members of a colony will only be breeding from March until June, daily visits by colony members and others occur throughout the year (Marshall and Coombs 1957), except for mid-summer and particularly bleak periods in mid-winter. Regular morning and evening visits occur, with sporadic visits at other times, and the activity whilst in the rookery depends on the time of year and to some extent upon the weather. From morning and daytime visits, the Rooks generally disperse to the surrounding fields to feed, and after evening visits either fly direct to the communal roost or to pre-roost assemblies (see section 2.5). As each rookery has a fairly fixed membership, such regular returns to a fixed point will influence to some extent where individuals concentrate their activities.

2.2.2 The communal roost

During the breeding season, those Rooks which are breeding pass the night in the rookery. Outside this period they utilize communal roosts, which are joint roosting places used by members of a number of rookeries. The catchment area of a roost is very variable in both size of population and area. Rooks may have a roost situated at their rookery, or they may fly up to 32 km (Harrison 1931) and population estimates of roosts range from 6750 up to 65000 (Patterson et al 1971).

A typical movement pattern is difficult to describe as much seasonal and year to year variation occurs. During the winter period (c. November-February) birds will depart from the communal roost at dawn and generally head for their respective rookeries, often accompanied by Rooks wintering in the area. They may form post-roost assemblies or even land in other rookeries en route, but normally they will appear in their own rookery, except during adverse weather conditions in winter, and during mid-summer. After the Rooks have gathered in the rookery, they will disperse to surrounding fields to feed, returning to the rookery on occasions during the day.

Return to the roost during the afternoon follows a pattern of coalescence which results in all the Rooks in the catchment area being assembled in a field close to the roost at dusk. ^{The birds from} ~~a~~ number of rookeries will gather together at a primary assembly point close to all the rookeries and each roost catchment area has a number of these primary assembly areas. In turn, the members of a number of these primary assemblies will move roostward to a secondary assembly point. This process continues until all the Rooks from a given catchment area are gathered close to the roost just before dusk (Coombs 1961b). It is not clear what happens to wintering birds not breeding in the area, it is possible that they attach themselves to one of the breeding groups. The roosting pattern shows much variation. The assembly points may vary in location (Burns 1957) as may the communal roost itself, for instance summer and autumn roosts may form on a more local basis, whilst non-breeders may form their own roost during the breeding season, or they may continue to use the winter roost (Coombs 1961b, Patterson et al 1971). True winter roosts may remain static for decades or they may move frequently (Patterson et al 1971, Munroe

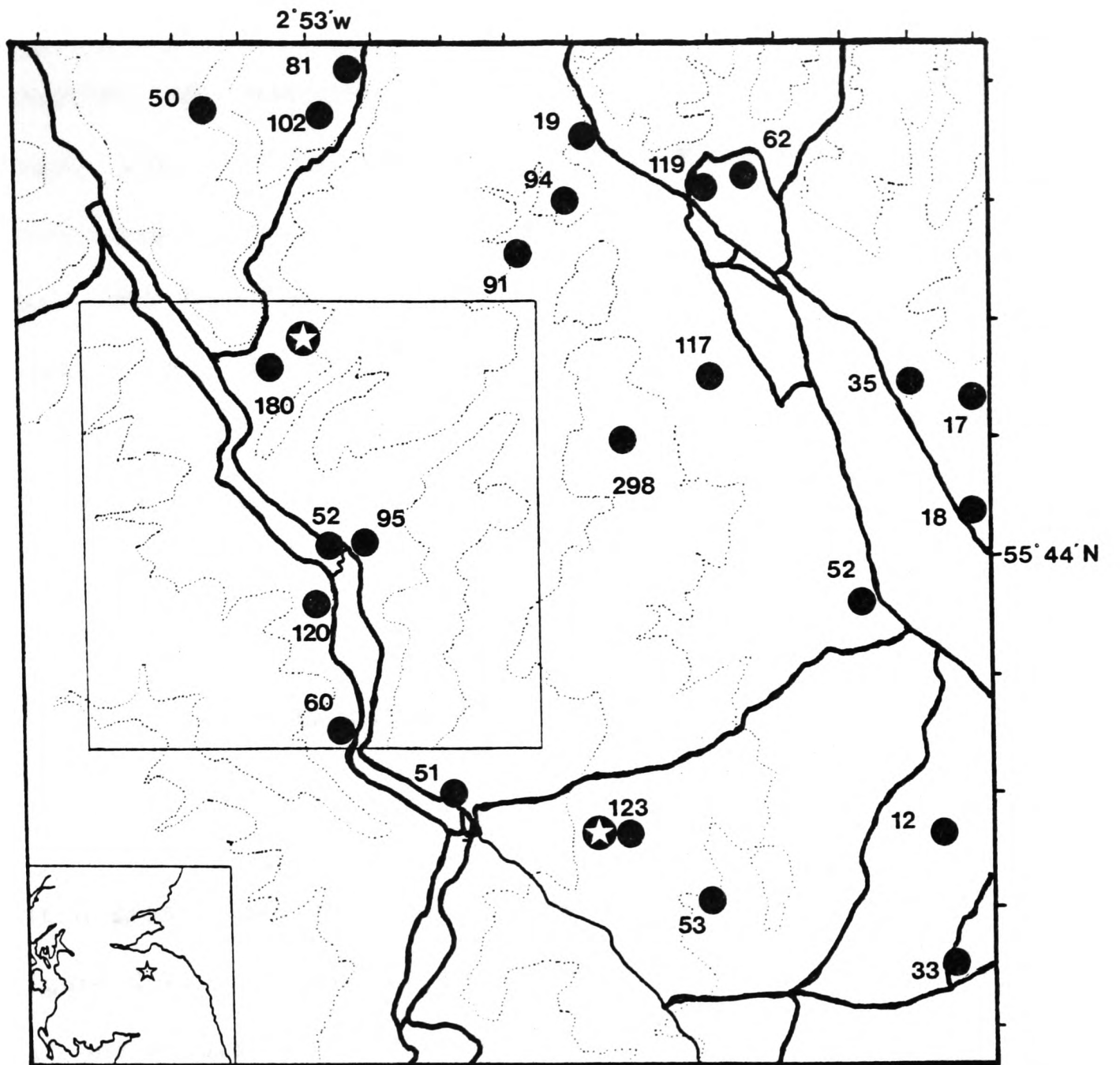
1948, 1971, 1975). Post-breeding, pre-winter communal roosts form during the summer, when rookery attendance is rare. The systematic afternoon regroupings typical of winter are therefore not shown during this period.

2.3 THE STUDY AREA

The extended study area is shown in Figure 2-1. The insets show its location and also that of the intensive study area. It is situated in the Borders Region of southern Scotland, 20 miles south of Edinburgh. The traps described in Appendix One are situated at 55°44' N, 2°54' W. Approximate proportions of field types in the intensive study area are 42% pasture, 25% cereals, 20% rough grazing, 10% woodland and the remaining 3% other crops, mainly turnips and other brassicas grown for animal feed. Spring sown oats and barley are the main cereals grown, and beef cattle and sheep are the only stock animals grazing the valleys and high ground. Altitude varies from 250m in the valley floor to 500m on the hill tops. The intensive study area covered five farms and emphasis on *land use* varied considerably from farm to farm. Fields varied in size from about 4 to 30 ha, although some much larger ones of rough pasture extended around some hill tops. The result for the Rooks is that a wide variety of foods are available. Extensive pasture is present to obtain invertebrates for the young, plenty of stubble is available for grain in the autumn and winter, and stock is fed outside all winter, providing easy pickings for the Rooks. The intensive study area extended over approximately 30 km² and contained approximately 550

Figure 2-1

Extended study area, with its location in Scotland (small inset)
and intensive study area (large inset)



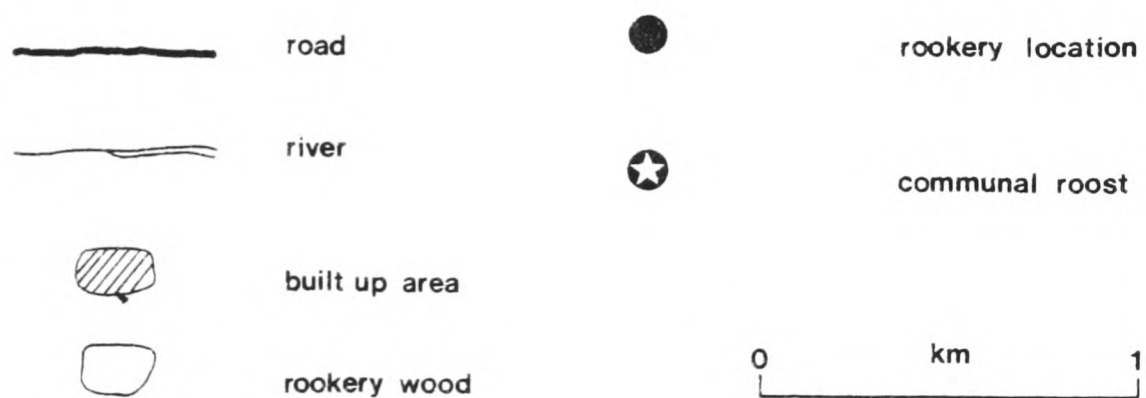
breeding pairs of Rooks. The extensive study area extended over 200 km² and contained approximately 2000 breeding pairs. This gives a breeding Rook population of 40 Rooks/km² in the intensive study area, and 20 Rooks/km² in the extensive study area. In addition, there are considerable numbers of non-breeding adults and juveniles. This density is very high. Feare et al (1974) found a density of 24 nests/km² in their study area in the Ythan Estuary in N.E. Scotland to be the highest yet recorded. So the study area is by all measures densely populated with Rooks, although precise figures will be affected by the siting of the study area with respect to the dispersion of the rookeries.

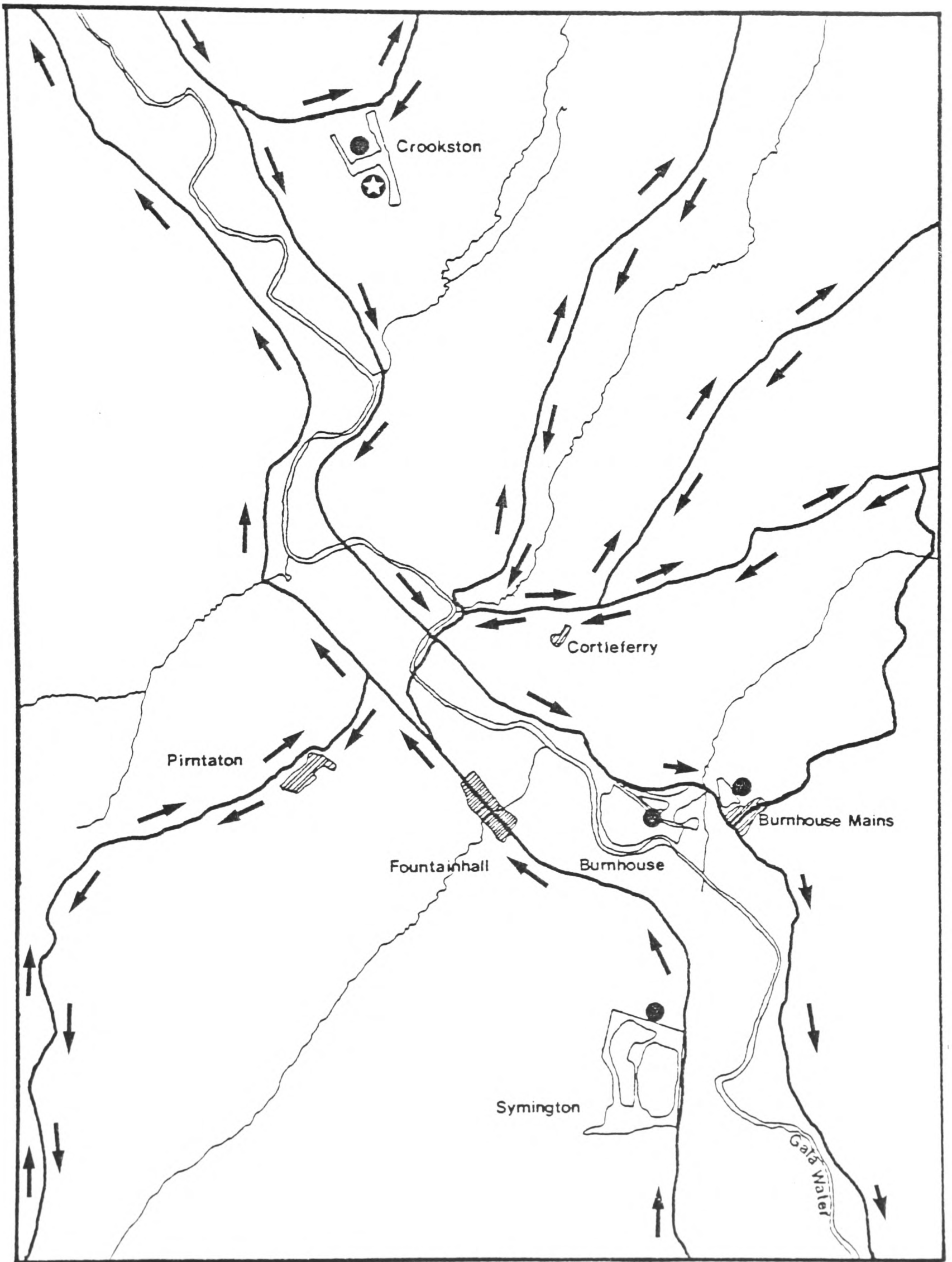
2.4 METHODS

The Crookston roost, used by all the Rooks in the study area is shown in Figure 2-2. It was not discovered by Munroe (1975) but he predicted that one should exist in this area (Munroe pers. comm.). These qualitative data were collected on 14 afternoons in November 1978 and 1979. Initial data were obtained in October 1978 when the Cortleferry assembly point was noticed and followed by steps until the roost was located. Thereafter, the origins of birds in each assembly area were located by going to their area of origin as postulated the previous day. Occasional checks were also made during December to March, and data were supplemented when in relevant areas during roosting time. Subsequent roosting behaviour of ^{rooks in} the extensive study area was made by watching from a 400m summit in the centre of the area coupled ^{with} by observations made from roads. An understanding of roosting

Figure 2-2

Intensive study area, showing location of roost and rookeries of the study population, and the transect as indicated by the arrows on the roads and tracks





movements was felt to be desirable if only to understand the occurrence of certain large aggregations of Rooks.

Colony membership was determined by systematic scanning of rookeries with a 15-60x zoom telescope and noting the presence of wing-tagged birds. Details noted included whether the bird was paired, whether it was defending a nest area and its general behaviour. The rookeries in the intensive study area were observed on most days from January to July in 1979 and 1980, and at any other time when Rooks were in the nesting colonies. Rooks seen repeatedly in the field, but never defending a nest in the rookeries, were classed as 'non-breeders'. Whilst it is possible that such birds may have bred in unobservable nests, other signs of breeding, such as a male seen filling his sub-lingual pouch or either parent with dependent young, were used to verify the status of birds. If these were seen, records were altered retrospectively.

To determine use of the study area by birds from different rookeries a standard circuit was driven as indicated by the arrows on the roads and tracks shown in Figure 2-2. 78 circuits were completed on the dates given in Appendix 4, between April 1979 and May 1980. The time of day of the circuits was not constant, and was varied between 0800 and 1400 hours. Using a 15-60x zoom telescope all flocks seen were counted and scanned for tagged birds whose identity was noted. Identification was possible up to a maximum of 500m in ideal conditions, although normally ^{WAS} less than this. Distance was a limiting factor in identification on a few occasions only, normally due to mist or heat haze, the dissected nature of the landscape being

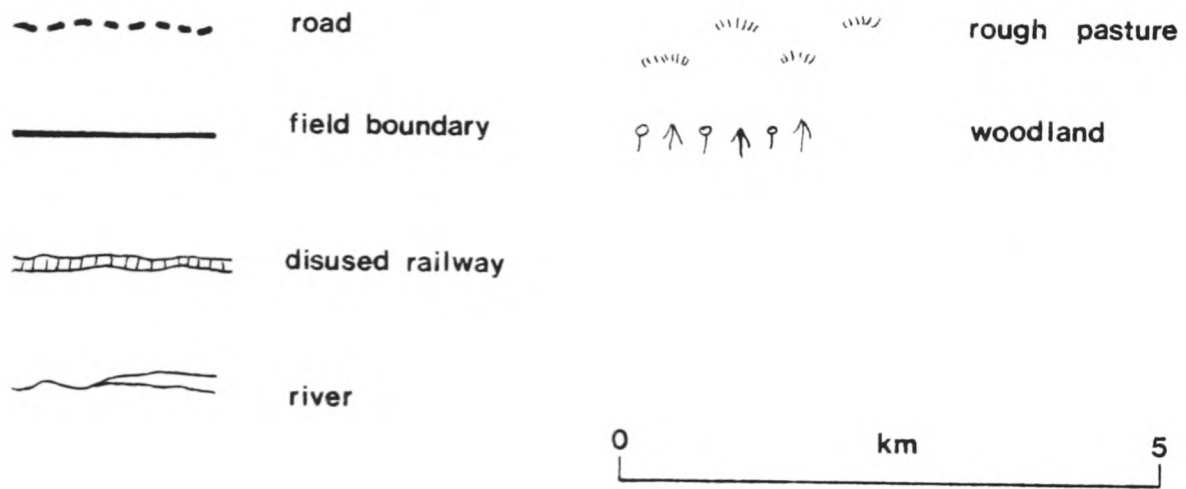
a greater problem. Figure 2-3 gives some idea of the field boundaries of the intensive study area, each field being numbered on a field map so that accurate location of feeding flocks could be quickly noted for subsequent analysis.

2.5 ROOSTING MOVEMENTS.

The movements of large numbers of Rooks from November to February are summarised in Figure 2-4. The Rooks from Symington, Burnhouse and Burnhouse Mains rookeries all utilized the same winter roost, and they gathered at an assembly point by Cortleferry Farm . They assembled here either by flying directly en masse from their rookeries or gradually moving in from surrounding fields. The factors affecting this were not studied. This assembly was normally joined by large flocks, totalling well in excess of 1000 birds, from the east of the study area. ^{THE TOTAL ASSEMBLY} would depart at about 30 minutes after sunset, its destination being a high ridge overlooking the roost wood (Figure 2-4). At this location the gathering would be joined by others from the north and east. Entry to the Crookston communal roost was extremely variable. Sometimes all the birds would lift as an orderly ribbon and settle in the trees, at other times they would wheel in the air to be joined by other groups previously on the ground, to drop very suddenly into the trees. At still other times they would move down onto the fields surrounding the roost wood, eventually moving rapidly up into the trees when the light was nearly gone. Factors affecting these behavioural differences were not

Figure 2-3

Field boundaries of the study area. Each field was numbered so that precise location of feeding flocks could be quickly noted



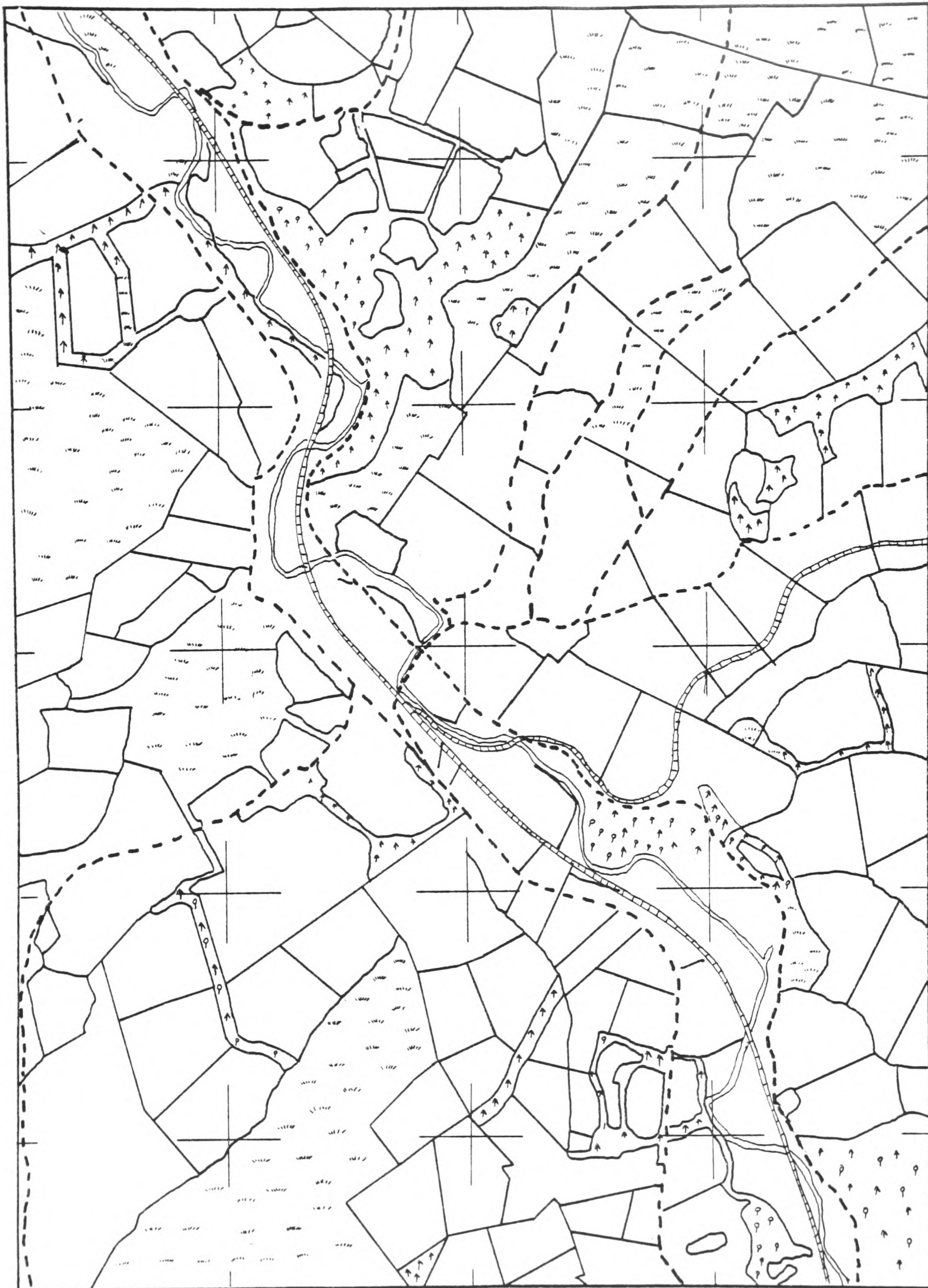
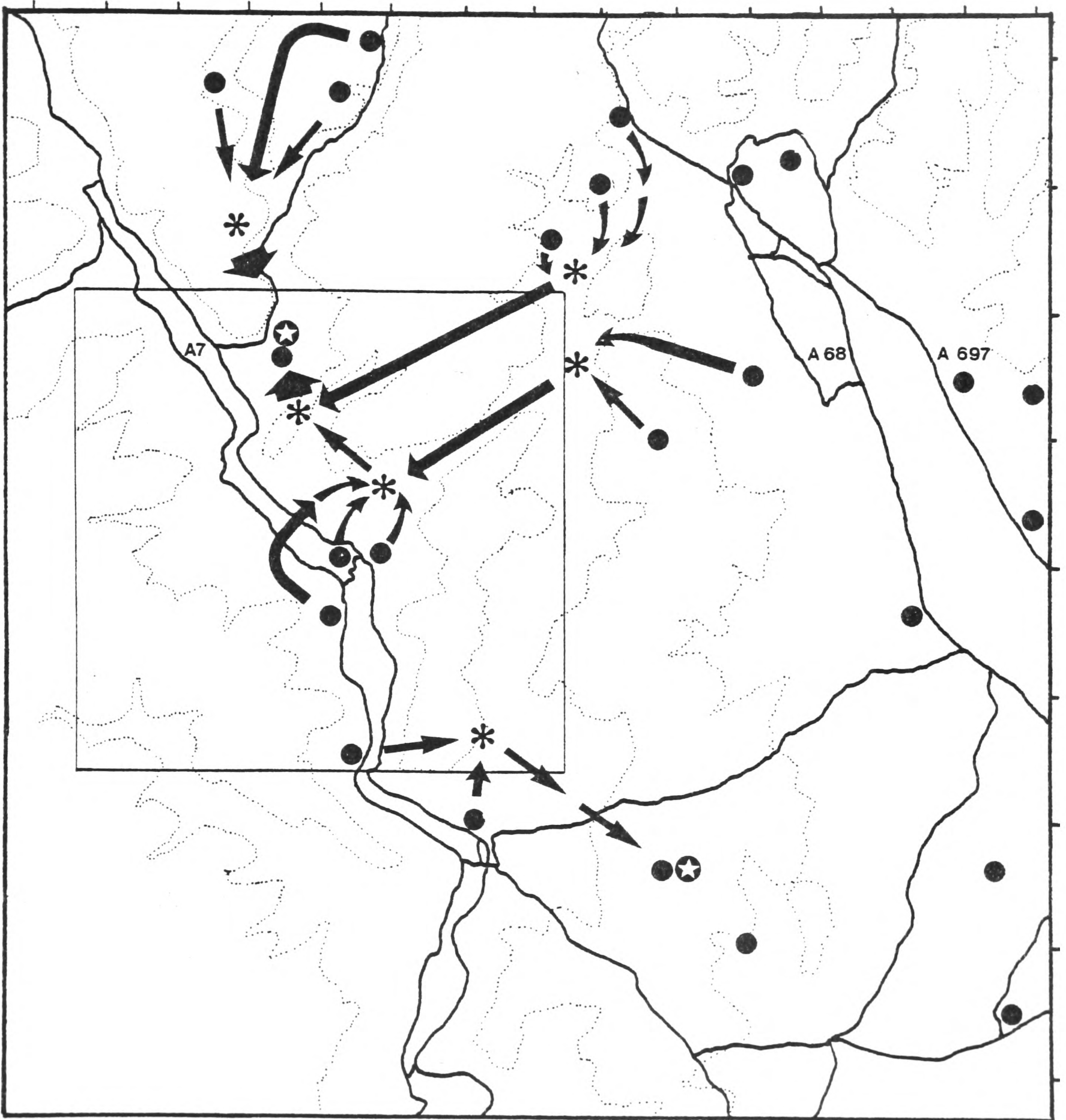


Figure 2-4

Summary of winter roost flights for the *INTENSIVE + EXTENSIVE STUDY* areas





Drawed in

studied. Similar variations in behaviour have been studied in Pied Wagtails by Fleming (1981), who offers no explanation for their occurrence. The mean time of entry into the roost was 39 minutes after sunset (range 13-65 minutes, S.D.=5.0, n=14). This is thought to be controlled mainly by light intensity (Swingland 1976), although other factors are involved since low light intensities, sufficient to cause early roost entry in the afternoon, do not cause this during the morning. Also, birds attached to a particular rookery a long distance from the roost begin the assembly pattern earlier in the day than those close to the roost (Coombs 1961b, Swingland 1976).

In

February, Rooks would fly directly to the roost from their rookeries. In early February, the colony would move as an integral unit, but as the month progressed individuals appeared to become more reluctant to leave, so that small groups departed roostward over a period of about 45 minutes. By mid March, when the first females are laying, breeding birds would roost in the colony. Non-breeding birds were known to roost in the Crookston communal roost as well as in a young pine plantation in Fountainhall village. The latter was first located as a result of returned tags found by local people, and was later confirmed by observations in late evening. No post-breeding summer roosts were located, although in September and October, woods by Burnhouse Mains were used as an autumnal roost by rooks from Symington, Burnhouse and Burnhouse Mains rookeries. Birds arrived here in small parties from the surrounding fields instead of flying to Crookston.

Pre-roost gatherings did not have an effect on the circuit results as most were done between the hours of 1000 and 1400, therefore not

including the later afternoon gathering groups. Dates when circuits were undertaken are listed in Appendix 3.

2.6 RESULTS ON FEEDING DISPERSION

2.6.1 Introduction

Sightings of tagged rooks are summarised in Figures 2-5 to 2-9. Each figure contains data for sightings of one class of bird (non-breeders, or breeders from Symington, Burnhouse, Burnhouse Mains or Crookston), and compares the March-June breeding period with the November-February winter period. Circuits made during the July-September summer period were too few to give meaningful results. Birds were very dispersed during this period, and a complete circuit gave very few sightings of tagged Rooks, which were often out of range for tag identification.

2.6.2 Seasonal differences

Sightings of Rooks breeding in the study area, as well as birds present throughout the study but not seen to breed, showed a more southerly trend in feeding areas during the breeding period than during the winter. Thus, fewer birds are found north near the winter roost at Crookston during the breeding season, and even those nesting there fed further south as breeding began. Those breeding to the

Figure 2-5

Sightings of tagged non-breeding birds on transects for breeding
and winter periods

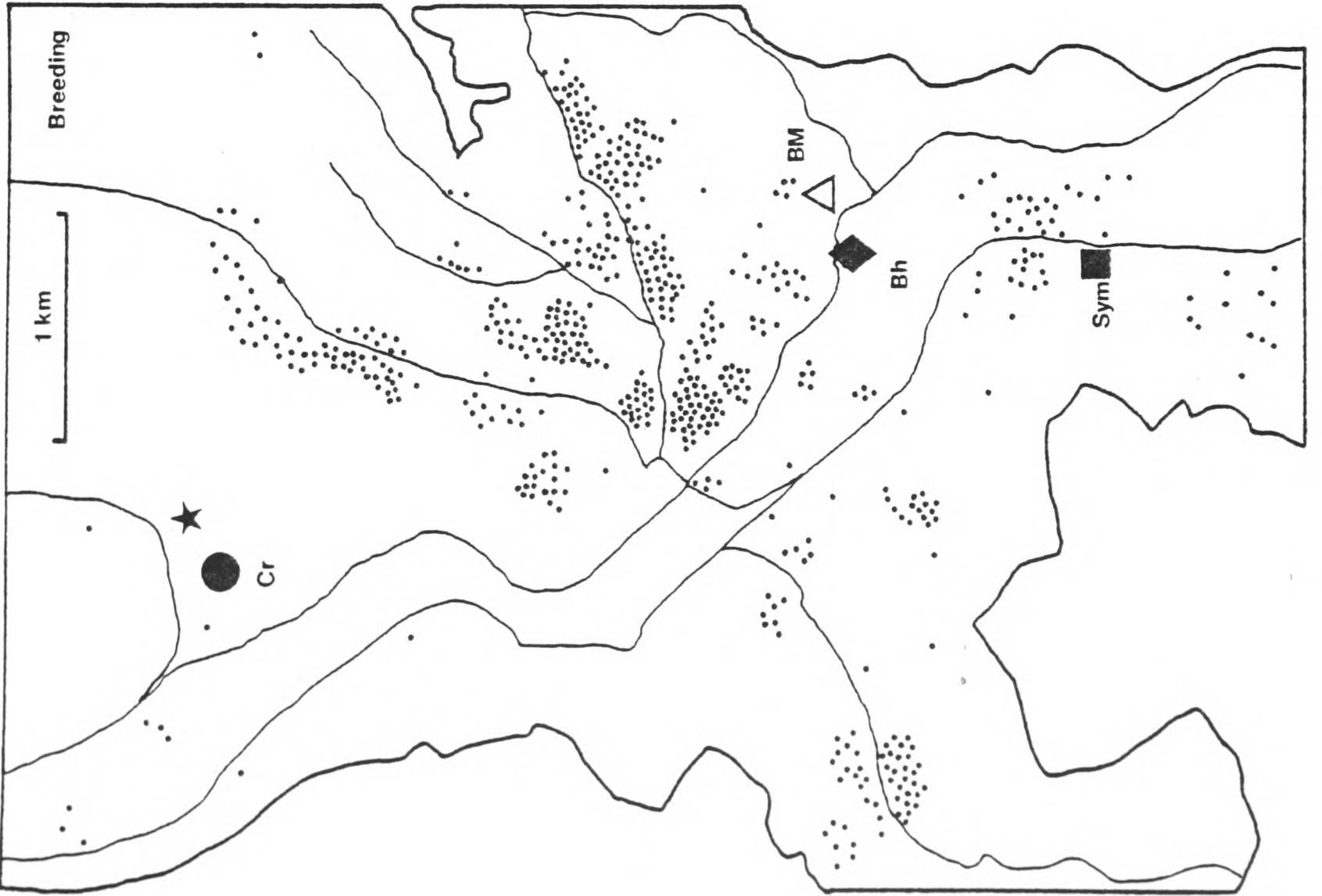
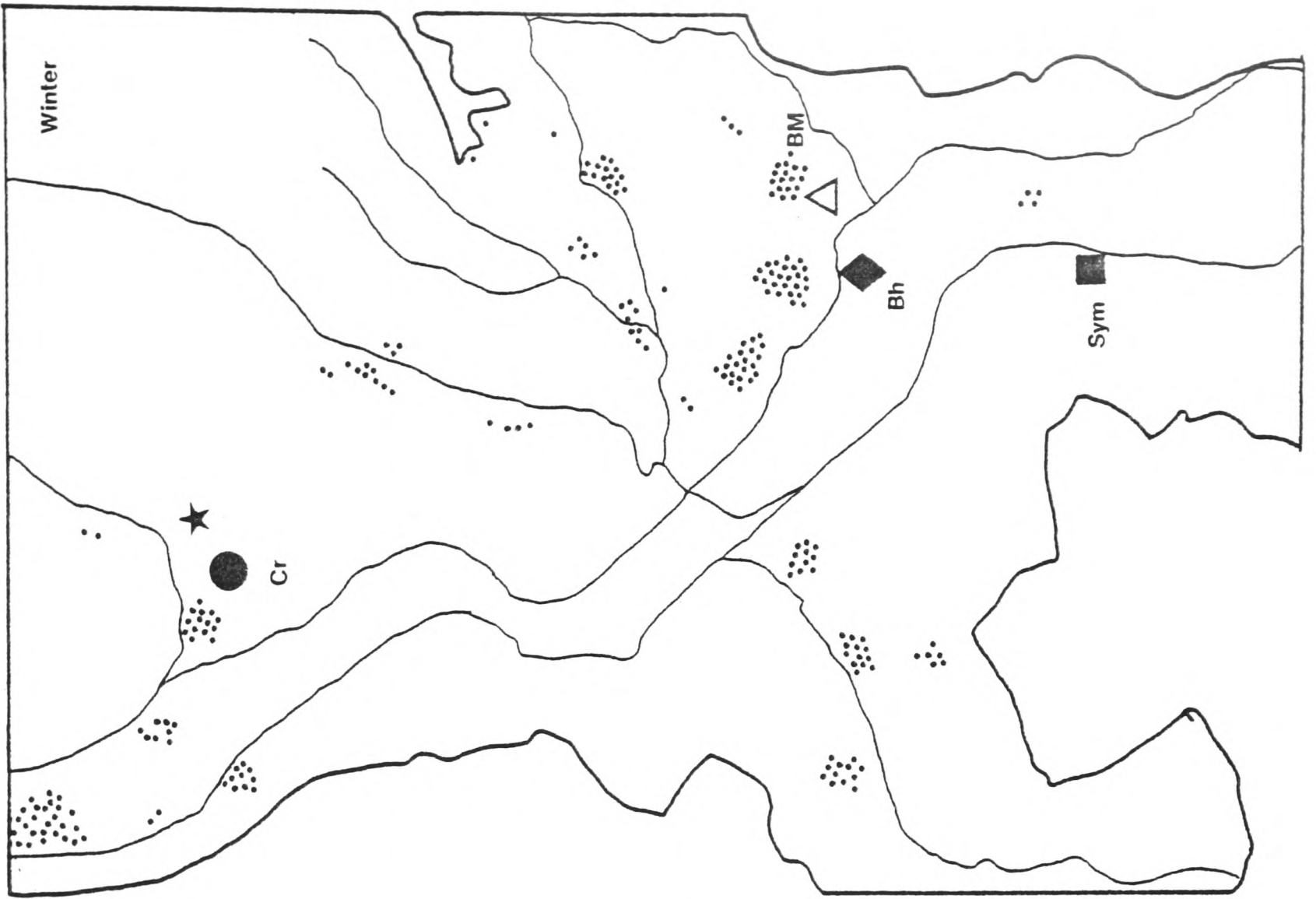


Figure 2-6

Sightings of tagged birds attached to Crookston rookery,
made during the breeding and winter periods

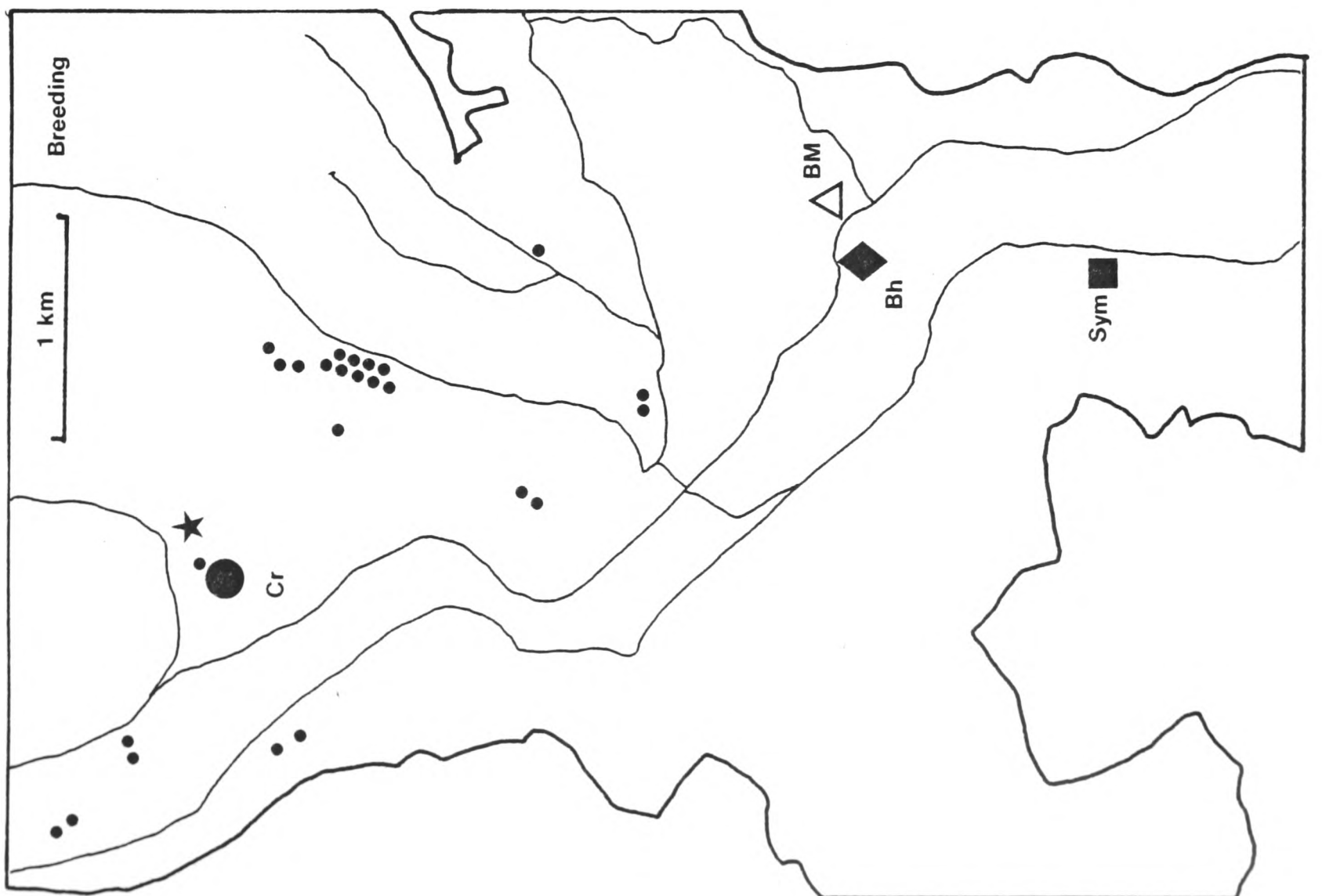
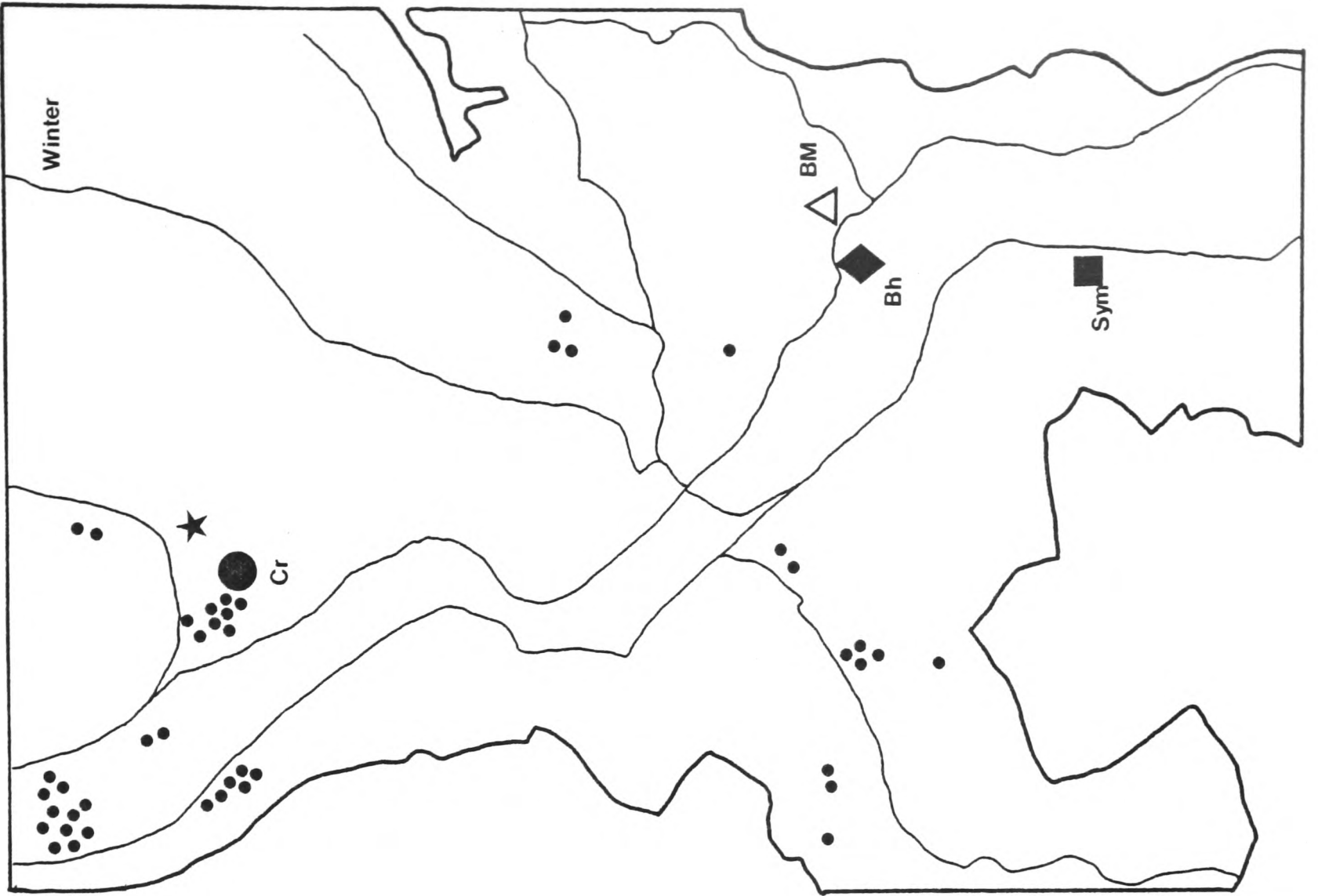


Figure 2-7

Sightings of tagged birds attached to Burnhouse rookery,
made during the breeding and winter periods.
Open diamonds are for the eastern nest group

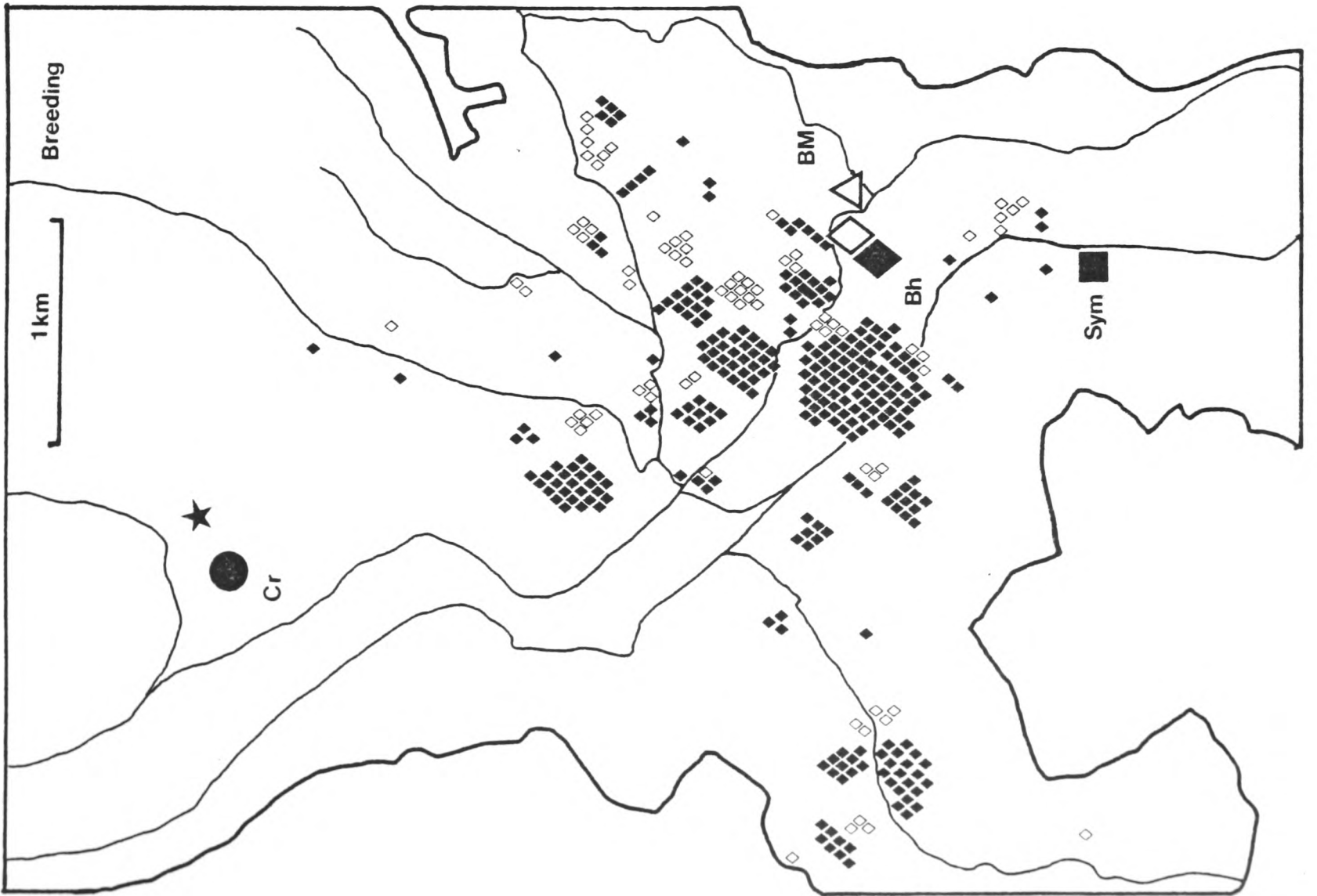
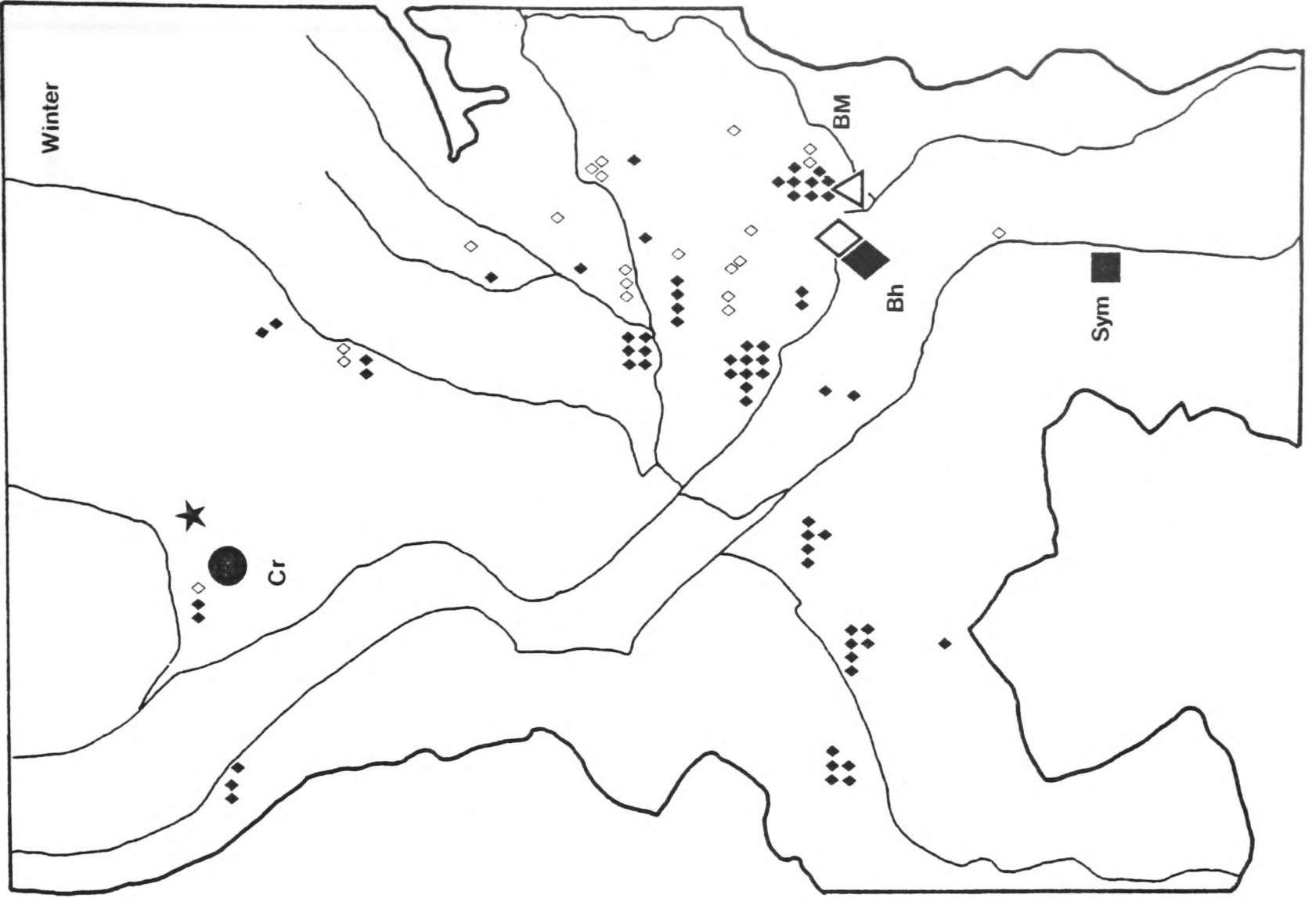


Figure 2-8

Sightings of tagged birds attached to Burnhouse Mains rookery,
made during the breeding and winter periods

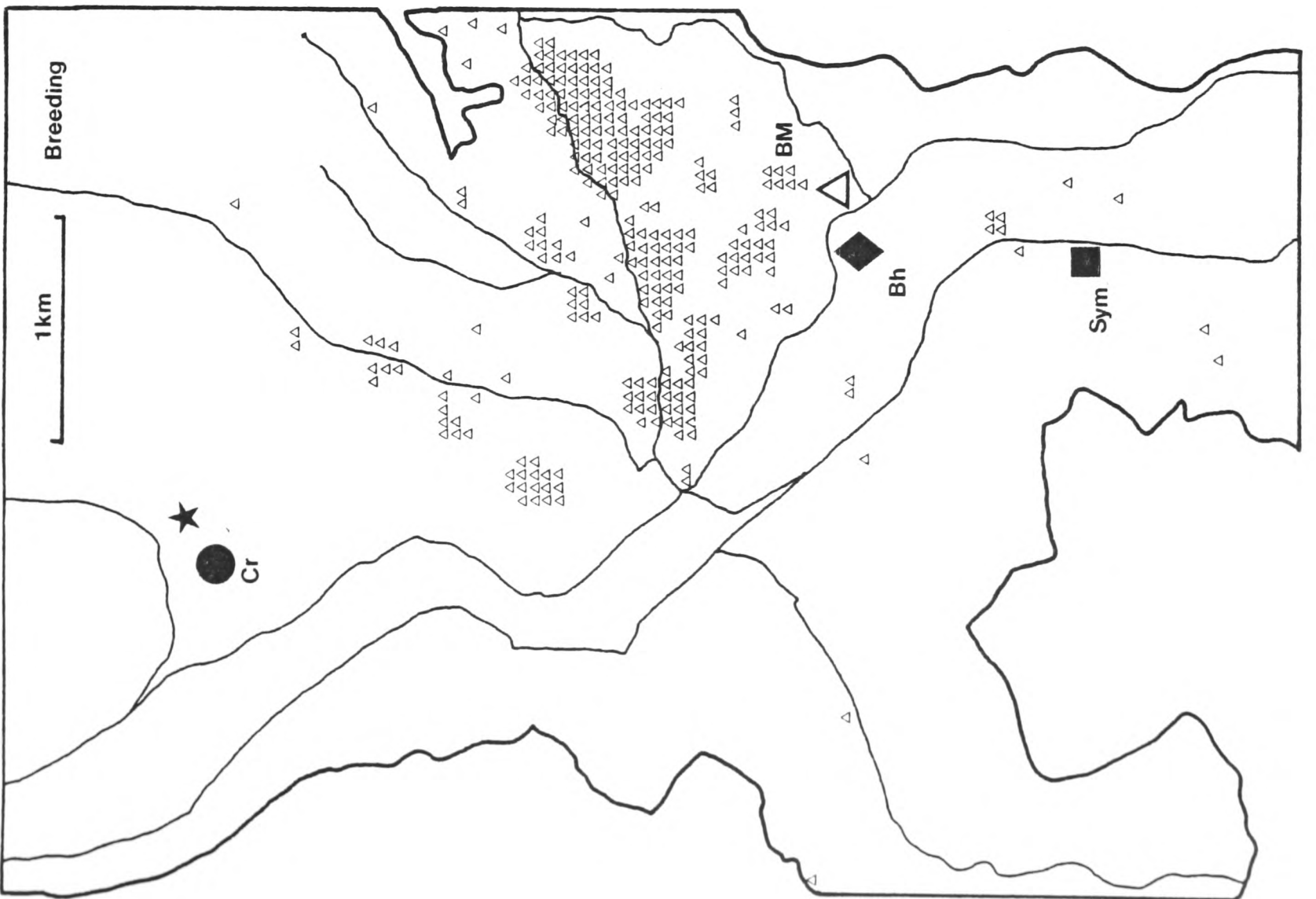
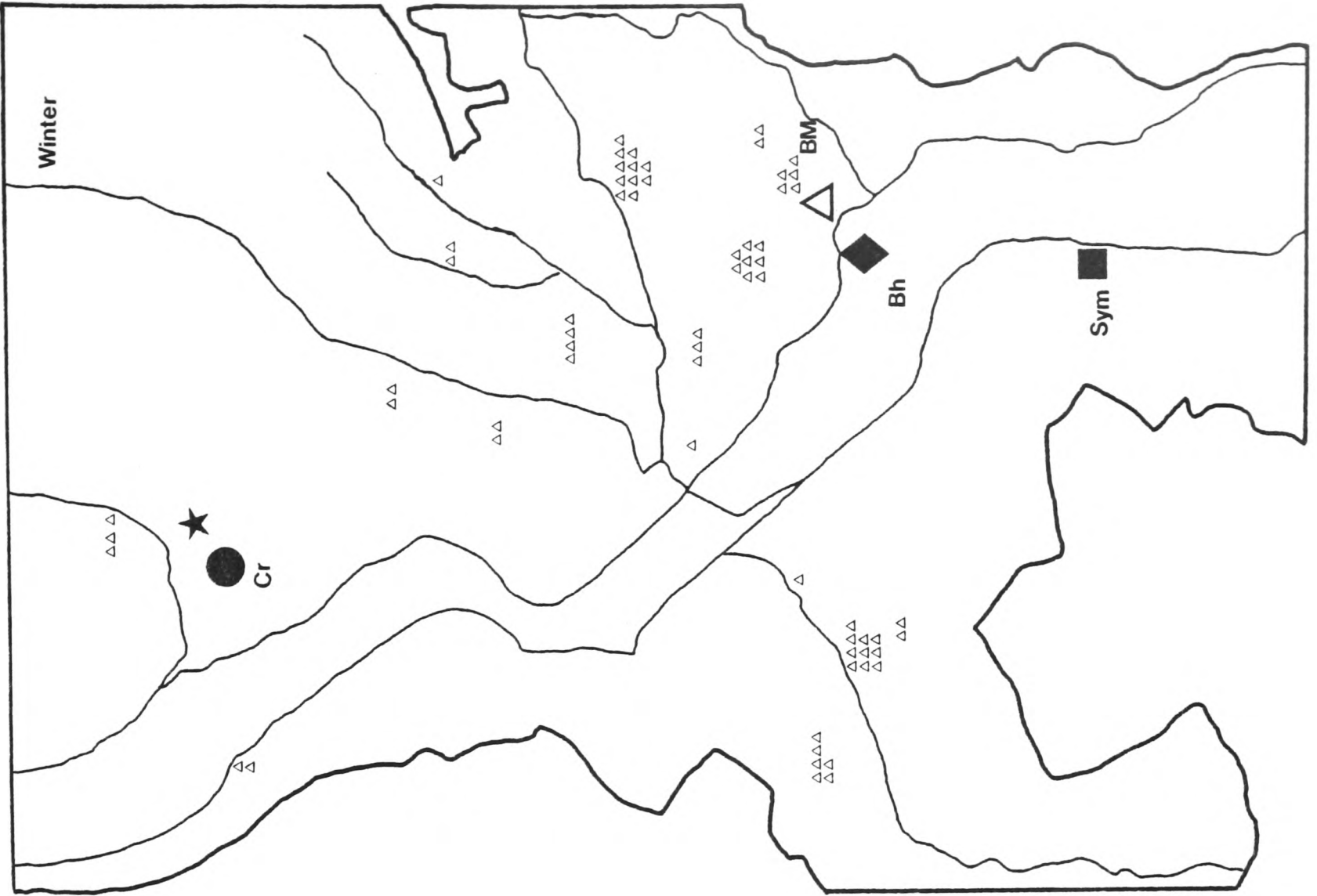
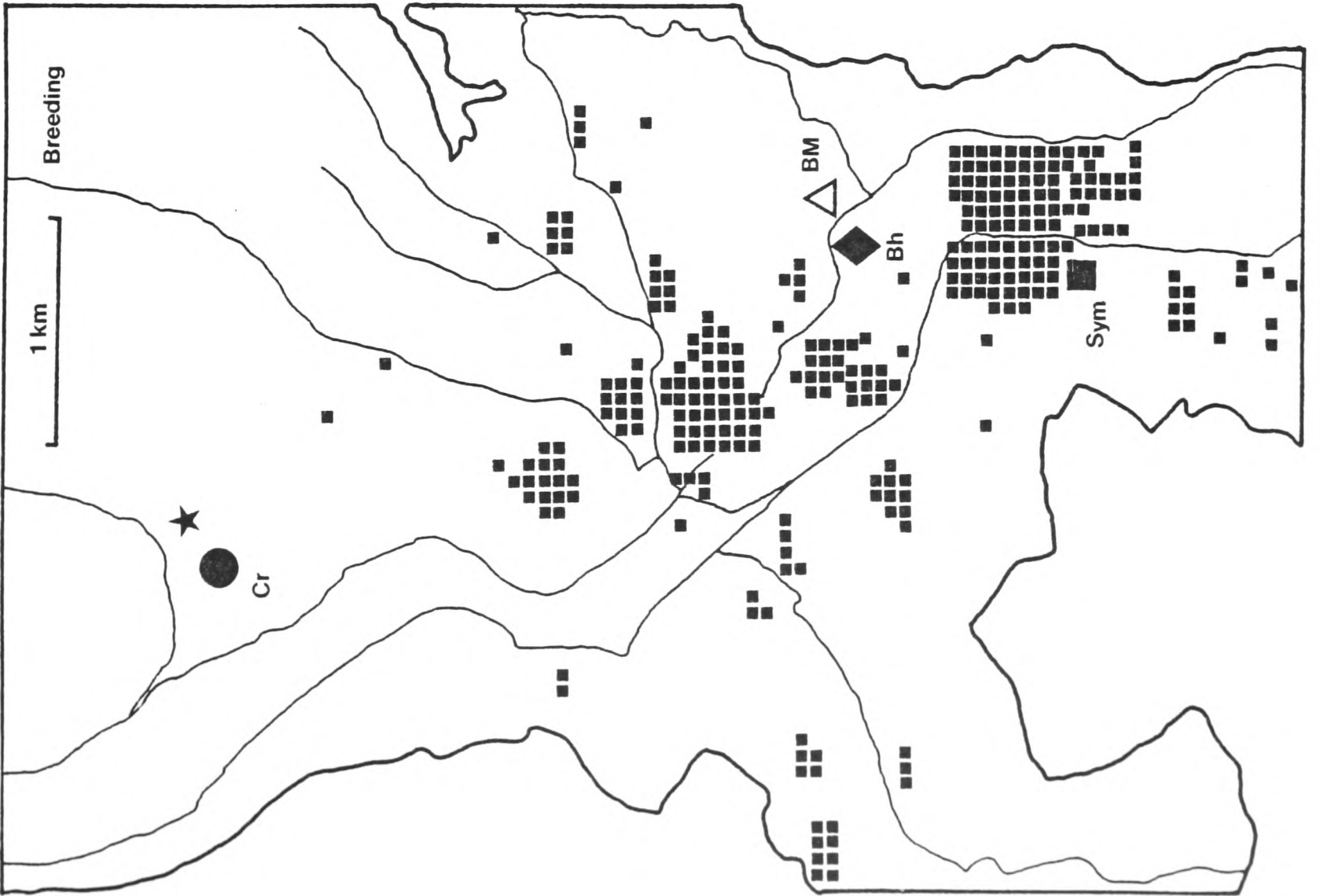
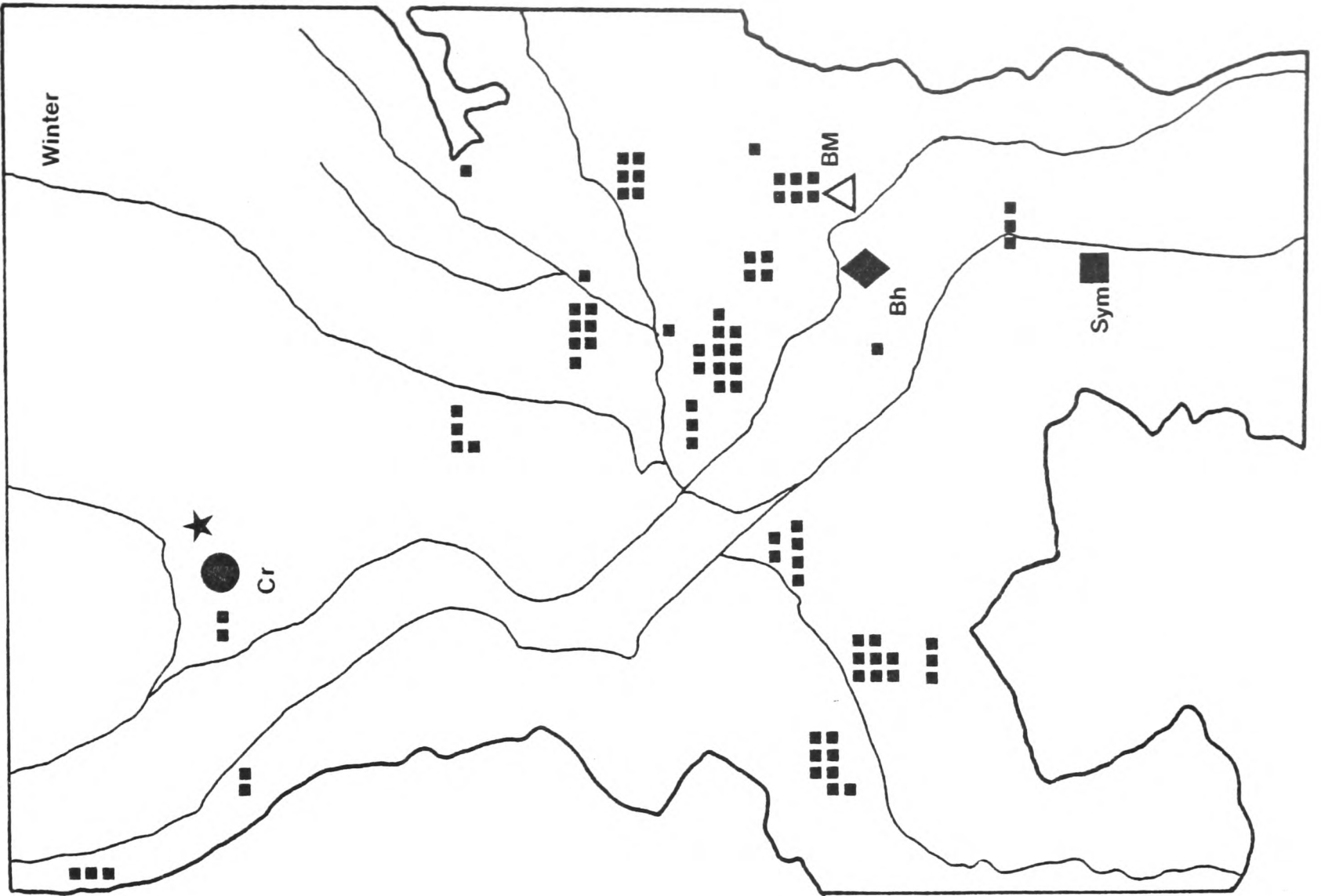


Figure 2-9

Sightings of tagged birds attached to Symington rookery,
made during the breeding and winter periods



south at Symington were never seen close to their colony during the winter, but fed very close to it in the spring. Those of intermediate breeding location, Burnhouse and Burnhouse Mains, fed more locally during breeding season, and were not found near the roost.

Such a trend is to be expected, since attachment to the roost is cut during the breeding season, and attachment to breeding colony is strengthened (see also Coombs 1961b). The most striking difference, shown by Symington birds, may be a reflection of farming practices, for livestock near their rookery is kept under cover during the winter. Livestock around the roost area is kept and fed outside all winter, so the shift probably reflects the availability of food, although no systematic study was made of this. Livestock food always had numbers of Rooks associated with it, and was probably a very important food supply in winter, especially when all other sources were under snow.

2.6.3 Colony differences.

During the winter, Burnhouse and Burnhouse Mains Rooks were found in the same areas as each other, and were also accompanied by Symington birds, see Figures 2-7 to 2-9. Crookston birds fed to the north, with a small amount of overlap.

There were colony differences during the breeding season, birds from specific colonies showed certain directional tendencies in their feeding ranges. Crookston birds fed in a more northerly part of the study area when compared to birds from other rookeries, see Figure

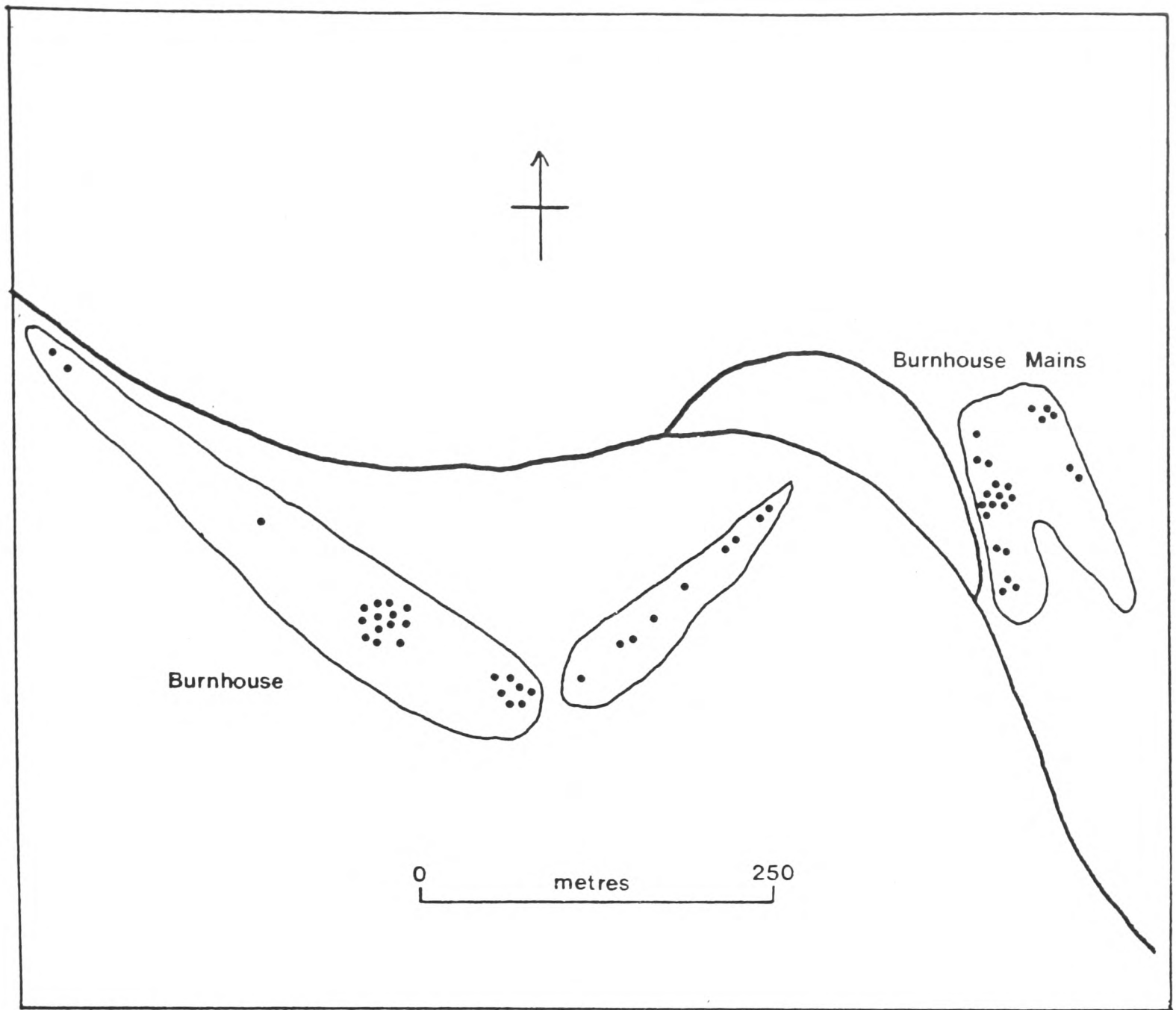
2-6. Burnhouse birds fed more centrally with a trend westward and northward from their colony, see Figure 2-7. Burnhouse Mains birds fed predominantly to the north of their colony, with an eastward bias, see Figure 2-8. Symington birds accounted for most of the sightings in the south of the study area, but could also be found spread throughout the areas used by all the other colonies, see Figure 2-9.

The Burnhouse and Burnhouse Mains colonies offer an interesting insight to the effect of nest site on feeding location. Figure 2-10 shows the relative positions of nests in these two colonies. The feeding areas used by these two colonies show a central shared core area, but with an eastward drift for members of Burnhouse Mains, and a westward drift for those from Burnhouse. A similar effect resulted at Symington: the sightings of birds to the far south of Figure 2-9 are mainly from a detached south section of the rookery. There is some evidence that even within a colony birds from certain groups of nests tend to feed more in some areas than in others. To illustrate this, I divided Burnhouse rookery into two parts for comparison, and the results can be seen in Figure 2-7. A greater proportion of the sightings of the eastern group of trees occurs in the eastern section of the study area than birds from the western section. This group of trees acts as a bridge between Burnhouse and Burnhouse Mains rookeries, see Figure 2-10. Yeates (1934) mentions an identical finding, how birds from certain sections of his study rookery tended to use specific areas more than others.

So during the breeding season, the birds from each colony have a home range which overlaps to a variable extent with the home range of birds from neighbouring colonies, who share the same communal roost.

Figure 2-10

Map of the proximity of Burnhouse and Burnhouse Mains rookeries
and the location of nests of tagged males



- location of nest of tagged bird

The location of the nest site within the colony is correlated with the *greater* use of certain areas of the colony's home range than others, so it seems probable that the colony home range is not used equally by all members of that colony.

Figure 2-11 attempts to summarise the seasonal differences of home range. These lines have been drawn to include all fields where more than 5% of sightings of tagged birds from each rookery have been seen. Overlap of feeding areas of the three different rookeries is almost complete during the winter, but shows more separation during the breeding period, with a core of overlap in the centre of the study area. Patterson et al (1971) using a similar methodology, found a shift in feeding areas during the breeding season, but their results were not interpreted in relation to use of the roost. The non-breeders in my population appeared evenly spread over the study area, occurring at all of the major feeding areas of the breeding Rooks, see Figure 2-5, suggesting that the sampling method was unbiased.

Representation of the results in this way has a number of limitations. Although it does reveal a shift of feeding areas, misleading results may occur from a number of sources. Large winter post-roost gatherings which never fragment, and super abundant food sources occurring in spring which all rookeries locate, are just two examples. For this reason, further quantification of sightings was desirable to see how rookery membership affects feeding areas and how this varies with season. This will be considered before possible reasons for this seasonal change in range are discussed.

Figure 2-11

Summary of seasonal range differences of birds
from each of the rookeries

2.7 DIVERSITY INDICES

2.7.1 Background

Application of Chi-square and 3 way analysis of variance statistics to the data is complicated by multiple resightings of certain individuals (i.e. samples not independent) and alternative analytical methods were considered.

Figure 2-11 suggests that the dispersion patterns of Rooks during the breeding period is affected by breeding location, and that as a result seasonal differences in range occur. Members of each rookery tend to be seen more frequently in certain fields than others during the breeding season, and so flocks seen in these fields should show less heterogeneity with respect to rookery membership of individuals when compared to winter flocks. Certain predictions therefore follow concerning the diversity of rookery membership of flocks, how this varies between seasons, and throughout study area within a season. For example, the central overlap area during the breeding season of figure 2-11 should have more diverse flock structures than say the area around Symington rookery to the south, for the former is being used by all rookeries at all seasons.

To measure this diversity, at the suggestion of W.D. Atkinson I used the Shannon-Weiner diversity index, as presented in Atkinson and Shorrocks (1977), and for each of the 259 feeding flocks observed a

diversity index was calculated. So that use of areas within the study area could be compared I divided this into five areas, see Figure 2-12. In itself, such a division is problematic, since any such arbitrary division could be made to suit the analysis. However, these areas were worked out from Figure 2-11, itself compiled by sightings of tagged Rooks from known breeding locations and so were considered to have real significance for the Rooks. Thus area 1 is an area of overlap of rookery ranges during the breeding season, the others showing varying degrees of overlap between particular rookeries. Rooks breeding in Crookston in 1980 were eliminated from the analysis because numbers were few, and comparison between years would have been impossible because of the different numbers of rookeries used in computing the diversity indices between years. No tagged Rooks bred in Crookston in 1979.

The use of the diversity index is being made only to quantify the apparent differences in range between Rooks from different colonies, and between seasons, as shown in Figures 2-5 to 2-9. ^{It} does not provide qualitative information about the contributory factors of the index. As a technique, it provides information only on how diverse flock structures are, and for information for why an area has diverse flock structures, reference must be made to Figures 2-5 to 2-9 and to the discussion in section 2.7.3.

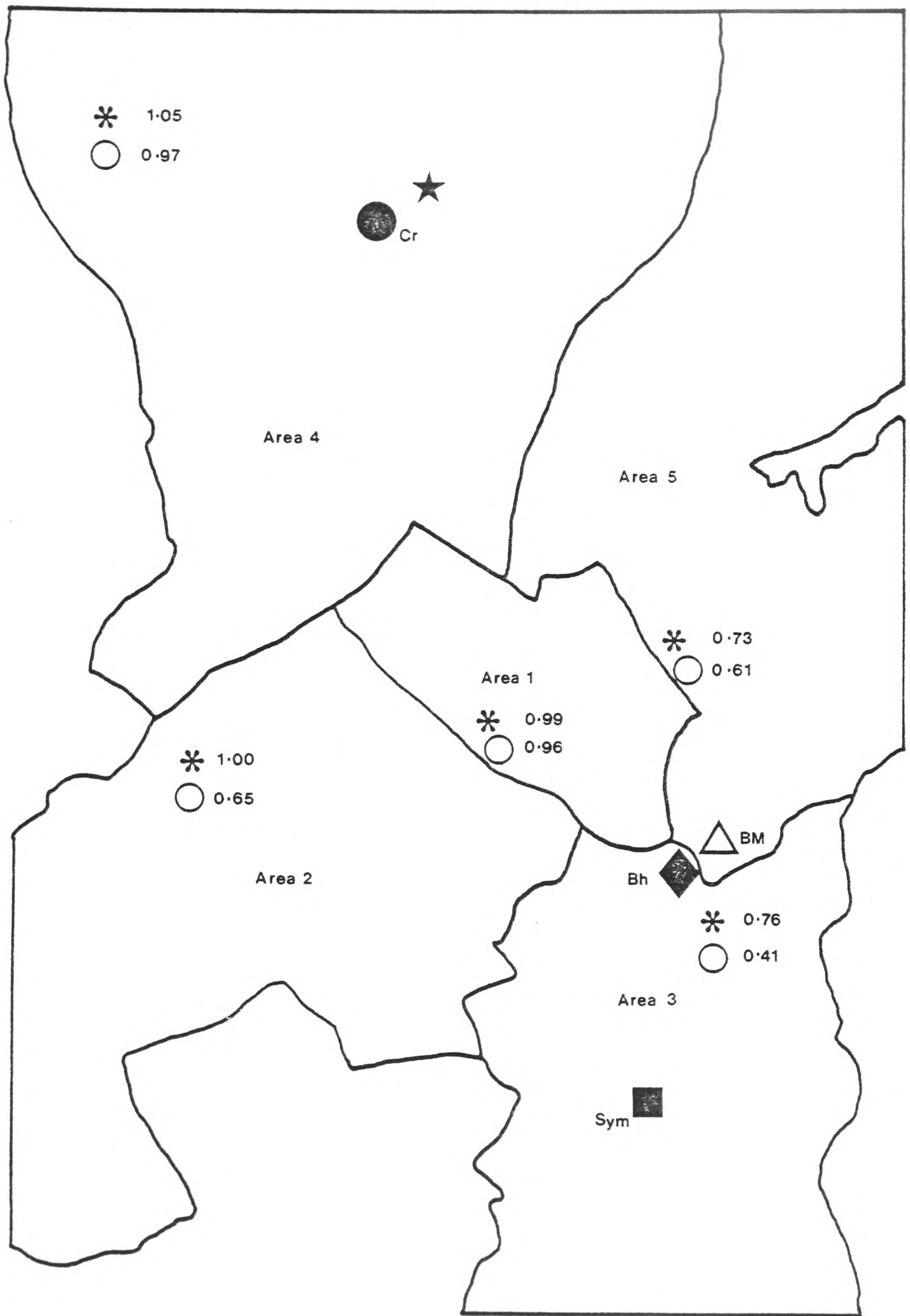
Although diversity indices are thought to have a normal distribution (Bowman et al 1971), I checked my own with a programme taken from Sokal and Rohlf (1969) which revealed them as non-normal. The diversity indices were successfully transformed by squaring

Figure 2-12

Division of the study area into areas for
Diversity Index comparisons.

Asterisk: mean diversity index of flocks for that area during winter

Open Circle: mean diversity index of flocks for that area during breeding.



($G_1 = -0.70065$, S.E. 0.27391; $G_2 = -0.55631$, S.E. 0.54146). Differences in diversity indices for area and season were tested by one way analysis of variance on the normalised data, and for significance levels between groups the Student-Newman-Keuls (SNK) multiple range test for unequal samples was applied (Sokal & Rohlf 1969). As tagging of new individuals continued during this data collection, a check was kept of the proportion of marked birds attached to each rookery. This did not vary significantly between months except for those from Crookston rookery, which was eliminated from analysis for reasons already explained.

2.7.2 Results

2.7.2.1 The effect of month on diversity index

One way analysis of variance revealed a significant effect of month on diversity index ($p < 0.05$). The SNK multiple range test did not reveal any significant differences between adjacent months at the 5% level. The diversity index for each month is given in Table 2-1. The trend is for greater diversity during the non-breeding months, breeding occurring from March until June. Two exceptions are the figures for October 1979, which corresponds to the autumnal sexual phase (Marshall and Coombs 1957), and the high figure for April 1980. The reason for this latter figure is unclear.

2.7.2.2 The effect of area on diversity index

One way analysis of variance on the effect of area within the study area revealed a significant effect ($P < 0.001$), and the SNK multiple range test revealed certain areas to be significantly different to others as shown in Table 2-2. Homogeneous subsets in the following tables are defined as 'subsets of groups whose highest and lowest means do not differ by more than the shortest significant range for a subset of that size' (Nie et al 1975). So in this context, some areas are revealed as being significantly more similar to each other than to other areas.

As month has an effect upon diversity, the area effect revealed in Table 2-2 was retested separately for breeding and winter periods. For the winter period, analysis of variance did not show a significant difference in the way areas were used ($p > 0.6$) and the SNK test revealed no significant differences of diversity index between different areas, see Table 2-3.

TABLE 2-1

Mean monthly diversity index for flocks seen in the study area.

The larger the diversity index, the more diverse the flock.

month	D.I.	month	D.I.
Apr 79	0.6549	Jan 80	1.0306
May 79	0.6631	Feb 80	1.0239
Jul 79	0.7906	Mar 80	0.7715
Oct 79	0.4195	Apr 80	0.8137
Nov 79	0.8783	May 80	0.6384
Dec 79	0.8103		

TABLE 2-2

Homogeneous subsets as revealed by SNK test
for diversity index differences between areas
for all season together.

Subset 1

Area 3, mean Diversity Index = 0.4161

Subset 2

Area 5, mean Diversity Index = 0.6223

Area 2, mean Diversity Index = 0.7117

Subset 3

Area 1, mean Diversity Index = 0.9623

Area 4, mean Diversity Index = 1.0044

TABLE 2-3

Diversity indices of flocks seen in different areas
during the November-February period.

Area 1	0.9883	Area 4	1.0448
Area 2	1.0017	Area 5	0.7327
Area 3	0.7621		

For the March to June breeding period however, analysis of variance did reveal a significant effect of area on diversity index ($p < 0.001$), and the SNK test revealed three homogeneous subsets, see Table 2-4.

2.7.3 Discussion of diversity indices

Birds from a given rookery associate with an area around that rookery during the breeding period, so the overlap of home ranges of birds attached to different rookeries decreases when compared to the November-February winter period when ranges show almost complete overlap (Figure 2-12). So a Rook is more likely to be found feeding with members of another rookery during winter than during the breeding period, with a consequent increase of diversity during the winter than at other times, (Table 2-1; compare also Table 2-3 with Table 2-4).

TABLE 2-4

Homogeneous subsets as revealed by SNK test
for diversity index differences between areas
in the March-June period.

Subset 1

Area 3 mean diversity index = 0.4070

Subset 2

Area 5 mean diversity index = 0.6103

Area 2 mean diversity index = 0.6490

Subset 3

Area 1 mean diversity index = 0.9564

Area 4 mean diversity index = 0.9740

These differences in flock diversity are likely to be a result of some aspect of the strength of rookery attachment by individuals. During the breeding season male rooks are strongly tied to their rookery by the need for regular return trips with food (around 53/day, Feare et al 1974), and unless an exceptional, super-abundant food source occurred some distance away, it would be expected that Rooks would cut their flying costs by utilizing equivalent sources close to the rookery if available. Indeed, Rooks have been shown to feed closer to the rookery during the breeding season (Coombs 1961b, Patterson et al

1971). The directional tendencies (i.e. Rooks do not have a circular home range whose centre is their rookery) may be explained by distribution of good feeding sites, and also by familiarity with land in the corridor between the rookery and winter roost. Thus Symington birds still use all the area utilized by them in the winter period, plus the areas close to their rookery.

During the winter, patterns of movement are very different. Although rookery assemblies occur in the morning and evening, throughout the day a gradual coalescence of flocks takes place, and large flocks build up on areas of high food density (Waite 1981). The rookery has less effect on movements (Figure 2-12), flocks from different rookeries converge, leading to an increase in flock diversity (Table 2-1). This is reflected too in flock sizes seen at different times of year, large flocks of over 100 rooks being most common from December to February and never occurring during March and April in a sample of 5583 flocks (Patterson et. al. 1971).

The low figure for diversity index for October may be related to the autumnal sexual period. The autumn photoperiod and the quality of the food available approximate that of spring, and various degrees of sexual behaviour occur, such as nest building and nest defence with corresponding development of gonads and resurgence of breeding hormone levels in some birds (Lincoln et al 1980). This response shows variation between individuals and in area, for in Scotland the hormonal response is less marked (Lincoln et. al. 1980) than in southern England (Marshall & Coombs 1957), where young have actually been hatched (Lockie 1954). Return to the breeding state leads to birds spending much of their time in the rookeries, with regular

visits during the day, resulting in a dispersion pattern similar to that found in the breeding season. A second peak of appearance of small flocks occurs at this time (Patterson et al 1971) which, in my study area, are homogeneous with regard to rookery membership (Table 2-1). During the winter there is no effect of area on diversity index (Table 2-2) but during the breeding season the differences between areas are large (Table 2-4). These differences could be anticipated from Figure 2-11 and result from the lack of ties to the rookery.

The area effect during the breeding period is more complex (Figure 2-11). Areas 1 and 4 have flocks of maximum diversity. Area 1 is used by all rookeries, and flocks therefore often contain birds from different breeding location, and thus the overlap zone of Figure 2-12 is not caused by temporal partitioning of the area. As for Area 4, if Crookston had^{had} sufficient birds for inclusion, it would probably have shown low diversity, but as these were excluded from the calculations all birds seen here come from either Burnhouse, Burnhouse Mains or Symington rookeries. It is out of the normal range of these colonies, and any flocks^{considered} here are likely to contain members of each of these, who will be familiar with the area due to the pre-and post-roost gatherings. The comparatively high diversity of these flocks are a result of a lack of a predominant local rookery (as manifested by tagged birds) rather than its extensive and equal use by several other rookeries. Areas 2 and 5 form a homogeneous subset of intermediate diversity, and this results from each area being utilized by two rookeries (Figure 2-11), Area 2 by Symington and Burnhouse, Area 5 by Burnhouse and Burnhouse Mains. Area 3 displays flocks of significantly less diversity than the others, as it is used predominantly by just one rookery, Symington.

Diversity indices therefore provide a useful tool with which to test the significance between seasons in Figure 2-11, albeit indirectly. To summarise, they show a difference between winter and breeding periods in the degree to which Rooks from various rookeries feed together, and also that during the winter there is no significant difference between various areas within the study area with respect to their use by different rookeries. Most importantly, during the breeding season the diversity of flocks seen is lower, supporting the *data* that each rookery has a feeding range which may only partially overlap with others.

2.8 DISCUSSION: THE DETERMINANTS OF HOME RANGE IN THE ROOK

Early studies on the range of Rooks were necessarily limited to observations of the interactions between rookeries and the roost, and between catchment areas of roosts (e.g. Harrison 1931, Philipson 1933, Burns 1957). With the development of marking techniques it has become possible to observe accurately how known individuals utilize an area with reference to the rookeries within a roost area. The only other study where this has been done was a long term study of Rooks on the Ythan Estuary, Aberdeenshire (e.g. Patterson et al 1971).

Adult Rooks in Britain are apparently sedentary and appear to remain in the same area over a period of years. Movement occurs in the first year of life. Although few Rooks move more than 30 miles (Holyoak 1971) this would normally be enough to place the youngster in a new roost area and group of rookeries, since roosts are

spaced at 5-10 mile intervals of 'good' agricultural land (Munroe 1971). Patterson et al (1971) suggest that some young Rooks return to breed either to their natal rookery or one close by.

Attaching the label sedentary implies that the animal is attached to some characteristic of an area, and therefore becomes part of the roost and rookery system of that area. The roost is a simplistic term, true winter communal roosts should be strictly defined as those occurring in the period prior to breeding, i.e. January onwards, but often extending back to November. After breeding finishes in June/July until the formation of the winter roost, communal roosts form which appear to involve all manner of associations between rookeries (Patterson et al 1971) ^{involving} much mixing of populations. The division of rook populations into true winter roost catchment areas ('parishes' in the traditional terminology of Rook natural history) has significance, for in both studies involving marked birds (this one, and that of Patterson et al) no observable mixing occurred in the breeding season between adjacent rookeries which happened to be in the catchment areas of different winter roosts. In the current study, Figure 2-1 shows a rookery of 60 nests to the extreme south of the intensive study area. Rooks from Symington rookery, the one to the north of this (120 nests), were never seen more than 0.5 km south of their rookery, whilst those of the southern rookery utilized areas to the south and west, as deduced from flight lines. There existed an area of land almost totally devoid of Rooks between these two rookeries, superficially ideal feeding areas for Rooks. Patterson et al (1971) have similar observations: their study involved a northerly group of three rookeries, with a pair to the south. These two groups associated in various post-breeding roosts, but separated into two

true winter roosts. Observations during the breeding season revealed some overlap between members of each group, but complete separation between northern and southern groups.

Burns (1957) and Coombs (1961) anticipated these findings concerned with relationships between roosts and rookeries, the latter ^{opening} a rookery on the edge of winter roost catchment area whose birds temporarily associated with Rooks from a neighbouring roost area in the autumn. Philipson (1933) located what he termed subsidiary roosts at the junction of roost catchment areas, but ^{did} not discuss temporal relationships.

The roost is therefore a dynamic entity, having a variable membership, depending on the time of year. It is possible that individual Rooks become attached to specific rookeries. To justify this, some idea of colony integrity may be gained from my sample of 1979 tagged breeding Rooks (see Appendix 4). Of 315 Rooks tagged in 1979, 85 were known to have bred. In 1980, of these 85, 10 were not seen again, 14 were present throughout the breeding season but did not breed, and 61 bred again. Of these 61, 12 bred in a different rookery within the study area. From these figures, there appears to be an adult survival rate of 88%, with 72% of birds breeding two years in succession, but with 19% of these changing rookery. Colony fidelity then can only be set at 53%, 'rookery group' ^{fidelity} (i.e. a group of rookeries in close proximity) at 72% and roost catchment area ^{fidelity} to 88%. The 12% remainder must contain all adult mortality, tag loss and emigration. As the birds which took a year out from breeding (14) were similar in number to those which disappear (10), it is possible that the main cause of not breeding is death of a mate and subsequent

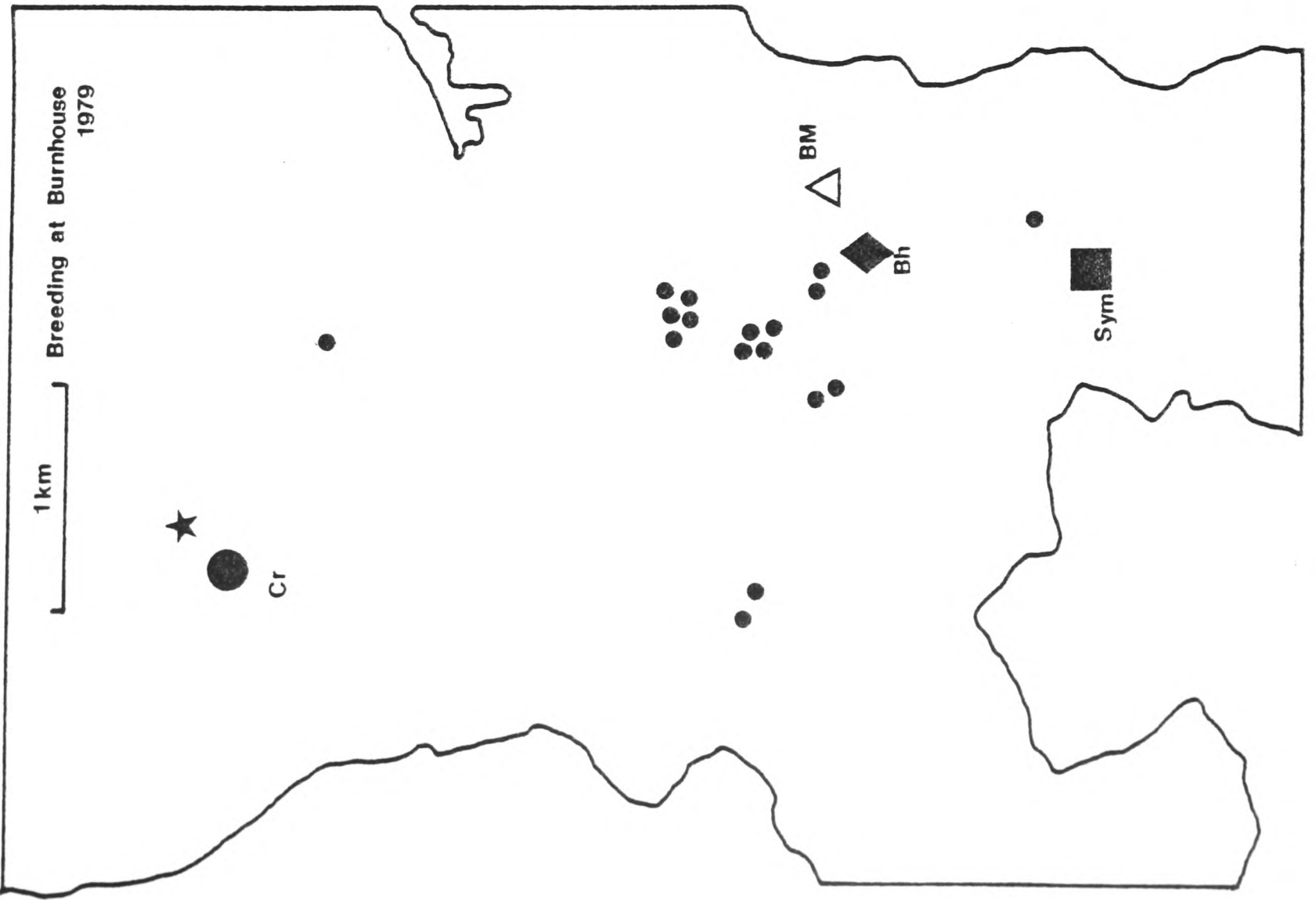
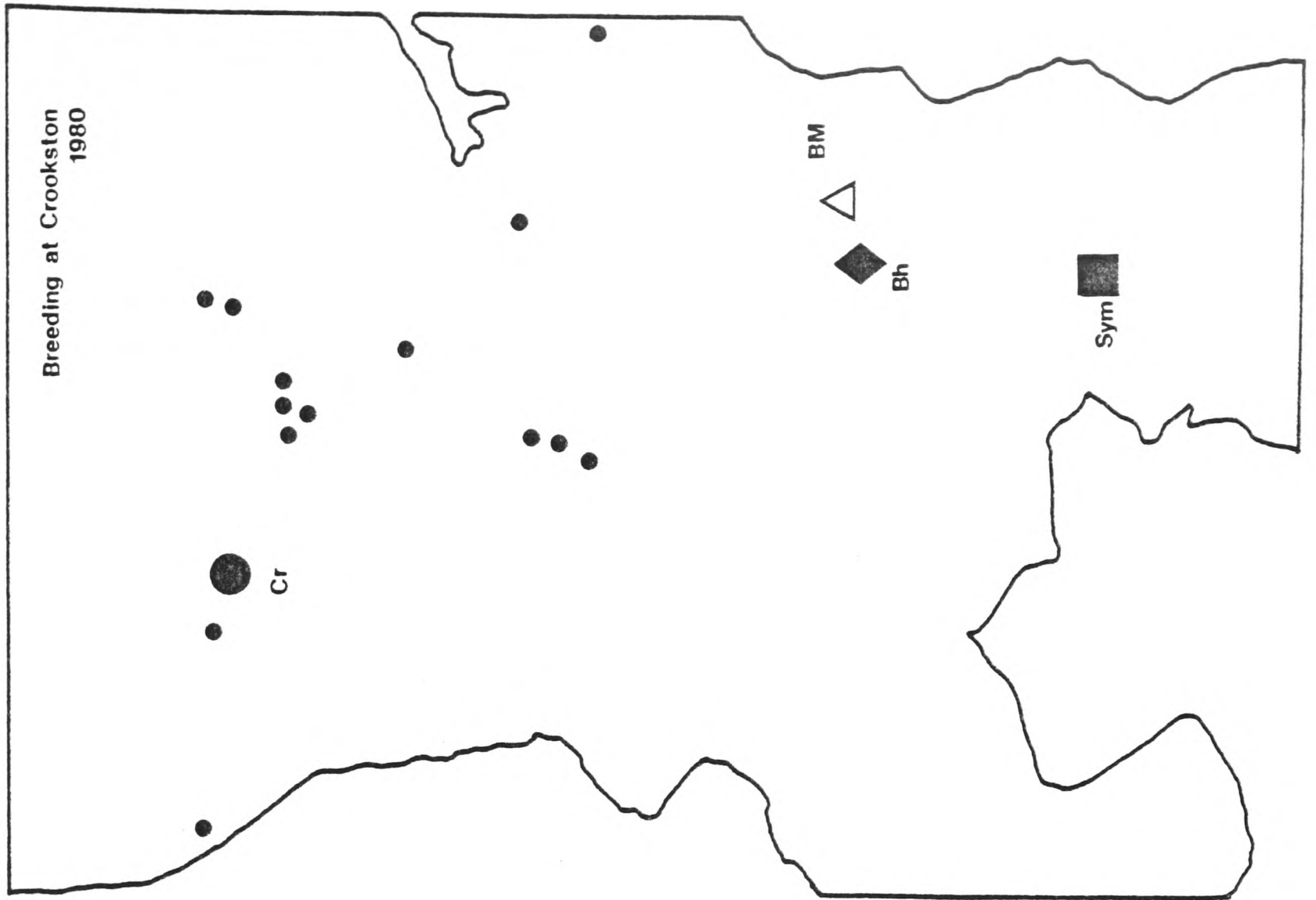
failure to re-mate. The possibility of 'non-breéders' being unobserved breeders has been covered in section 2.4.

The location of a rookery also appears to influence the feeding range of breeding birds attached to it. The range is not a simple circle around a rookery, other factors are involved (Figure 2-11). Furthermore, birds which change rookeries between years change their feeding range also and conform to the pattern typical of that rookery, as shown by Figure 2-13. The only movement between two rookeries which involved more than two birds and hence gave a reasonable number of sightings was from Burnhouse to Crookston. The sightings of these three birds are shown in Figure 2-13 and show a shift correspondant with the use of land by those rookeries. Thus some factor intrinsic to the rookery appears to determine the specific rookery range, which appears to disappear in the winter. The difference in range is especially obvious when one considers the proximity of Burnhouse and Burnhouse Mains rookeries, see Figure 2-11, and the differences in their ranges, see Figures 2-7 and 2-8.

Adult Rooks seem therefore to be most strongly attached to the pre-breeding true winter roost, in that 88% of the tagged sample were present in two consecutive years. When this roost does not exist (post-breeding period), the rookeries must represent the basic social unit, for these remain discrete throughout the autumn period with their daily gatherings. However, as a proportion (19%) switch rookeries between years and breeding birds are sometimes seen in other rookeries at all times of year, it seems likely that a social unit of *neighbouring* rookeries must also exist, as originally suggested by Patterson et al (1971) but which proximate rookeries are involved

Figure 2-13

Difference in feeding areas of Rooks when they switched breeding location from Burnhouse to Crookston rookery during the breeding season.



probably depends upon the roost catchment area.

To summarise, a complex hierarchy of attachment for a Rook exists, the winter roost serving as a central gathering point from around November until March, but dispersion is generally around the local rookery complex. The local rookery complex serves as the centre for breeding activities, there being slightly over 50% chance of a Rook breeding in the same rookery from year to year with approximately a 19% chance of moving into a nearby rookery. There is a 16% chance of the Rook taking a year out of breeding, and if it does so it seems to spend the time in the home range of its past breeding rookery.

2.9 SUMMARY

1. The determinants of home range of Rooks as given by past workers is reviewed, and the relative effects of roost and rookery are considered.
2. The study area is described in detail, and roosting movements of local birds are given.
2. Standard circuits of the study area revealed effects of colony location and season on feeding dispersion of birds for which breeding location was known.
4. The significance of these differences was tested indirectly by the use of a diversity index on rookery membership of feeding flocks. Each colony tended to use certain areas during the breeding season with some overlap of neighbouring colonies.
5. This range difference disappears during the winter period, but is apparent during the autumnal sexual period.
6. The validity of various social units is discussed, and a grouping of proximal rookeries as an intermediate unit between roost and rookery is postulated.

CHAPTER THREE

RADIO TELEMTRY

3.1 INTRODUCTION

Radio telemetry is a means by which an animal's movements may be followed by tracking a radio signal transmitted by a small package attached to the animal. The aims of its use in this study were to be able to follow a breeding Rook out from the rookery to the feeding fields, where its feeding rate could be measured using an event recorder (see Appendix 6) and to see how this affected where it went on subsequent feeding trips. In short, I wished to gain insight into how a breeding male Rook may make decisions concerning where to go to gather the next meal for its young.

3.2 METHODS

3.2.1 Equipment

All equipment used was manufactured by the AVM Company of Champaign, Illinois, U.S.A. Each package attached to a Rook contained an SM1 radio transmitter (wt. 0.6g), a mercury cell power source of 8 milliamp day capacity (wt. 2.4g) and a 12 inch two strand whip antenna. The assembly was attached to a 30mm x 25mm x 1mm piece of PVC plastic (Darvic) sheet, see Figure 3-1a, by means of Araldite epoxy resin, through which had been threaded two 300mm lengths of 10mm wide woven 'knicker' elastic. The package weighed less than 5g, approximately 1% of the total weight of the bird. This set up has a theoretical life

Figure 3-1

Components of the radio transmitter package.

A. Darvic base with slots for elastic harness straps

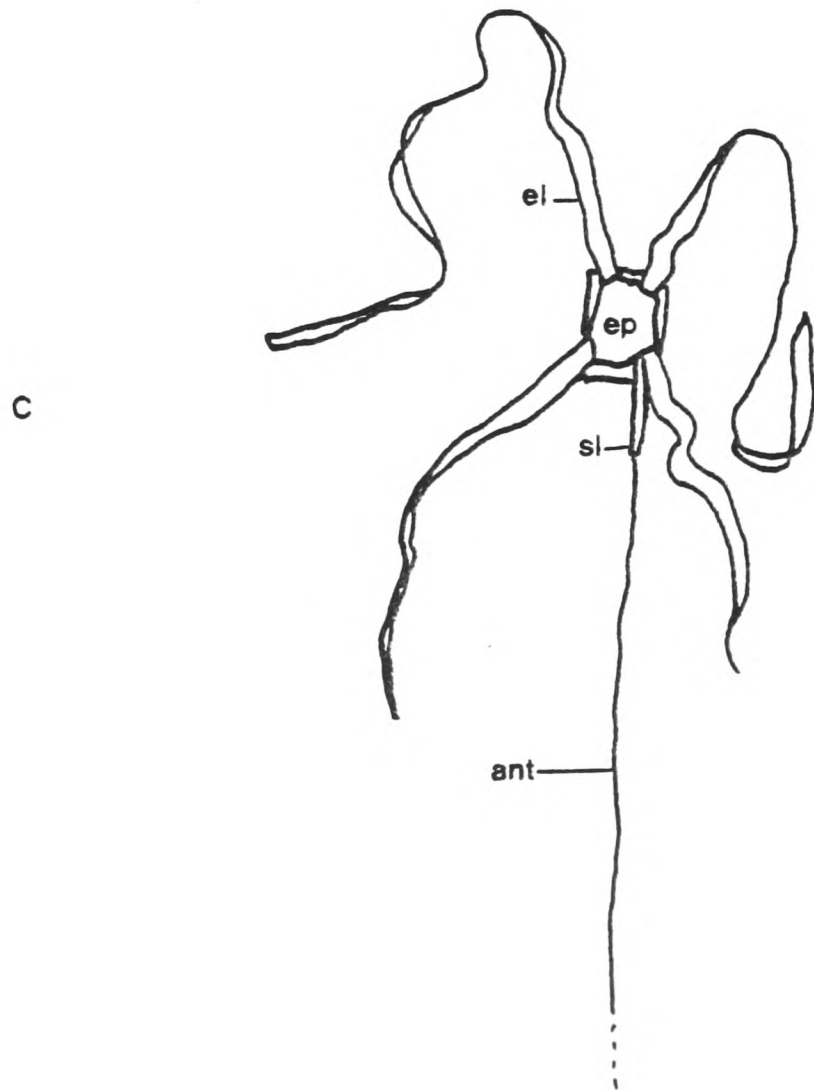
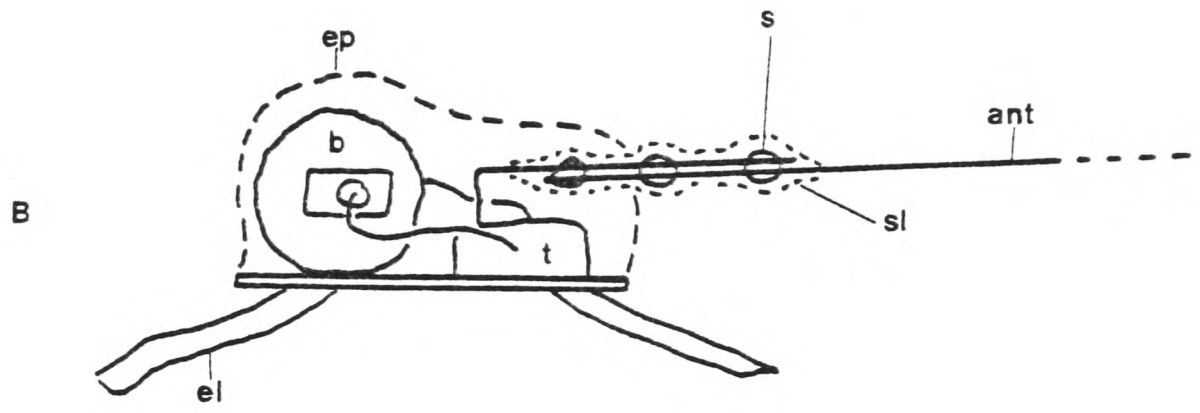
B. Assembled components of harness assembly

ant - antenna, b - mercury cell power source,

el - elastic harness strap ep - epoxy resin matrix, s - solder join,

sl - heat shrink plastic sleeve, t - radio transmitter unit

C. Completed assembly



of approximately four months, calculated by the drain imposed by the transmitter (.06 milliamps) on the capacity of the power source (8 milliamp days). Tracking equipment consisted of one hand-held 3 element yagi antenna, connected to an LA12 receiver equipped with headphones. Each transmitter had a unique frequency, spread between 173.335 and 173.475MHz, and a unique number of sound pulses emitted per minute, so that different radio tagged birds would not be confused. The only previous study involving radio tracking of a member of this genus is by Loman (1980) on the Hooded Crow Corvus corone cornix in Sweden. He used larger 27 MHz transmitters which are heavier (30g), have a shorter range (up to 800m), and shorter life (up to 10 days), but more robust in not requiring a long antenna, transmitting on a shorter wavelength. He gives no details of equipment.

3.2.2 Choice of bird

Packages were attached to 8 male Rooks known to be breeding by virtue of their wing tags, and one non-breeding second year, which were recaptured in the traps described in Appendix 1. In 7 cases, the package was a back pack as described, see Figure 3-1c, and was attached to the bird by passing the two ends of each elastic strap around the bird and tying at the front with a reef knot, see Figure 3-2. The tension on the elastic was just sufficient to prevent the package from slipping; great care is needed not to overtighten it. The two front straps are passed in front of the wing and knotted to its diagonal opposite on the ventral surface of the bird, see Figure 3-2b. The first assembly was tried on a bird in captivity to check

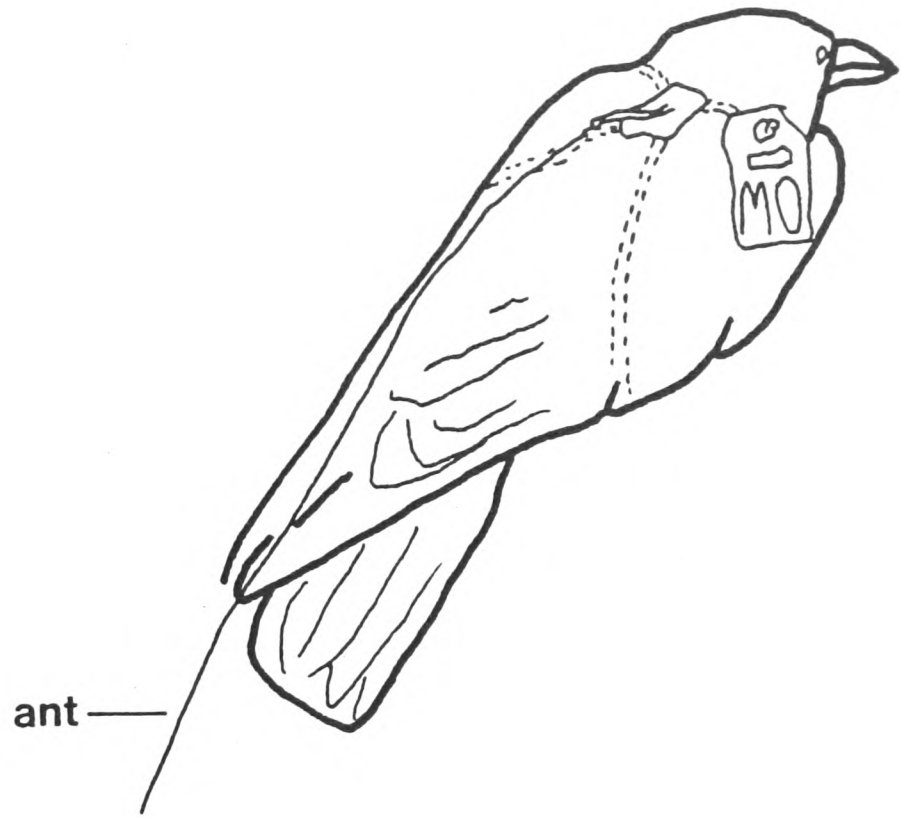
Figure 3-2

Rook with transmitter package attached

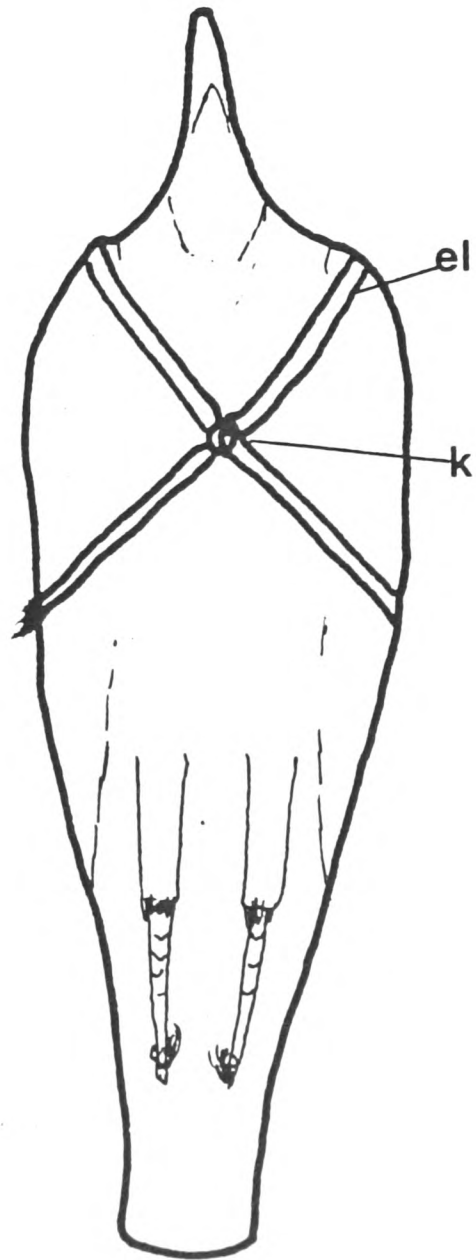
A. Dorsal view

B. Ventral view showing knotted elastic straps

A



B



that the system was satisfactory. This is a design adapted from that used on Herring Gulls by Richard Sibley, who showed me the details of its attachment. In one instance, an assembly not attached to the Darvic base but including thread set into the epoxy resin matrix, was attached by the method described by Kenward (1978) to the bases of the two central tail feathers.

3.2.3 Following procedure

Tracking was done by remaining at the rookery where a particular Rook was known to be breeding, and once it had returned keeping a radio and visual fix. Upon departure, the bird was kept in visual contact for as long as possible, after which it was relocated using the radio receiver.

The technique of relocation involved a sweep with the antenna until a strong signal was picked up. When the antenna was directed at the transmitter, maximum strength of signal was obtained, manifested by volume of the transmitted sound pulse. By making sweeps at intervals from a vehicle whilst progressing along a road, it was usually possible to pinpoint an animal fairly rapidly, especially if its point of disappearance from view and flight direction at this time was known. Once relocated, the Rook was kept in visual contact until it moved, either to another field or to the rookery.

3.3 RESULTS

3.3.1 Limitations of the method

It should be noted at the outset that the results which were obtained from this method were minimal, radio telemetry requiring an extremely large time investment for a small return of information. Apart from late delivery of equipment, which meant that only one season's use could be made of it, and budgeting of my own time and labour, other factors presented problems. The deeply dissected nature of the terrain of the study area meant that signals from the birds were often obscured or completely blanked out by the hills, so that direction had to be anticipated in order to relocate. This often resulted in loss of the bird for a period of time. The presence of rock faces in valleys could often give misleading results by reflecting signals. However, this phenomenon could actually be used to advantage, as it was possible to sound along a winding valley, sometimes obviating the need for a long drive.

The largest problem was that the equipment was not sufficiently robust for the animal. None of the 8 transmitters fitted to birds had a useful life approaching the theoretical maximum of four months. The principal reason for this was with the transmitter antenna, which broke off at its point of emergence from the shrink fit plastic sleeving, presumably as a result of normal preening actions of the bird. Antenna loss was first confirmed by retrapping of the first experimental bird, MO red. Subsequent loss by others was confirmed by close range observation using a telescope, after it was suspected from

poor signal strength. A twin twisted-flex antenna was used whereas a traditional single core 'guitar string' antenna may have been more durable. A transmitter without antenna tends to give a good signal at a range of up to 500m but has little directionality, thus all such a transmitter will do is to indicate presence within a 500m radius. The maximum line of sight in the study area was approximately 2 km, and an intact transmitter assembly could be clearly detected at this range.

Details of birds to which transmitters were attached were as follows.

- 1) M0 red, a male of Burnhouse Mains, transmitter attached 23.3.80., antenna lost in 3 days.
- 2) OM red, a male of Symington, transmitter attached 1.3.80., antenna lost within 3 days.
- 3) V4 green, a male of Symington, transmitter attached on 2.3.80., and worked for 19 days before failing.
- 4) SA red, a male of Burnhouse, transmitter attached on 2.3.80., antenna lost in three days.
- 5) T0 red, a non-breeding second year Rook, transmitter attached 9.3.80., and when next seen on 30.3.80. had lost antenna.
- 6) O9 blue, a male of Burnhouse, transmitter attached 28.3.80., and provided signals for 5 days.
- 7) OV yellow, a male of Burnhouse, transmitter attached 11.5.80. and lost antenna by following day.
- 8) SV green, a male of Burnhouse, transmitter attached 12.5.80., and antenna lost by 13.5.80.

The attachment of radio transmitters to these birds had no obvious

effects on their behaviour. All breeders continued to breed and successfully fledged young, and all breeding birds were seen again in a brief tour of rookeries conducted in April 1981. The biggest effect on behaviour was after initial release, when typically a bird would roll over on its back in a field, and manipulate the knotted elastic for a period of up to one hour. The day following attachment of transmitters all birds were seen feeding young and flying normally. There is therefore no indication of detrimental behavioural changes in the short or long term resulting from the attachment of radio transmitter harnesses, although measures of the frequencies of various behaviours before and after attachment of the transmitters were not made.

Despite the limitations imposed by antenna loss, 5 good records of several hours duration of the movements of two individuals were obtained during the latter part of the breeding season. It was not possible to obtain feeding data of tracked birds at their feeding sites, since these were often far away from a road. The results discussed below refer to 4 records of Rook V4 green for the 4th, 11th, 15th and 21st of April 1980, and for 09 blue on the 1st May 1980.

3.3.2 Description

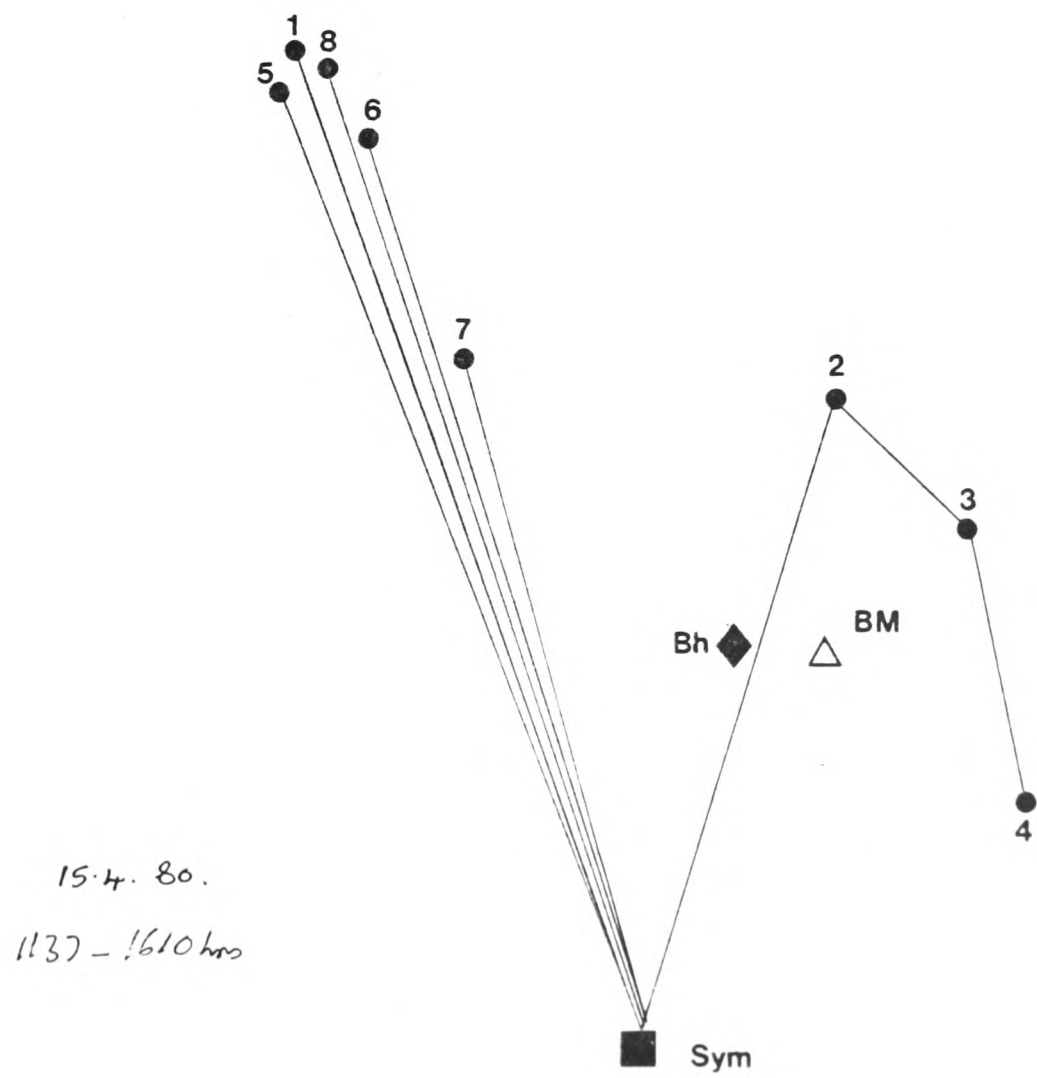
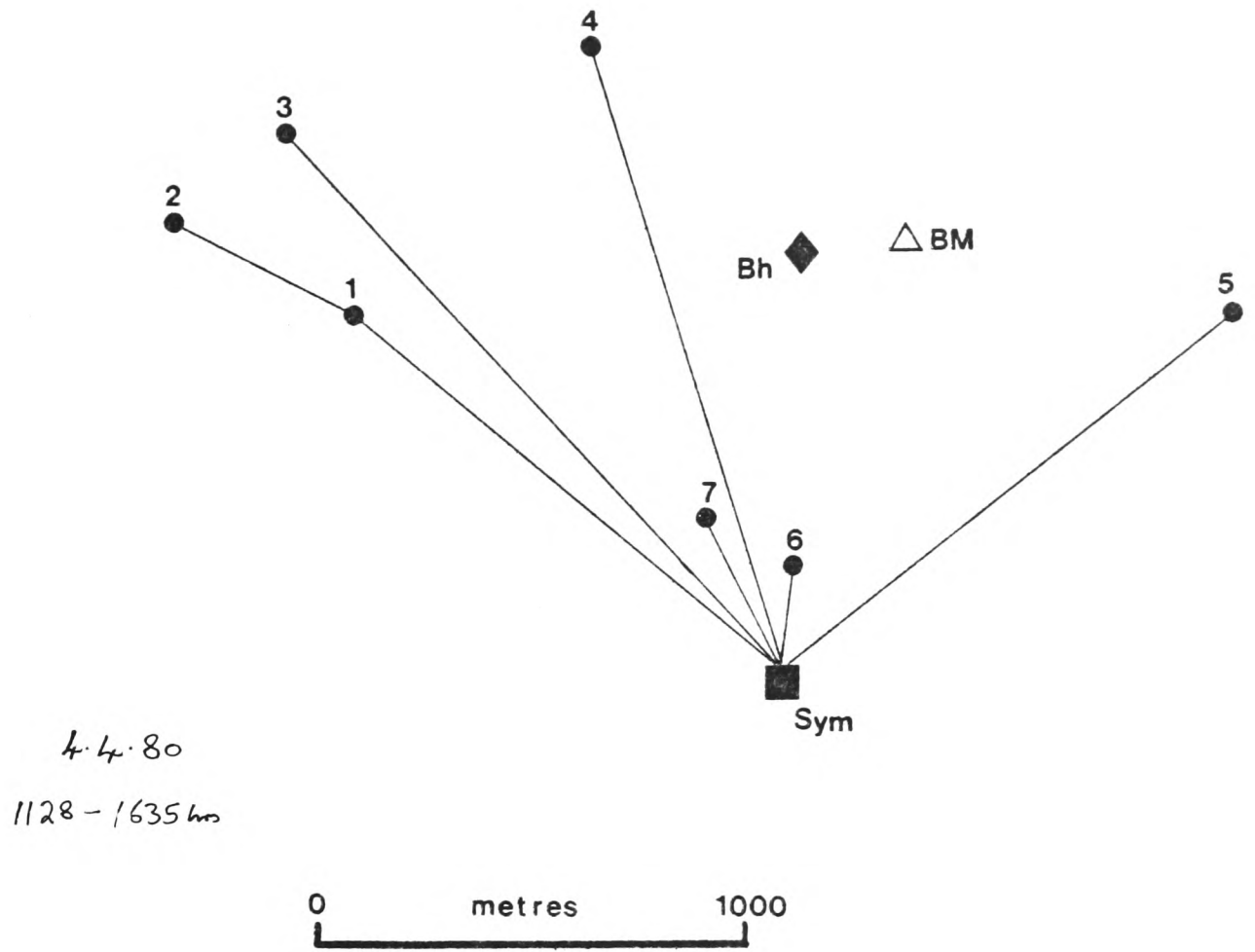
Figure 3-3 represents the movements of Rook V4 green on the 4th and 15th of April 1980. From a purely descriptive level, a pattern in the Rook's feeding sorties shows a sequential use of different fields on subsequent journeys out from the rookery. Most sorties (defined as the time between departure from, and return to, the colony) consist of

Figure 3-3

Sequence of feeding locations of breeding male V4 green.

4.4.80 is the typical pattern

15.4.80 shows result when a good food source is available



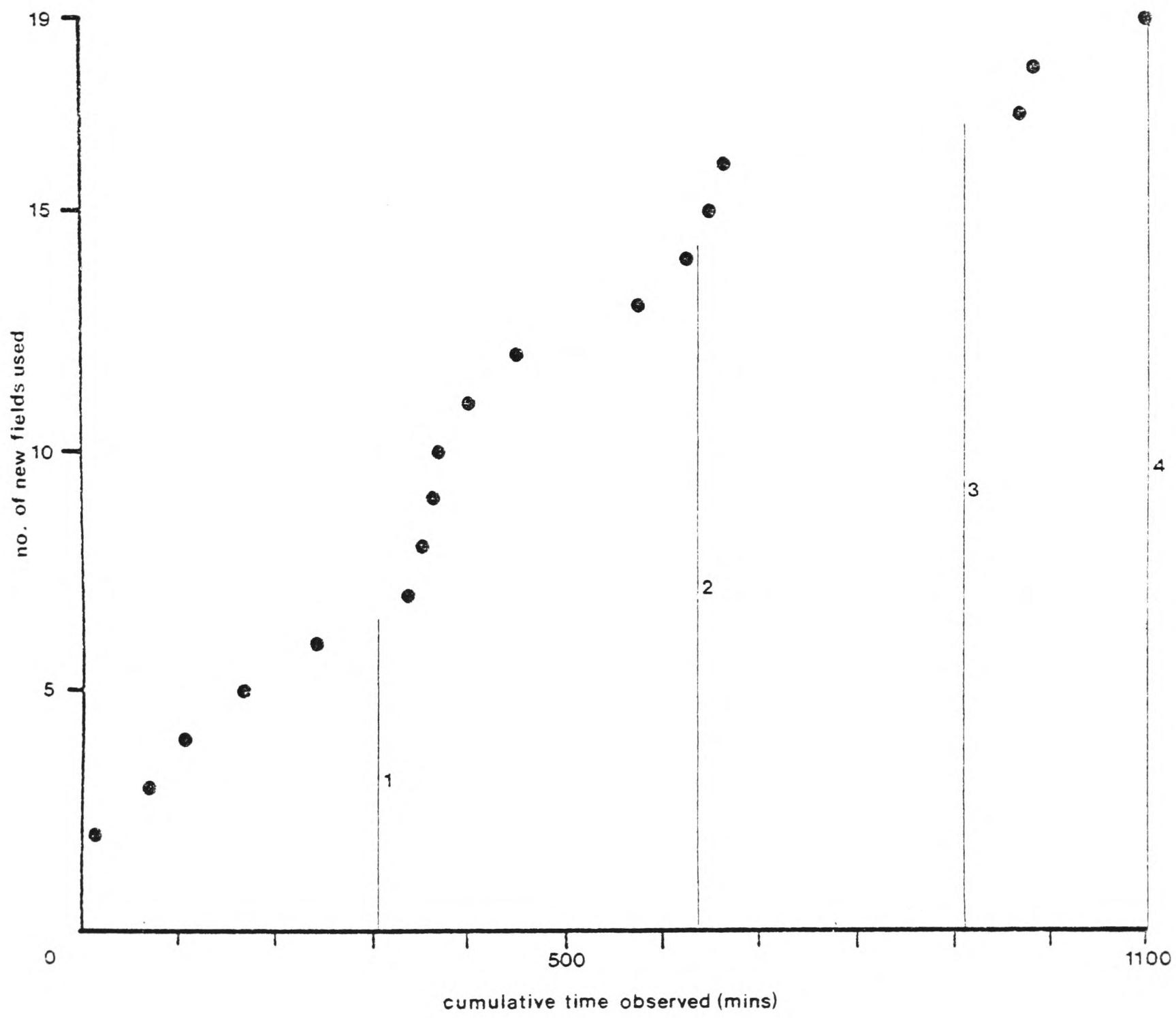
a flight direct to a field, a period of feeding in that field (defined as a bout) followed by a direct flight back to the rookery. Of 27 sorties observed of both birds, 21 were of this type, the remaining 6 involved feeding at more than one field before returning. Only rarely (4 occasions from 27) did the Rook return to the same field on two consecutive occasions, and three of these were to a field being ploughed, which, as discussed in chapter 5, is the most plentiful source of invertebrate prey. This situation is represented in the movement for April 15th, where feeding bouts 1, 5, 6 & 8 were on one field which was being ploughed. An interesting point revealed by this example is that the sortie involving bouts 2, 3 & 4, which was long in duration, followed a visit (1) to the field being ploughed during the ploughman's lunch when invertebrate food was presumably not so available. During a lull in ploughing, the numbers of Rooks on a field declines rapidly. In contrast, on 3.4.80 no ploughing was observed in the study area during an earlier circuit or during the radio tracking.

3.3.3 Area Used

Figure 3-4 represents the area utilized by the Rook V4 green, as defined by number of different fields plotted against cumulative time under observation. If a near complete picture of range of an individual was approached, the graph would show a plateau effect as relatively larger periods of observation would be needed to observe use of a novel field. After a cumulative total of 20 hours observation the plateau effect is not obvious, thus more than this period of time is needed in observations to obtain a true estimate of

Figure 3-4

Cumulative number of new fields visited with time. Numbered vertical lines represent the end of one day's observation



range of the Rook at this season. The graph reveals the large number of fields used by an individual, and Figure 3-3 the spread of these and therefore the broad knowledge it must have of the field types within its range.

3.3.4 Feeding flight distance

The 24 direct flights by V4 green observed were to one of 4 field types, namely cultivation in progress (plough or harrow), recently cultivated (bare broken soil exposed), stock food and grass pasture. The mean and S.D. of distances flown to these fields are given in Table 3-1. The mean flight distance of 1325 m is comparable to the overall mean calculated from Patterson et al (1971) of 1384 m for the breeding season (March-May). Differences in distances travelled for different field types were large, and is to some extent dependant upon location of field types i.e. fields used for grain were generally away from the valley bottom where the rookeries were located. However, it would only be worth a Rook's energy in flying to distant fields if the benefits were great, for instance better prey availability or quality than present locally. My own data for intake rate for field types will be discussed in chapter 5, but at the level of calorific intake for different field types as calculated by Feare et al (1974), cultivation in progress yields 1.27 kcal/min, stock food 0.31 kcal/min, cultivated 0.44 kcal/min and grass 0.56 kcal/min.

TABLE 3-1

Mean distances flown by Rook V9 green to different field types

field type	mean distance (m)	S.D.	N
grass	838	681	9
rec.cult.	1583	380	5
stock food	1650	37	5
cultivation	2445	368	5
all types	1325	758	24

Rooks therefore fly furthest to the best yielding supply of food. The rookeries were surrounded by grass fields, so distance travelled to them is correspondingly small (about 33% of the figure for fields undergoing cultivation). That birds fly furthest to high yielding food sources is a logical prediction from optimal foraging theory (e.g. Krebs 1978) and the problem then becomes one of location of that food without counter-productive search time. The advantage gained from such a field is rapid filling of the sub-lingual pouch and therefore less time per feeding bout and ultimately better survival of nestlings.

3.3.5 Time spent in rookery vs time spent feeding

Some information concerning temporal organization of behaviour can also be obtained from these data. The mean duration of nest visits by the male Rook V9 green was 19.4mins (S.D.=15.75, n=23). Figure 3-5 indicates that the mean length of periods of nest attendance decreased slightly during late morning and early afternoon.

The mean length of feeding bout (i.e. time spent in a field feeding) was 27.9 mins (S.D.=16.6, N = 23), and Table 3-2 gives a breakdown of these feeding bouts related to field type.

TABLE 3-2

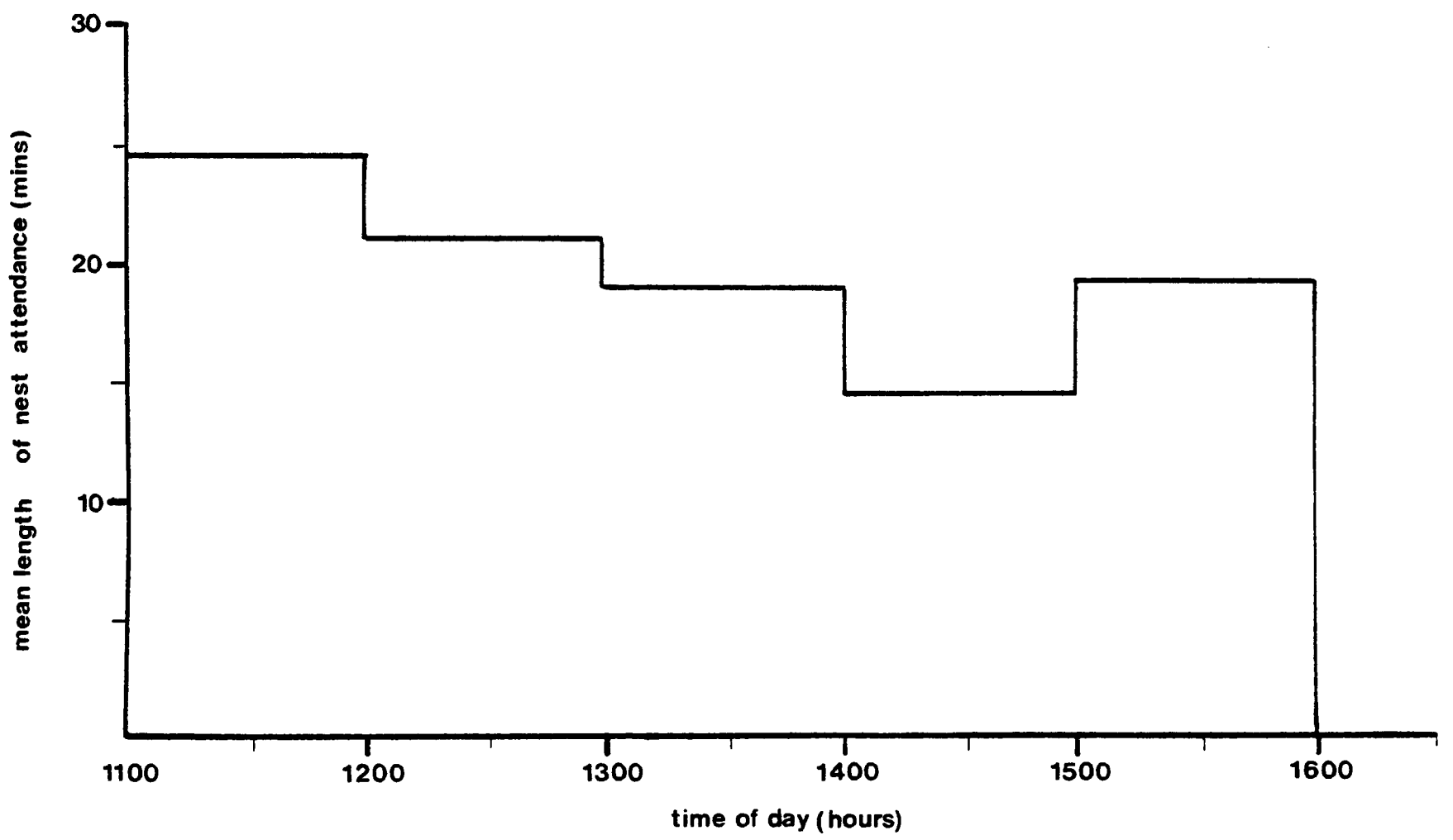
Mean length of feeding bout in minutes according to field type used

	grass	rec cult	stock food	cult
mean (mins)	35.4	29.0	28	15
S.D.	(18.2)	(19.8)	(15.3)	(6.7)
N	9	4	4	6

The sample sizes are small, but a trend emerges which reveals short stays on those fields undergoing cultivation which yield most invertebrate food/minute (Feare et al 1974). On the 3 occasions where the Rook returned to the same field on consecutive occasions, the

Figure 3-5

Proportion of time male Rook V9 green spent by his nest in
relation to the time of day



initial feeding bout lasted a mean of 15.6 (S.D.=16.6, n=5) mins compared to 29.8 (S.D.=16.9, n=22) mins for bouts which were followed by a feeding bout on a different field. This suggests that if a field is particularly good, the likelihood of returning is high. However, some other short forays on fields were not followed by a return. It is possible that these fields had a low prey density and were left more quickly.

There was also a positive correlation between the time spent feeding and time spent in the rookery upon return (Spearman rho = 0.51, $p < 0.01$). This is discussed below and again in Chapter 4, where similar data collected in a different manner are analysed.

3.4 DISCUSSION

The small amount of information revealed from radio telemetry has provided some information on how a breeding male Rook utilizes its range, and provides some insight into those factors which might be important. A study with radio telemetry as its central feature is merited with an improved design of equipment. This method reveals a better picture of use of space than the circuit method of spotting tags, since it can utilize proximate cues available to the Rook in its decision on where next to go for food.

The sequential use of fields by these Rooks suggests that they are sampling the environment for feeding sites. That the only times a

bird was seen to return to the same field twice sequentially (and also in the same 5 hour time period) was to a ploughed field (giving the highest intake rate) suggests that intake rate is a very important cue. The presence of feeding conspecifics is also very important (see Chapter 4), itself probably a reflection of high intake rate and a useful cue when deciding where to land.

In his study on foraging decisions, Tinbergen (1981) showed that Starling landing patterns were extremely aggregated in space, and showed that the proximity of two sequential landings was determined by the intake rate of the first bout, itself determined by prey density. Starlings have a small foraging range when compared to a Rook, normally within 800m of the nest. If a feeding bout was good, they returned to a feeding site next to, but not on, the previous feeding location, suggesting systematic search. If the bout was bad, the consecutive bout was over 3.5m from the first one, and often over 20 m away, showing avoidance of the bad area. This may contribute to the pattern seen in Figure 3-3, the record for 3.4.80 shows extensive sampling, that for 15.3.80 returns to the same field. Tinbergen also showed that, although a Starling knew the location of the best feeding site, it need not necessarily use it, (see for example trip (2-3-4) on 15.3.80). It is possible that a dilemma exists for the Rook (i.e. this patch is good, but how do I know it's the best?). Sampling is therefore an important strategy for an animal so that it quickly becomes aware of a new food source. Thus Loman (1980) radio tracking Hooded Crows, found that each individual sampled its entire territory every day, and Green (1977) that in an hour a flock (average size 12) of Rooks had searched an entire 8.5ha field.

It seems therefore that an important cue for Rooks deciding on where to go to feed is intake rate of previous trips, perhaps coupled with reactions to foraging flocks. Higher order factors may also account for feeding locations. Tinbergen found that the decision of whether to forage for low cost (in terms of time taken to catch each prey item) high calorie leatherjackets or high quality (in terms of protein content and prevention of excessive nest fouling) high cost Cerapteryx sp. caterpillars depended on the hunger of the nestlings. Such factors may be important for Rooks, but inaccessible nests make such data difficult to collect. In years of poor earthworm availability, as judged by climatic conditions, Lockie (1959) found a switching of nestling diet away from earthworms, the deficit being made up by grassland caterpillars (Celaena sp.) and the remaining shortfall by grain. Nestling influence on adult foraging behaviour is clearly an important new area of investigation with implications for optimal foraging models.

The partial dependence of the time spent by the male at the nest upon the length of the previous feeding bout may be because after a long period feeding, the male needs a longer period for maintenance activities. These include preening, resting and social interactions etc. Also, the female is subject to 'mass rape' by other males when her mate is absent (Coombs 1961a). Another possibility is that if a bird has been away for a long period it may have been unsuccessful at locating a good food patch, as suggested by the data for length of time spent on a field of good food availability, Table 3-2, and it remains in the rookery to see where other birds are going to feed. If it has been successful at locating food it may return almost immediately to the field. The correlation for this effect may be

greater than appears at first sight because some of the longer feeding sorties may have involved feeding in a number of fields before finding a good feeding site. Thus a good feeding site may be located after a long foraging bout, a site which may be returned to after a short nest visit.

A male remaining by the nest for a particular time span is probably caused by a number of factors, for example interactions with other birds at the colony. However, the significant positive correlation found here is matched by a non-significant positive trend for similar data presented in Chapter 4.

3.5 SUMMARY

1. Radio transmitters were attached to 8 Rooks, 7 by means of a harness, and 1 as a tail mount.
2. Most transmitters were inactivated as a result of the bird breaking the antenna within 3 days.
3. To obtain a true picture of a breeding male's range, it needs to be followed for a cumulative period in excess of 20 hours.
3. Results showed that Rooks normally switched feeding fields between subsequent sorties, and it is probable that a field was used twice in succession if it gave a high intake rate (e.g. a field being ploughed).
5. Rooks travelled further to fields undergoing cultivation than to any other type, and least to grass pasture. The feeding bout length was much shorter on the former than on grass.
6. A positive correlation was shown between time spent away on a feeding bout and the subsequent length of time spent by the nest.

CHAPTER FOUR

LOCAL ENHANCEMENT BEHAVIOUR

4.1 INTRODUCTION

In Chapter Three, studies using radio telemetry revealed that, during the breeding season, male Rooks sample large areas in their search for food each day. Several factors which might affect the location of each foraging bout were considered, and one of these, namely local enhancement, is considered further in this chapter.

Local enhancement is a type of social learning which increases the tendency of an individual to respond to a part of its environment as a consequence of the response of another to that part (Hinde 1970). In the context of Rooks feeding, this could occur at three levels. By following other individuals to a distant feeding location from a central gathering point (colony or roost), a Rook may find a good feeding area within its range. Once in that general area, it may respond to a feeding group on a specific field. Finally, once on a field, it may approach other individuals on the field. At each level, local enhancement can be seen to direct an individual to progressively finer areas of the environment. Only the first two levels will be considered here, beginning with the finer of the two.

4.2 LOCAL ENHANCEMENT TO A PARTICULAR FIELD

4.2.1 Introduction

The review of prey collected for young Rooks in section 1.3.2 shows that the most important prey type, earthworms, occur in cryptic, sub-surface patches which are hard to locate, the patches shifting in a manner which may be unpredictable to Rooks (section 1.3.3). By reacting to other birds feeding, individual Rooks could reduce search time, which could result in greater rate of food delivery to their young, thus increasing fitness. Other reasons for joining others may be to decrease the proportion of time spent in vigilant behaviours, thus increasing the time available for feeding or, by being with others, the probability of being eaten by a predator is reduced by one of the several processes reviewed in section 1.2. As predation is rare, this is difficult to quantify.

Due to methodological flaws, data collected in 1980 to test between the two food-related hypotheses (i.e. does joining a flock result in increased food intake through locating better food patches, or through increasing the proportion of time spent feeding), cannot be presented and instead reference will be made to work by Waite (1981) for Rooks feeding on grassland in winter.

4.2.2 Methods.

To measure whether birds did prefer to land with others I watched one grass permanent pasture field for a total of 9.5 hours over a two

week period from 10-24 April 1980, a time when feeding bouts by males were high (young in nest, female still brooding). The measures taken were the response (land or fly on) of Rooks flying out of the rookery over the field, together with the number of birds in the field at the time of the response, their spacing, and, if the bird landed, the distance to its nearest neighbour. NNDs (mean nearest neighbour distances) were calculated by estimation of number of Rook lengths, and later dividing by two to give an approximate distance in metres. This method has been successfully used in the past (Waite 1976, Green 1977) and shows good inter-observer reliability.

4.2.3 Results

4.2.3.1 Preference for the flock

Figure 4-1 reveals that the likelihood of an aerial bird landing is influenced by the number of birds in the field (Chi square = 86.2, d.f. = 7, $p < 0.001$). Flock sizes 6-10 and 11-20 were lumped due to small sample sizes of these larger flocks. This effect could also have been produced by birds independently returning to the field, because of a high prey density. However, I never observed a male Rook return to any grass field on any two successive sorties (Chapter 3).

The effect of NND as shown in Figure 4-2 is not significant (Chi square = 10.54, d.f. = 5, $p < 0.1$) but this obscures an interesting effect. Figure 4-2 reveals that birds are less likely to land if

Figure 4-1

Influence of flock size on attracting birds to land

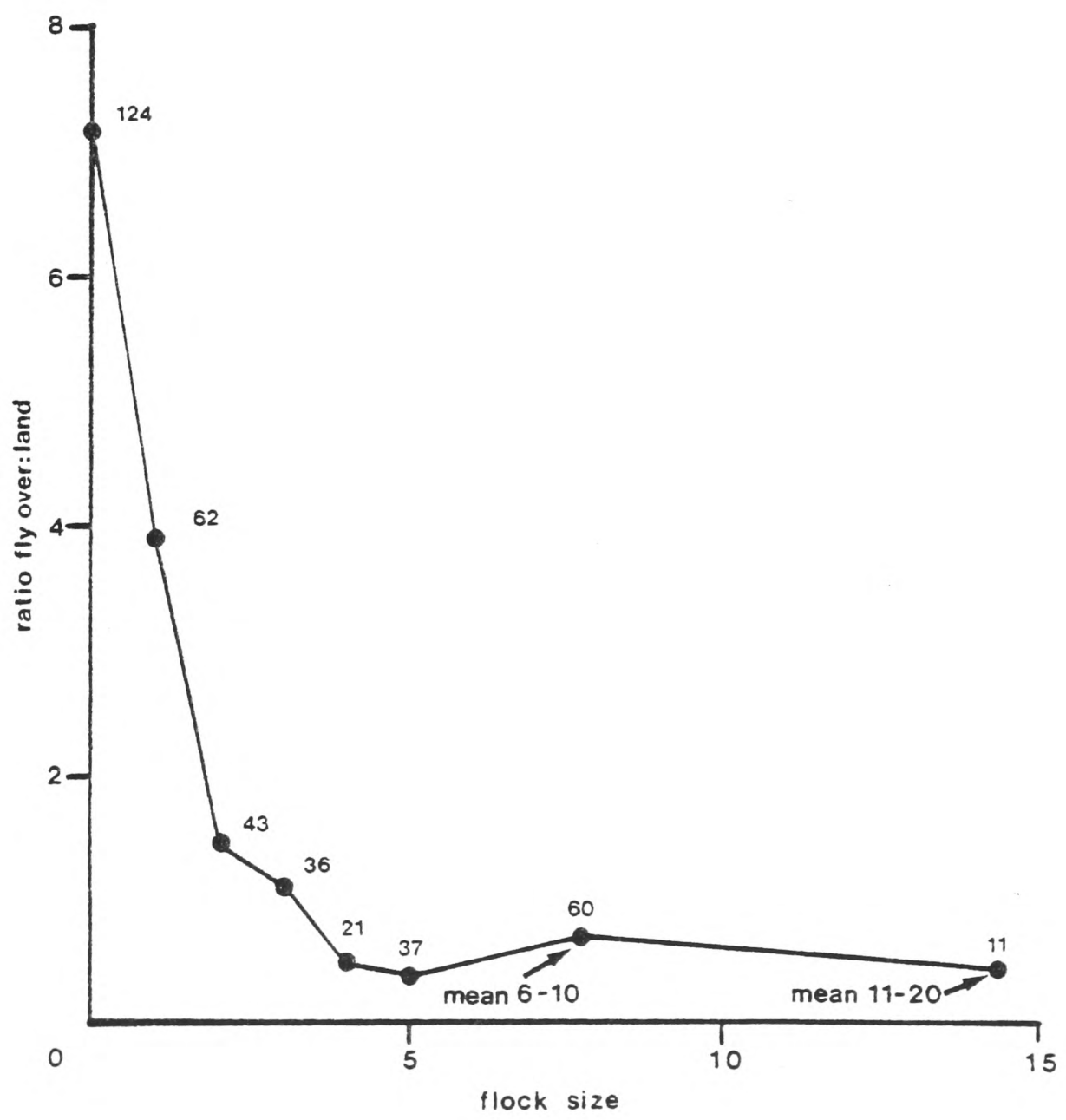
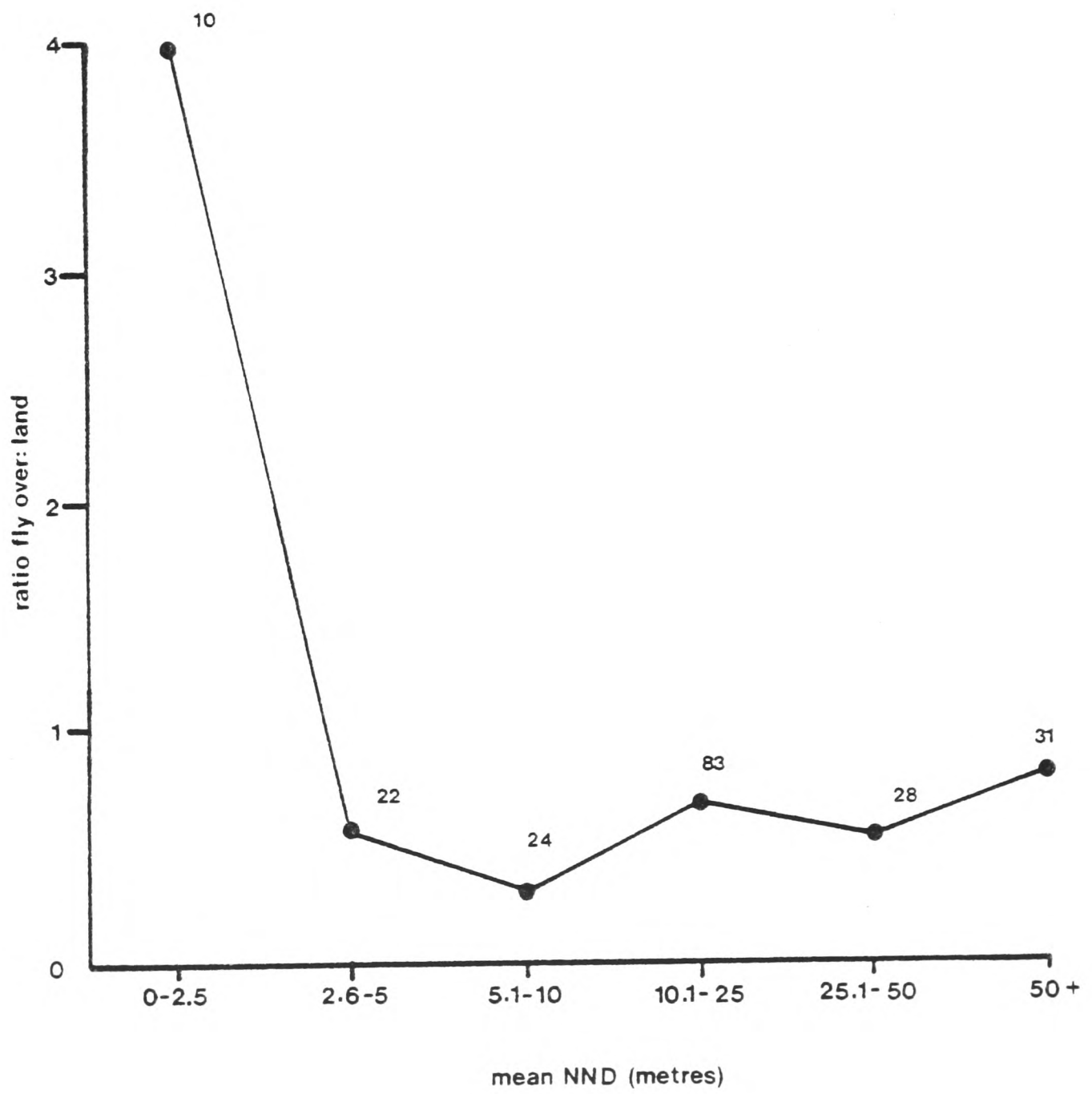


Figure 4-2

Influence of mean nearest neighbour distance
on attracting birds to land



birds are close, that is between 0-2.5m, than at higher NNDs. This is puzzling, because Figure 4-3 reveals that mean NND decreases with increasing flock size ($\rho = -1.0$, $p < 0.01$) thus lower NNDs occur with the more attractive larger flocks. This result may be partly explained by small sample size, but also the original data reveals that all the points of small NND (0-2.5m) occurred with pairs of birds, in several cases exhibiting overt sexual displays. It seems likely that a courting pair is recognized as such by aerial birds and avoided as a nucleus of a feeding flock. Table 4-1 shows that only at large flock sizes (~~3~~11) does NND have any significant effect on the attractiveness of the flock to birds flying overhead. The decrease in NND as flock size increases is not caused by constraints of the field, since at any one time the flock covered only a small proportion of the field.

Figure 4-3

Relationship between flock size and mean
nearest neighbour distance

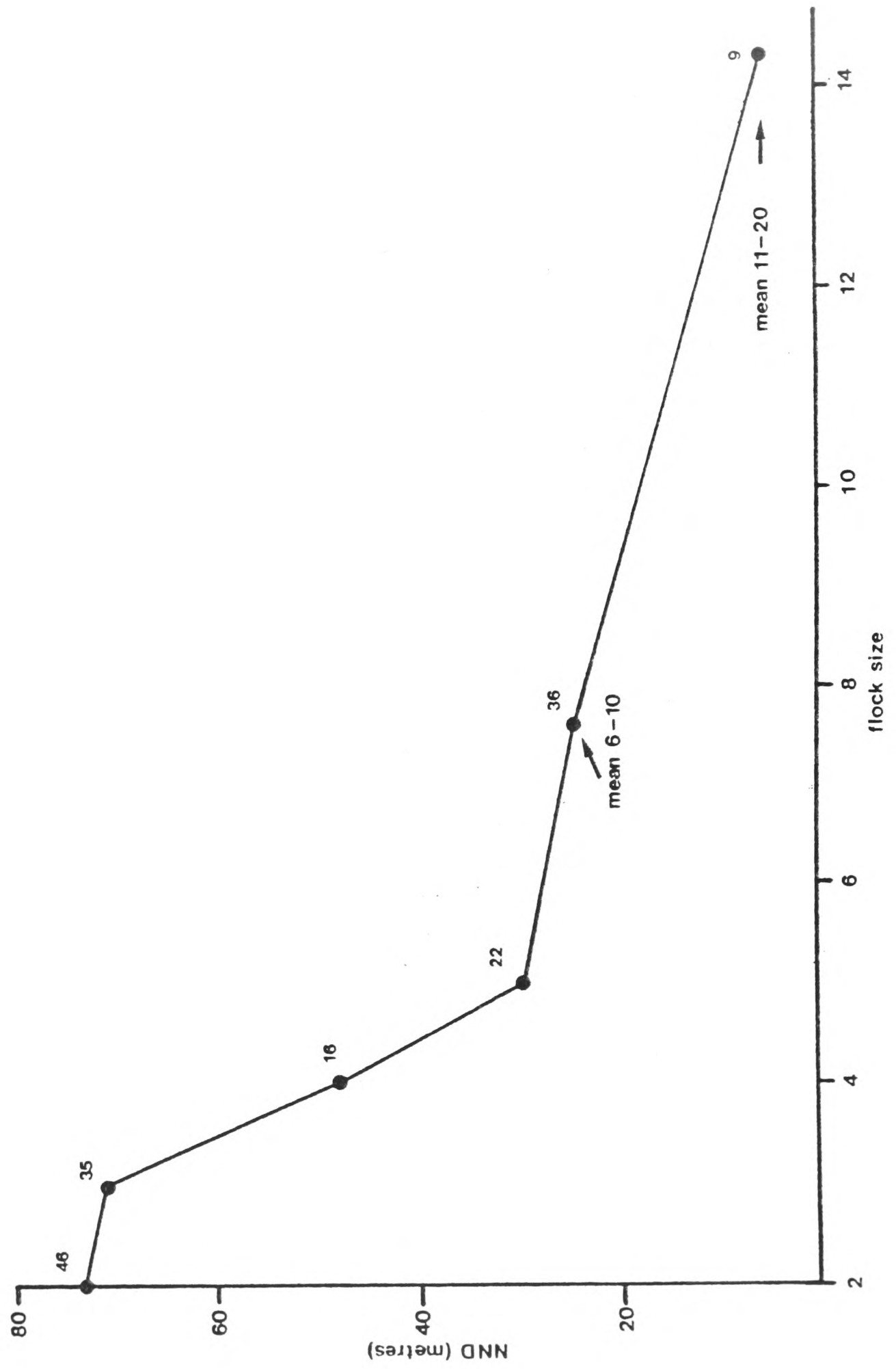


TABLE 4-1

Difference in mean NND (in metres) when aerial Rooks landed and flew over a feeding flock, for different flock sizes.

FS	NND land (m)	NND fly over (m)	t	P	d.f.
2	117	66	1.69	N.S.	25
3	83	64	0.39	N.S.	19
4	40	45	0.19	N.S.	18
5	24	22	0.55	N.S.	34
6-10	17	22	1.04	N.S.	52
11-20	8	14	4.13	<0.01	13

To summarise, birds are more likely to land in a field if it contains birds than if not, and the effect increases with the number of birds in the flock. Furthermore, at larger flock sizes, flocks with closer spacing between individuals were more attractive.

4.2.4 Discussion: medium and fine scale local enhancement.

Results similar to those above have been presented by Krebs (1974)

for the Great Blue Heron Ardea herodias feeding on fish in estuarine pools, by Barnard (1980) for House Sparrows Passer domesticus feeding on spilt barley grain, and by Waite (1981) for Rooks feeding on earthworms on grass fields in winter. Each of these authors went further and studied the inter-relationships between variables measured from the birds in the flock and of the flock itself, in order to understand which had the greatest effect on intake rate. The variables included intake rate, vigilance behaviour, prey density, flock size, individual spacing and short flights. By multiple regression techniques, they were able to construct models to explain how individuals gained by joining a flock.

Traditionally, the negative correlation between flock size and vigilance has been regarded as the causal mechanism, by allowing more time for feeding (e.g. Abramson 1979). However, in the three studies quoted above, prey density was shown to be the greatest predictor of ingestion rate, with no link between flock size and ingestion rate. On similar prey densities, birds do no better in a large flock than in a small one.

Larger flock sizes occur on higher prey densities as a result of local enhancement. High prey densities result in a high intake rate by individuals, who stay put longer and attract more birds to the area. In this way, flocks build up on areas of high prey density, and a bird would experience a feeding advantage by landing with others than on its own, notwithstanding any of the anti-predator advantages mentioned in section 1.2. Waite (1981) has shown that local enhancement occurs in Rooks at this intermediate level, but also at a finer scale. Rooks take off more frequently on areas of lower

earthworm density than on areas of high earthworm density, and on 60% of occasions land within 5m of another individual. The effect of this shuffling is that individuals aggregate on the small, high density patches within a good general area (Waite 1981, Chantrey in press).

This work by Waite and Chantrey was initiated by observations on a flock of Rooks during March (Green 1977), which revealed that as a flock searched a field, its members alternately spread out and closed up. Plotting mean NND against flock size revealed a scattergram of small flock size with highly varied NND, but larger flock sizes had small NNDs, the latter not being constrained by field size. This link between NND and flock size appeared with both artificial food (Green 1977) and with natural food (Waite 1978) and at the time it was suggested that the two flock dispersal patterns represented searching and feeding flock types. Subsequent work by Waite (1981) has shown that ingestion rate increases as mean NND decreases when feeding on sub-surface prey, as a result of local enhancement to high prey density patches, and that aerial birds do use this small inter-bird spacing as a cue to a good feeding area (see also Table 4-1). However, in the data presented here (Table 4-1), at the larger flock sizes, the ratio of fly on:land does not reach zero, as would be predicted from the effect of an attraction to others feeding. 37.5% still fly on in the larger flock sizes and from Waite's (1981) data at flock sizes of 25 in winter, 10% still fly on. So other factors must be involved in the decision process of a Rook seeking a place to feed, apart from the combination of numbers on a field and their spacing pattern.

Breeding Rooks are continually sampling areas to feed (Chapter 3),

rarely returning to the same place at least for several hours unless that place is very good. It is likely that Rooks, ^{like} other species, remember where feeding has been good in the past (Croze 1970, Murton 1971, Safriel 1975, Smith and Dawkins 1971, Smith and Sweatman 1974, Zach and Falls 1976a,b,c, Tinbergen 1981), and an active sampling procedure enables the individual to assess the relative profitability of feeding locations.

Tinbergen (1981) made the unexpected finding that nestling demands may dictate the feeding location of adult Starlings, and that even though an adult may know where the best feeding location is, it may not always use it due to constraints imposed by the need to sample new areas or collect a different food type. Those birds which fly past a feeding flock may be going on to join a larger flock they can see elsewhere, or they may be going to sample a field without conspecifics. In the latter case, memory of past good areas, and utilization of other cues (tractor, surface features, are two possibilities) may be some of the components they consider. Whether a flock then builds up may be the result of several factors. One will be the length of stay, for the longer a bird stays, the greater the probability of another joining. This feature, which is undoubtedly important in winter flocks feeding on grassland (Waite 1981) is complicated in the breeding season by the need to return and feed the young. A high prey density could result in a short stay, due to rapid filling of the pouch, or a long stay due to collecting food for itself. More study is required to see how long a Rook needs to assess the food quality of a field, and how this compares with the shortest stay on a low prey density. Another factor which might affect whether a flock builds up on a field may be whether the initial exploiter

returns to it. In Chapter Three, Rooks discovering a very good feeding site returned to it, and the implications of this are considered in the next section.

4.3 LOCAL ENHANCEMENT ON THE COARSE SCALE

4.3.1 Introduction

During the field study, it was noticed that some of the largest feeding groups during the breeding season were occurring on fields which were being ploughed or harrowed. Since some birds on these fields were from colonies 2.5km or more away, across hilly terrain, in areas where birds from these colonies were rarely seen (Chapter 2), it was possible that local enhancement to that area was occurring by following other birds out from the colony. A study of recruitment patterns to those fields was done in order to see whether this might be the case.

4.3.2 Background

In Chapter 3, Rooks were shown to travel furthest to those locations giving the best intake rate (i.e. fields being ploughed or

harrowed) and only returned to a field on a subsequent feeding bout if it was very good. Since time spent feeding at these good sources was much shorter than a trip to a grass field, the effect of locating a good source on a Rook's movements will be to cause a more rapid than usual sequence of flights to and from the colony, concentrated in one bearing. It is possible that other Rooks in the colony could detect this change, and follow the successful individual to the good feeding area, an example of local enhancement occurring at the coarse scale.

During 1979, the measurement of ingestion rates of birds feeding on different field types revealed that fields being ploughed yielded on average over twice as much food as pasture fields (mean plough = 20.5 items/minute; mean pasture = 9.1 items/minute: $t = 2.91$, $p < 0.001$, $df = 98$). Other indications of the generality of this finding include Feare et al's (1974) data which show that the calorific yield of fields under cultivation was double that of pasture fields. No measures were taken of fields being harrowed, but it is assumed their yield is somewhere between that of pasture and fields being ploughed, as such fields attracted large numbers of Rooks. Also, Rooks will fly further to fields which have been recently harrowed than to pasture fields (Chapter 3).

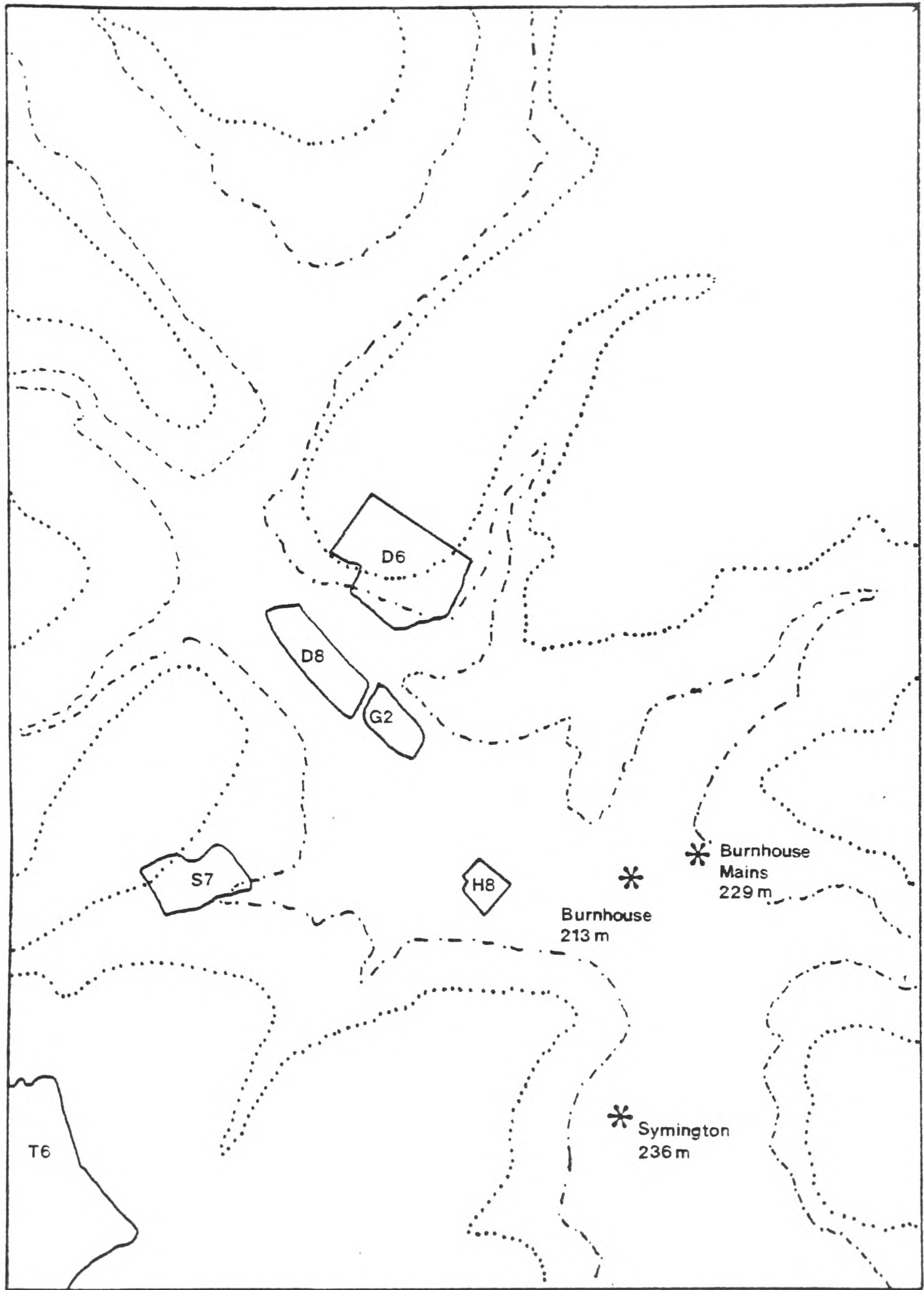
In the study area, very few fields were winter sown. Stubble was left over winter, and ploughed the following spring, although conditions rarely allowed this to happen before March. Ploughing continued until May, which coincided with the Rooks' breeding period. This practice supplies the Rooks with grain during early winter and a plentiful supply of high protein invertebrate food for nestlings in the spring.

4.3.3 Methods

As part of the transect programme, during the nestling period of 1980, a visit was made in the early morning to those fields due to be ploughed (based on information from the farmers). If a tractor was observed 'tooling up' the field was observed, irrespective of whether birds were already on the field, from when the ploughman started until he stopped, or, in some instances, until all the birds disappeared. Observations consisted of scanning the fields for tagged birds every five minutes, or however long it took to note all tagged birds present, whichever was the longest. Later analysis therefore revealed the rate of arrival of adult breeding males from each of the colonies and their return to the field after a visit to the rookery to feed their young. Raw data for analysis for each field observed for each scan consisted of 1), the number of wing tagged Rooks from each colony on the field, 2), the number of new wing tagged recruits from each colony appearing on the field during the previous interval, and 3), the number of wing tagged birds returning to the the field which had previously been sighted but had been absent during the previous time interval. A possible source of error in this method is that a tag could possibly be missed in a scan, and therefore counted as a return on the next sighting, but the large number of duplicate sightings of individuals during a single scan suggests that this error is small. A total of 10 such fields were located and observed, although 3 observations were terminated due to heat haze rendering the reading of tags unreliable. The location of these fields in relation to the rookeries is shown in Figure 4-4.

Figure 4-4

Location of rookeries containing tagged male Rooks, and the fields being ploughed or harrowed observed for arrival patterns



..... 274m contours
- - - - - 243m

1 km

4.3.4 Results

Statistical advice for this section was given by Dr. A. Renshaw, Department of Statistics, University of Edinburgh.

4.3.4.1 Field D8, 17.4.80, commencing 1311hrs.

Only tagged birds are used in the following analysis. As birds are recruited to a field, there are less potential new recruits at the colony, thus with a constant recruitment rate at the field there will be a tail off in the number of new birds arriving with time, simply because there are progressively fewer unrecruited birds remaining. The following method was therefore used to adjust the calculated rate of new arrivals from a specific rookery at a field. If the number of tagged males at a colony is, for example, 50, and 10 have already visited the field, there are just 40 left as potential recruits. If a scan of the field revealed that 8 new birds from the colony had arrived, this was scored as the proportion of potential new recruits which actually arrive in the set time interval, in this case 0.2. Figures 4-5, 4-7 and 4-9 are cumulative plots of such proportions against time from the start of recording.

The arrival rate of tagged individuals from each rookery at field D8 is given in Figure 4-5, together with a cross section of the terrain between the colony and the field under observation in Figure 4-6 to give an idea of visibility. The important comparison to make is the elevation of slope in Figure 4-5 before and after the first tagged Rook returns to the field after a trip back to its rookery, i.e. the slope of the plotted line either side of the vertical line to

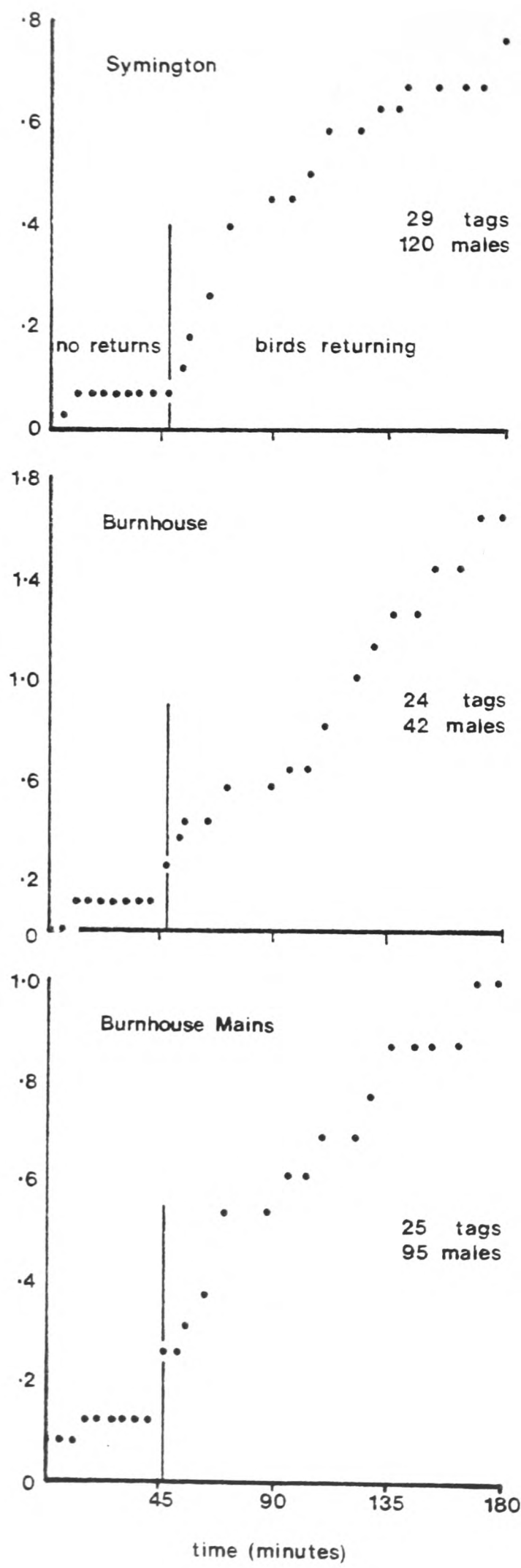
Figure 4-5

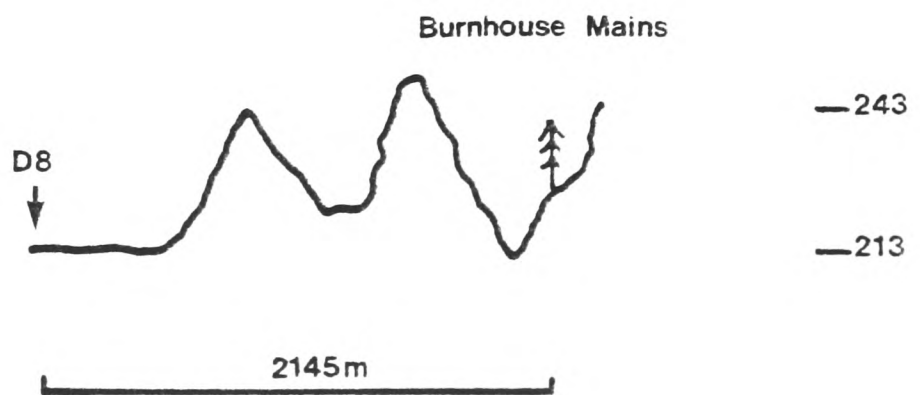
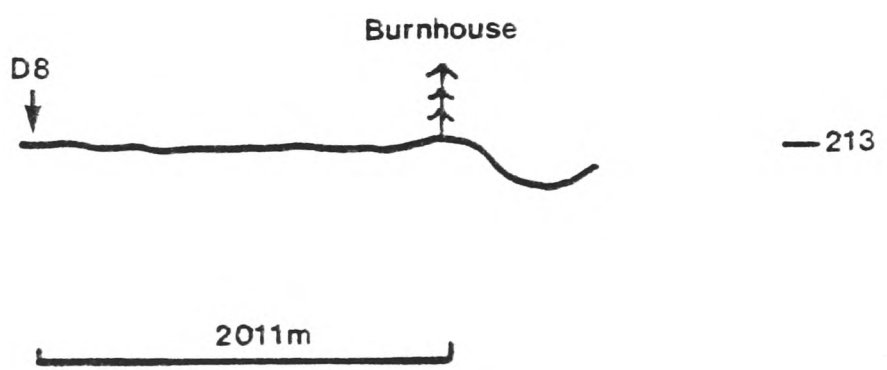
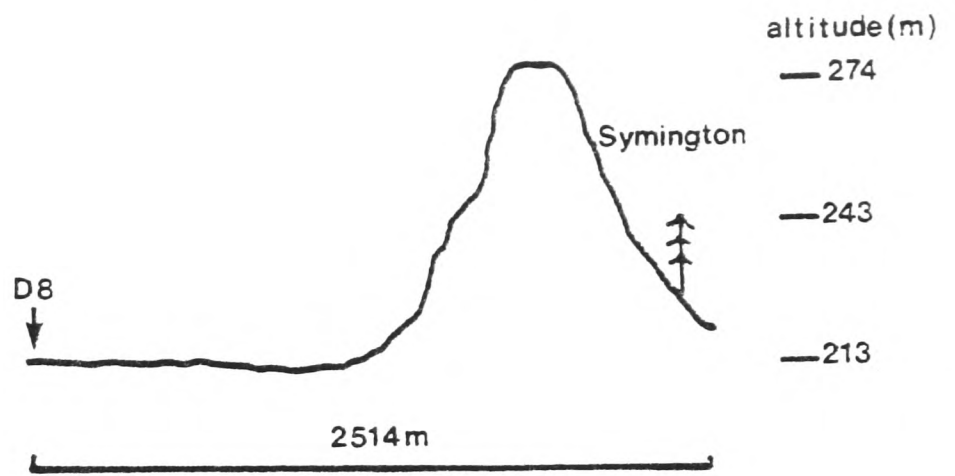
Arrivals at field D8 being ploughed from each of three rookeries. Time zero when ploughing begins. Vertical line in graph indicates time of last scan when no bird on the field had returned to feed after a trip to its rookery. The caption 29 tags, 120 males indicates that, in the rookery concerned, 29 of the 120 breeding males were wing tagged. These captions refer also to Figures 4-7 and 4-9.

Figure 4-6

Cross section of the terrain between field D8 and each rookery.

proportion of new recruits available which arrive during time interval (cumulative)





the right of the Y axis. Birds from Symington, whose view of the field, which is 2.5 km distant, is completely obscured by a bluff in the valley, show an increase in recruitment to the field after the first return of a tagged individual, and a fall off after approximately 2 hours. The trend for Burnhouse birds is less marked, there being an upturn ^{at the time of} the first return, Figure 4-5, with no decline through time. Burnhouse Mains birds showed a similar result. Testing to see whether the difference in arrival rate before and after the first return is statistically significant is not easy. The most apparent test of fitting regression lines to the rates either side of the first return line and testing for differences in the slope is not valid for a number of reasons. Observations before and after the first return are not independent and the lines produced by the graphed data are not straight. Similarly, large differences in the variance before and after the first return renders application of T-test to the data invalid, and the tail off in arrival rate towards the end of observation introduces problems for the median test. The difference in arrival rates before and after the first return are given in Table 4-2.

TABLE 4-2

Arrival rate, expressed as proportion new recruits available which arrive per minute, before and after first return, for field D8, see Figure 4-5.

Rookery	rate before return	rate after return
Symington	0.015	0.060
Burnhouse	0.006	0.012
Burnhouse Mains	0.006	0.006

Even with a tail off in the proportion of new recruits available which arrive per minute towards the end of the recording, the proportional arrival rate after the first return from Symington shows a four fold increase. The proportion of available new recruits arriving from Burnhouse rookery show a doubling after the first bird to return. For Burnhouse Mains rookery, there is no difference in recruitment rate before or after the first bird returns.

4.3.4.2 Results: Field D6, 24.4.80, commencing 1018 hrs.

This field was being harrowed while observations were made. Symington birds did not gather on this field. Both Burnhouse and

Burnhouse Mains rookeries are in view of the field, Figure 4-8, and Figure 4-7 shows that birds from neither rookery display the upsurge of arrival rate after the first known return. Table 4-3 gives the arrival rates before and after the arrival of the first return.

TABLE 4-3

Arrival rate, expressed as proportion of new recruits available which arrive per minute, before and after the first return, for field D6 on 24.4.80, see Figure 4-8.

Rookery,	rate before return	rate after return
Burnhouse	0.008	0.167
Burnhouse Mains	0.005	0.005

4.3.4.3 Results: Field H8, 2.5.80, commencing 1000 hrs.

This field was being harrowed while observations were being made. Figure 4-9 shows that no rookery exhibited the increase of recruits after the first return, and Figure 4-10 shows that only Symington was out of sight of the field. Both Symington and Burnhouse showed a steady rate of arrivals, although Burnhouse Mains, in direct line of sight, showed little utilization of the field, and no recruitment after the arrival of the first return. Table 4-4 reveals no large increase in arrival rate after the first known return, and a reduction

Figure 4-7

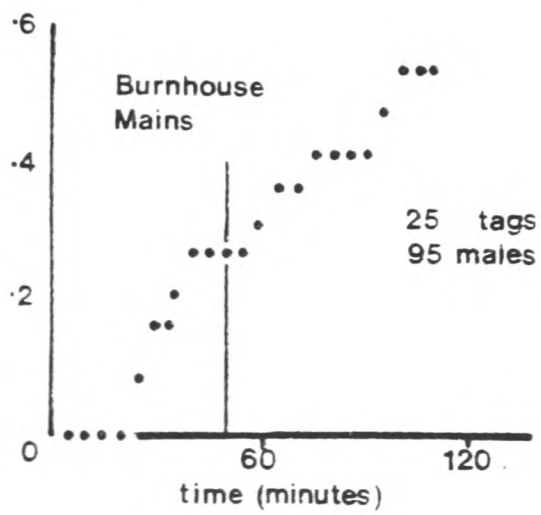
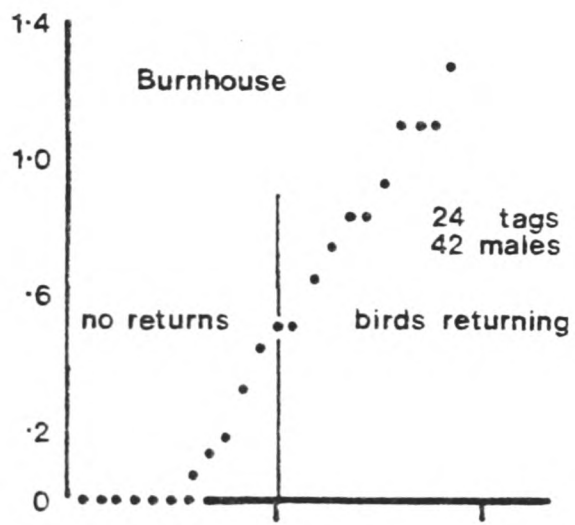
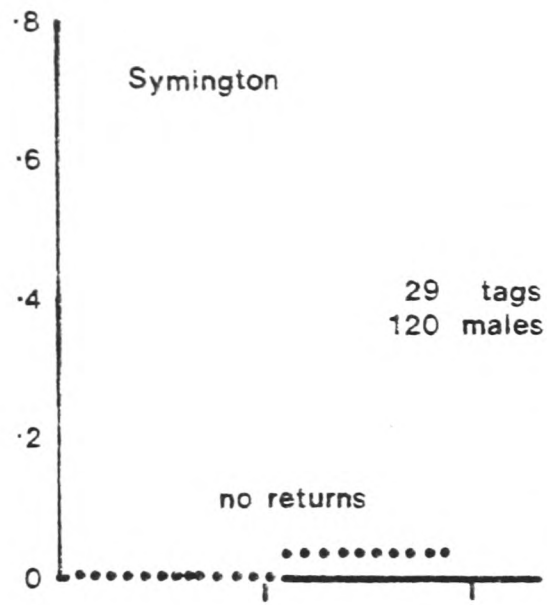
Arrivals at field D6 being harrowed from each of the three rookeries.

Other details as for Figure 4-5

Figure 4-8

Cross section of the terrain between field D6 and each of the rookeries.

proportion of new recruits available which arrive during time interval (cumulative)



altitude m

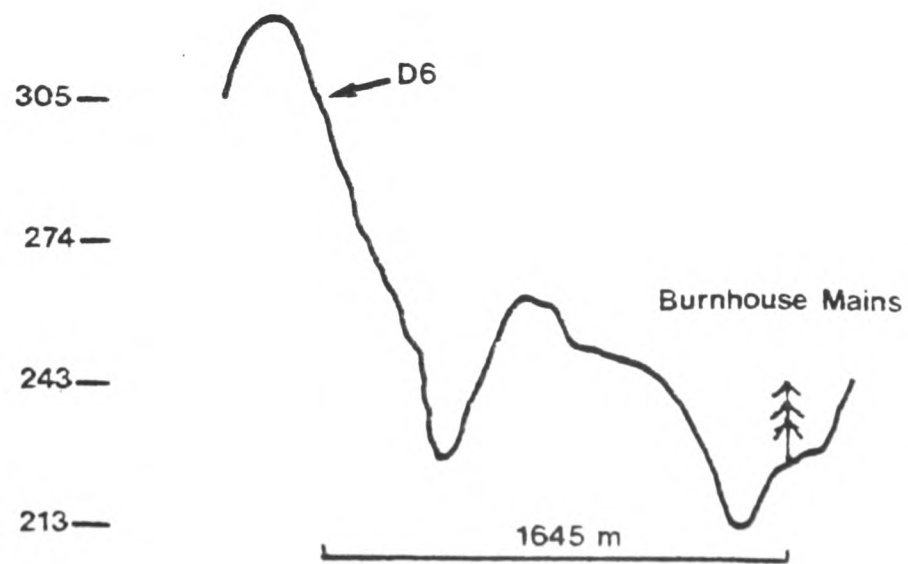
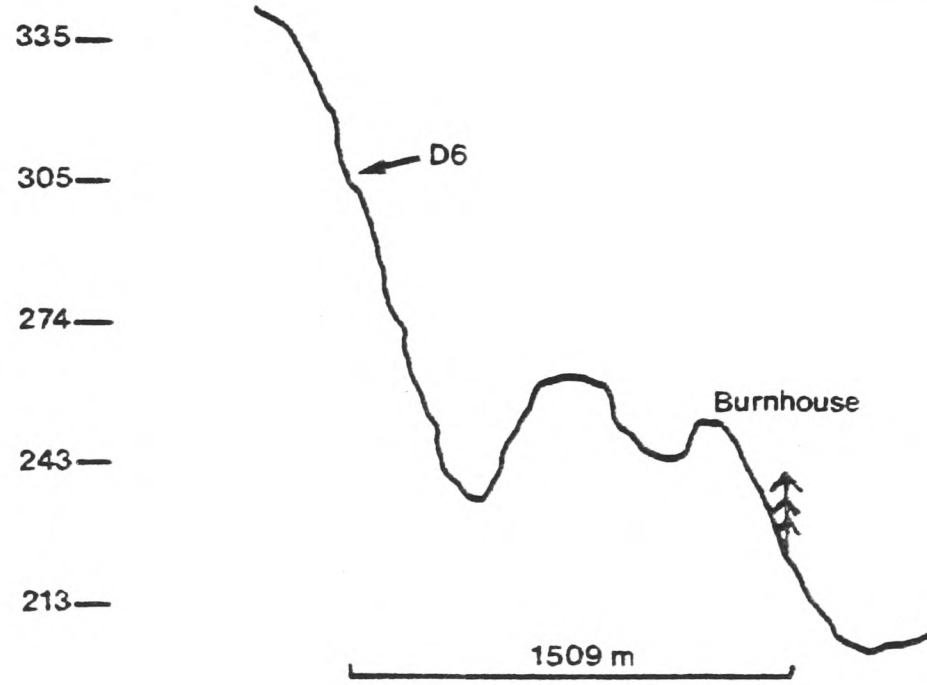
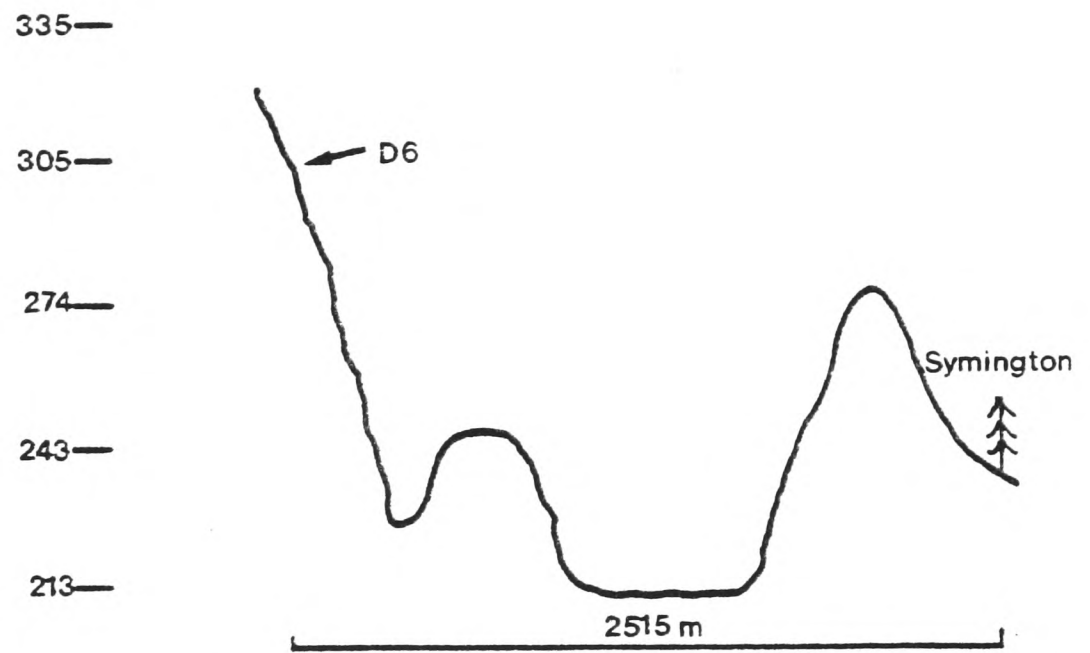


Figure 4-9

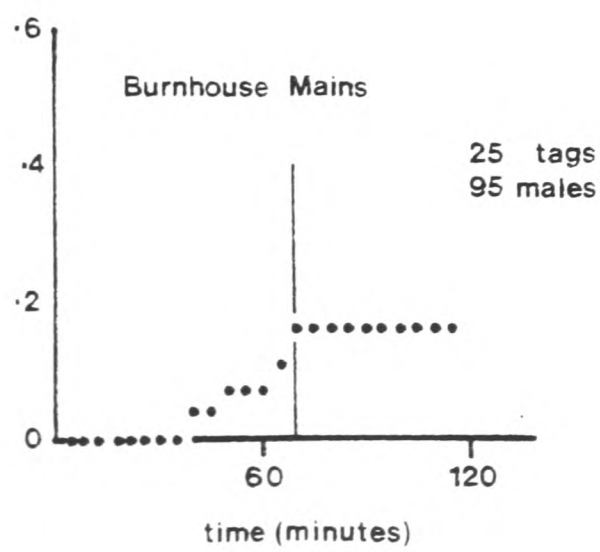
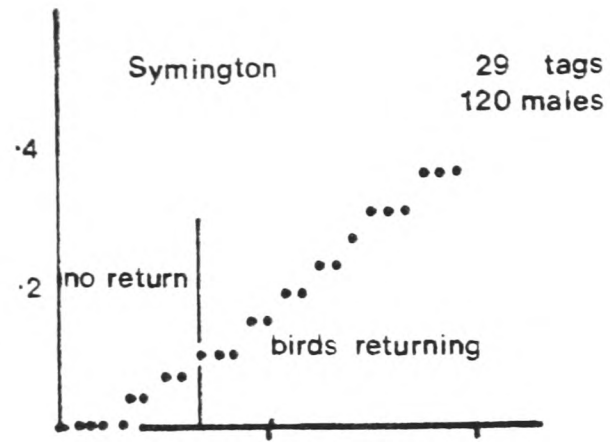
Arrivals at field H8 being harrowed from each of the three rookeries.

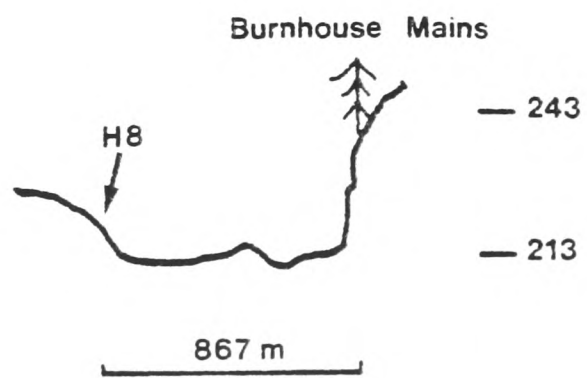
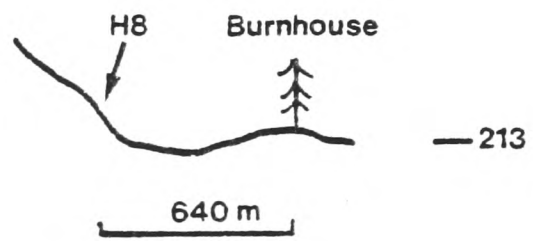
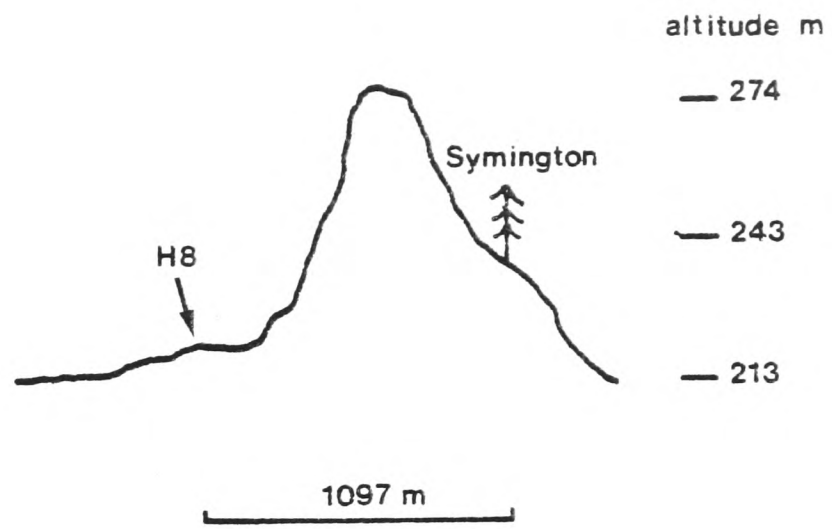
Other details as for Figure 4-5

Figure 4-10

Cross section of the terrain between field H8 and each of the rookeries

proportion of new recruits available which arrive during time interval (cumulative)





in the case of Burnhouse Mains.

TABLE 4-4

Arrival rate, expressed as proportion of new recruits available
which arrive per minute, before and after first return,
for field H8, 2.5.80, see Figure 4-7.

Rookery	rate before return	rate after return
Symington	0.003	0.004
Burnhouse	0.009	0.014
Burnhouse Mains	0.002	0.0

4.3.4.4. Results: Other fields

Field G2 was observed for one hour whilst being ploughed on 18.4.80. When the tractor stopped, only one bird had returned to the field.

Field S7 was observed during rotovation on 7.5.80 for 1412-1535 hours. Only 6 returns were made, 2 from each rookery, and no new birds arrived after their return. Total numbers on the field dwindled from 50 soon after starting, to 6 at the end of the session.

Field S7 was watched again on 12.5.80, from 1255-1510 hours, this

time being harrowed. Only one bird was seen to return, and at no time were there more than 10 birds on the field, often dropping to just 2.

Field T6 was watched from 0900-1200 and 1300-1600 on 5.4.80. Only untagged birds arrived, attaining a maximum flock size of 3 at any one time.

4.3.4.5 Discussion of field experiments

Explaining these results is problematic, since many influences are apparent and probably exert their effects to varying degrees in each case.

First return

It is clear that birds from Symington recruit to D8 much more rapidly after the first bird returns, the rate increasing by a factor of four after the first return. Trends in the same direction can be seen also for Burnhouse and Burnhouse Mains birds, although the change does not coincide exactly with the return of the first tagged bird. The differences in rate are less in Burnhouse, and non-existent for Burnhouse Mains birds, for there is an increase in arrivals before first return (Figure 4-5). The increase is very close to the time of the first return.

Noise

Noise exists in the system in the form of untagged birds. It is possible that untagged birds from the same rookery have returned to

the field before the first observed tag returns, and thus an increase in the arrival rate of new tagged Rooks could be caused by the return of an untagged bird arriving just prior to the return of the first tagged bird. In fact this is very likely, since there were always more untagged than tagged males attached to a rookery. In all cases this could be the cause of a point of increase before the return of the first tagged bird, although it is also possible the first returned bird may have been missed during a scan. Another source of noise is the recruitment of birds from nearby fields. Although the results of this will be small, from the results of radio telemetry presented in Chapter 3, it is a factor which could be usefully controlled in future experiments.

Perhaps the best evidence for a recruitment mechanism which does not utilize direct visual cues comes from the birds of Symington rookery, see Figure 4-5. Here, 55% of all tagged birds of a rookery 2.5km away completely obscured by hills, visited one field during a 3 hour period, and increasingly so after the first return visitor. It is difficult to see how else such recruitment could have occurred, except by individuals following others from the rookery.

Visibility of feeding site from colony

The effect of a feeding location being in or out of sight of a colony, which one would logically expect to have a strong effect, appears to have little influence on the first set of results. Burnhouse and Burnhouse Mains represent in and out of sight rookeries respectively, yet show essentially similar recruitment patterns (Figures 4-5 and 4-6). Furthermore, the tabulated recruitment rates are in the opposite direction to that predicted by birds following

each other from the Rookery (i.e. the in-sight rookery shows a greater difference after the first return than the out of sight colony). For the field D6 harrow, 24.4.80, the effect of being in or out of sight of the colony again seemed to have little effect upon recruitment patterns, for Burnhouse Mains is in a direct line of sight from the field, and birds from this colony showed the same steady rate of recruitment as birds from Burnhouse rookery, whose line of sight is obscured.

Plough or harrow?

The fact that D6 was harrowed on 24.4.80 introduced another variable to be considered, namely the difference between ploughing and harrowing with respect to food quality. Although no measure of the feeding rate of harrowed fields was made, it seems likely that a field being harrowed is less good than a field being ploughed due both to the nature of the original substrate (undisturbed soil will have a higher invertebrate population than weathered ploughed soil), and the degree of soil disturbance of harrow against plough (Evans and Guild 1948). As a result, it is possible that better food sources were available elsewhere simultaneously, to which birds may have been recruiting. Nevertheless, D6 harrow was much utilized by Rooks.

Table values

Table 4-3 does reveal a doubling of the proportional arrival rate after the first return from field D6. However, these table values may be misleading since they do include the initial pre-discovery phase, i.e. that time between the commencement of observations and the arrival of the first tagged breeding male, which will depress the initial arrival rate. However, they are valid when comparing

discovery rate against a 'random search' model, since if search was random, one would expect a constant arrival rate. However, recruitment to grass fields shows that the largest differences in the effect of feeding birds causing others to land occurs in the flock size range between 1-4, and this could give rise to results presented in the table, so birds could just be using local enhancement to others on the ground, although given the distance from the colony of some fields, this seems improbable. Another reason for an initial lag could be that birds only started looking for food after a period of time had lapsed since observations commenced. This is not a realistic explanation, for birds start feeding soon after dawn (Coombs 1961b) and observations were started well after this time. Interestingly, only 1 Symington bird was observed on the field, and it did not return, which could have been because other better sources had been discovered closer to that rookery. There is likely to be some kind of cost-benefit analysis by the Rook between the relative quality of the food source for that day, and the distance flown to feed (see Chapter 3, also Tinbergen 1981).

Other fields

The lack of consistent effects of feeding locations in and out of sight of the colony occur again in the case of H8 harrow, 2.5.80. Symington is out of sight, Burnhouse is in sight, and both show similar patterns of recruitment, bearing no especial relationship to the time of the first birds to return. Burnhouse Mains shows a more rapid recruitment before any birds return, but then after the first return, recruitment stops. This colony shows much less utilization of the field than either of the other colonies, indicating that factors apart from the number of birds on a field, in full view of a colony,

affect recruitment. After an initial pair of birds returned to the field, only one other was seen to return from Burnhouse Mains. So the situation of birds returning regularly without causing recruitment, which would show that local enhancement from the colony was not occurring, was not observed.

The four fields which failed to recruit may represent a reaction of Rooks to a stimulus (tractor disturbing surface) which often represents a good feeding location, but which failed to produce the goods. In one instance, G2, time was probably the factor preventing recruitment, since the processing of the field soon stopped. The two records for S7, 7.5.80 and 12.5.80. probably represent a poor food resource. This field was ploughed the previous autumn, and presumably few surface invertebrates remained during the spring harrowing. The fact that the absolute number of Rooks was never high and then declined, supports this view. Field T6, 5.4.80, was also a poor food location, for observation of one bird over a 3 minute period indicated a low intake rate, a total of 6 items (i.e. a mean of 2 items/minute compared with a mean of 21.7 items/minute for all ploughed fields, see section 4.4). In all cases, birds had probably found superior sites elsewhere, and may have been recruiting to those. The difference between ploughing and harrowing is further complicated by the use of the field being processed. Hence a field being harrowed which had been pasture for five years prior to ploughing may have a better prey density than initial ploughing of a field which has been under grain for five years.

From these results it is clear that there is no simple mechanism of recruitment to a new good food resource, (for example, that birds

locate a good field from the numbers of Rooks using it, unless it is out of sight, in which case they follow 'purposeful' individuals out from the colony). It is apparent from only one graph, Figure 4-5, that recruitment is occurring, and not by simple random discovery.

Further interpretation of the results is limited by the original data, for only 2 of the fields watched were being ploughed, the rest being harrowed. So whilst the harrowed field was being watched, a better field being ploughed may have existed elsewhere, and food quality of a harrowed field may have been insufficient to promote a Rook utilizing that field to return. I was not able to simultaneously sample the environment for all fields being cultivated whilst monitoring recruitment rate and intake rate on one field.

Local enhancement occurring in this way has been formalised into the information centre hypothesis. This has been reviewed most recently by Mock (in press), and briefly states that certain aggregations (colonies, roosts) serve to aid individuals locate food where their search has been unsuccessful. No study has shown that this actually occurs, and the two most recent studies where members of a roost (Fleming 1981) and a colony (Andersson et al 1981) have located a good food source, fail to bring new birds to the food on their return. The problems of falsifying this hypothesis are considered further in Chapter Six.

4.7 SUMMARY

1. Rooks are more likely to land in a field if it contains Rooks than if it does not, and this effect increases with the number of birds on the field.
2. The effect of flock density on the likelihood of a bird landing depends on flock size, and only at larger flock sizes (11-20 birds) is there a significant effect of spacing between birds on the attractiveness of the flock.
3. Whether individuals were using others to locate distant out of sight food sources was investigated by watching arrival patterns at known good novel food sources.
4. Results were extremely variable. In one case a sharp increase in the number of new arrivals coincided with the first bird to return to the field. Because in most cases it was possible that better food sources occurred elsewhere, further interpretation is problematic.
5. Whether a food site was in or out of sight of a colony had little effect upon the pattern of recruitment to a feeding location.

CHAPTER FIVE

DEPARTURE PATTERNS FROM THE COLONY

5.1 INTRODUCTION

Results presented in Chapter 4 of observations at feeding sites do not allow full evaluation of how important local enhancement is at the colony to aid in locating distant food sources. Another manifestation of the process will occur at the colony, for the easiest way for one individual to take advantage of a good feeding location discovered by another is to follow it from the colony. If this occurs, departure of individuals from a colony should be temporally clumped.

5.2 INITIAL INVESTIGATION - MACKIMRICH ROOKERY.

Initial investigation of departure patterns was done during April-May 1978 at Mackimrich rookery located approximately 7km north of the study area (see Figure 2-1, the rookery top left marked 80 nests). Initial observations involved monitoring all departures from the rookery, but it soon became apparent that birds which left simultaneously did not all head in the same direction. Indeed, often a number of birds departed together but soon split and headed in several directions. This indicates that one bird leaving the colony may facilitate the departure by others, so stricter criteria must be used when trying to assess whether birds are following each other from the colony in an attempt to find food.

5.2.1 Methods

To overcome this, I spent some time observing the destination of birds departing from the Mackimrich colony, which could be easily categorized because Rooks restrict themselves to a few distinct 'flight lines' from their rookery (Patterson et al 1971), so their destination could then easily be predicted soon after departure. The method then adopted was to observe from a position approximately 300m from the colony (see Figure 5-1) the time of each departure to the nearest second, and as soon as it became apparent the destination of that individual was also noted. The results from these observations consisted, for each destination, of the time at which each individual Rook left the colony. From this data set, the time interval between each departure was calculated and these used to test for aggregation in time. If Rooks are leaving their colony for a specific feeding ground on a random basis, the departure intervals for that specific feeding ground should conform to a random pattern which will take the form of a negative exponential distribution (Andrzjewski and Wierbowska 1961). Any tendency to aggregation will take the distribution away from this. The distribution of departure intervals was tested using the W exponential statistic (Shapiro and Wilk 1972) which is defined as follows:

$$W = n(\bar{y} - y_{\min})^2 / (n-1)S^2$$

where

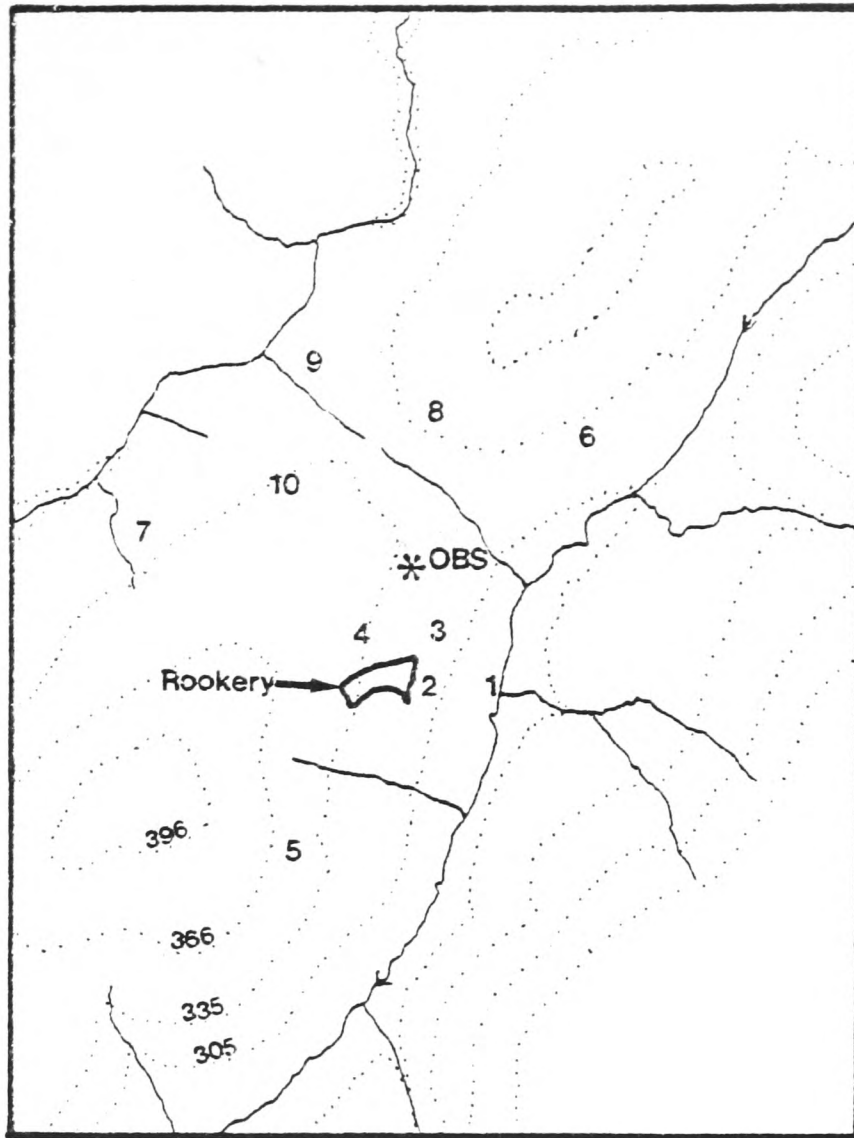
$$S^2 = \sum_{i=1}^n (y_i - \bar{y})^2$$

n = number of inter-departure intervals

\bar{y} = mean inter-departure interval

Figure 5-1

Feeding areas of Mackimrich rookery used in preliminary observation
of departure patterns.



1 - 10 = feeding locations

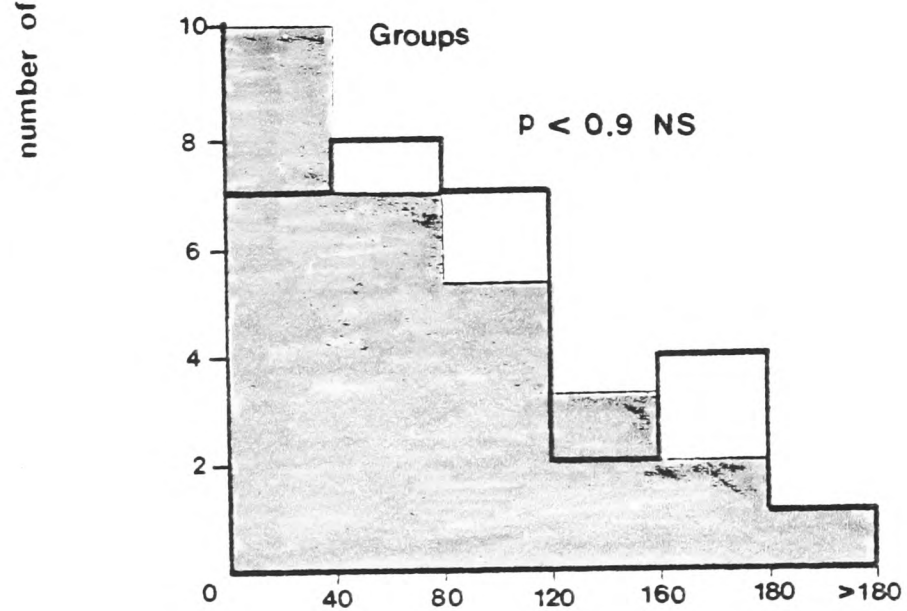
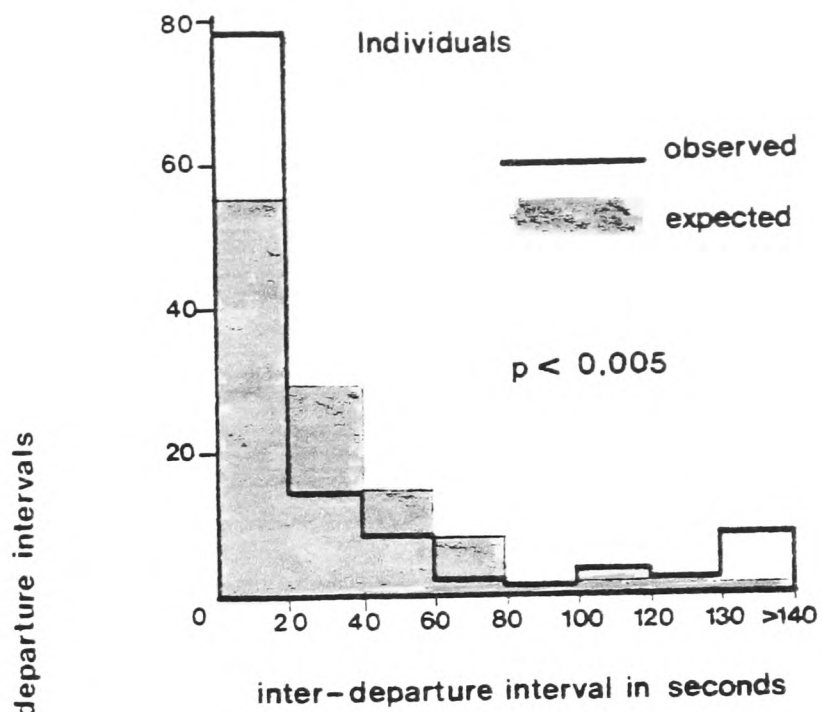
y min = shortest inter-departure interval

The W statistic calculated is then compared to values in tables for the appropriate N (number of inter-departure intervals) given in Shapiro and Wilk (1972). All results for temporal clumping are analysed using this formula, which has also been used to analyse for clumped arrival times of Ospreys Pandion haliaetus at their feeding grounds (Prevost 1977).

If clumping does occur its meaning is best explained by referring to Figure 5-2. These histograms show pictorially the distribution of departure intervals to area 5 in Figure 5-1. The expected values are calculated from the formula in Andrzejewski and Wierbowska (1961) cited in Krebs (1974). In the top figure of Figure 5-2, referring to departure intervals of individuals, there are far more short and long inter-departure intervals, with fewer of intermediate length than would be expected in a random situation. This indicates that birds are leaving in groups (many with short intervals between departures) with long periods between these. The lower figure of Figure 5-2 shows the distribution of departure intervals between these groups, where a group is taken as any individual departure or group of departures separated by more than 40 seconds from another. The figure of 40 seconds was arrived at by watching individuals leaving the colony, because after 40 seconds they were normally out of view of myself and in most cases from the rookery also. The distribution of the inter-departure intervals of these groups is not significantly different from a random pattern.

Figure 5-2

Pictorial representation of clumped and unclumped departure patterns
using data for Rooks from Mackimrich rookery on 5.5.78., feeding
on area 5



5.2.2 Results.

The location of the feeding grounds are shown in Figure 5-1. Departure patterns were only analysed if more than 7 flights (arbitrary figure) were seen to that area during the observation period. The results for this set of observations are given in Table 5-1.

The number of flights to different areas varied greatly from day to day, suggesting that different areas were used on different days (Chi square = 434, d.f. = 35, $P < 0.001$, lumping areas 8, 9 & 10). Departures to the distant regions 5-10 were significantly clumped in 11 of 15 occasions, whereas only 6 of 12 departures to the closer feeding areas were significantly clumped. This difference between departures to close and distant feeding grounds is not significant (Chi-square = 1.65, d.f. = 1).

It is possible that time of day could have affected the results if Rooks used different areas at different times of day, for instance by avoiding areas subject to frost first thing in the morning. The first two days' observations were made between 0800 and 0900 hours, and the last four between 1400 and 1500 hours. However, testing each of these two groups also revealed a significant effect within each group between days. Chi-square for 14.4.78 and 19.4.78. was 44.93, d.f. = 7, $p < 0.001$. Chi-square for the last four days, necessitating lumping of areas 1 and 2, was 248.2, d.f. = 14, $p < 0.001$.

TABLE 5.1

SUMMARY OF DEPARTURE PATTERNS FOR MACKIMRICH ROOKERY DURING 1978.

		area									
date		1	2	3	4	5	6	7	8	9	10
14.4.78	W	.0269	.0508	-	-	.0642	.0254	.0036	-	.026	-
	P	.005	NS	-	-	NS	.01	.005	-	.005	-
	N	10	19	7	6	15	15	68	4	13	0
19.4.78	W	-	.0474	.0270	.0120	-	.0155	.0809	-	-	-
	P	-	NS	.01	NS	-	.01	NS	-	-	-
	N	0	17	15	12	2	34	8	0	3	0
21.4.78	W	-	-	-	.0145	.0076	-	-	-	-	-
	P	-	-	-	.005	.005	-	-	-	-	-
	N	0	2	6	33	64	3	0	0	0	0
24.4.78	W	-	-	-	.0505	.0155	-	.0072	-	-	-
	P	-	-	-	NS	.005	-	.005	-	-	-
	N	0	6	2	14	25	5	47	0	1	5
25.4.78	W	-	.0223	-	.0186	.0132	-	.0297	-	-	.0180
	P	-	.005	-	.005	.005	-	NS	-	-	.005
	N	0	15	6	18	29	6	17	0	0	19
28.4.78	W	-	.0164	-	.0203	-	.0233	-	-	-	.0410
	P	-	.01	-	NS	-	.01	-	-	-	NS
	N	1	28	7	37	4	19	0	0	0	21

W = Shapiro-Wilk statistic

P = Significance level

N = number of flights observed during 45 minutes from rookery to feeding areas

5.2.3 Discussion

It is arguable that departures to the nearby areas of 1-4 should never show a significantly clumped departure pattern, and the fact that it does occur suggests that other factors may be at work in promoting group departures than simply following a knowledgeable bird. However, at the time of departure from the colony, a follower may not know where the initial bird is going, thus it could also be argued that no difference would be expected, the only difference being picked up at the arrival of birds at the feeding field. Here, one would predict a less clumped arrival pattern at a field visible from the rookery since the field would be recruiting by a mixture of local enhancement to others present by direct sight, as well as by following others out of the colony. In reality, if birds are following each other, such group departures will occur at certain times only in relation to the development and decline of a feeding location. Thus if a number of good food sources are in simultaneous use, a less clumped departure pattern would be expected as each bird would presumably return to its own favoured source without following. If birds do sometimes use others to locate food, they may not do so all the time, but if only a few food sources are available, i.e. first thing in the morning after overnight snow, the clumping should be far more extreme. Only in those cases where a guaranteed food source can be seen close to the rookery would one actually predict a comparatively unclumped departure pattern, assuming that the clumping is being caused by active following by naive individuals.

In summary, these initial results show two things. Rooks concentrate their feeding to a few areas at any one time, which change

from day to day. Departure patterns are sometimes very clumped in time, suggesting that one mechanism by which Rooks latch onto their particular feeding area may be by following others. Sometimes departure patterns are not clumped, and there appears to be little relationship between this and the distance of the food source from the colony.

5.3 FOLLOW UP INVESTIGATION - MAIN STUDY AREA

5.3.1 Introduction.

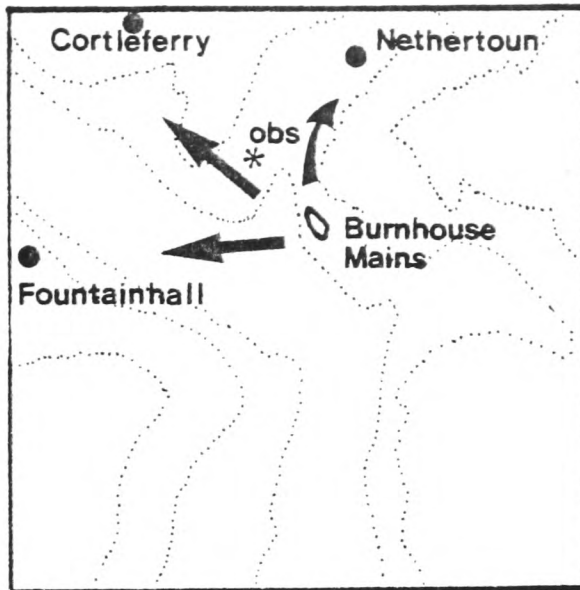
During 1979 and 1980, the type of data collection applied to Mackimrich Rookery during 1978 were applied to Burnhouse and Burnhouse Mains rookeries, in order to check that clumped departure patterns were not unique to Mackimrich rookery. In addition, other detailed records were kept of arrivals and departures at individual trees. Activity of individual birds in the rookery ~~were~~ monitored in an attempt to identify cues used to follow birds, and to measure departure patterns on the small scale. A brief look at arrivals at certain fields was also undertaken to see whether birds which actually leave in groups arrive at the feeding grounds in groups also.

5.3.2 Methods.

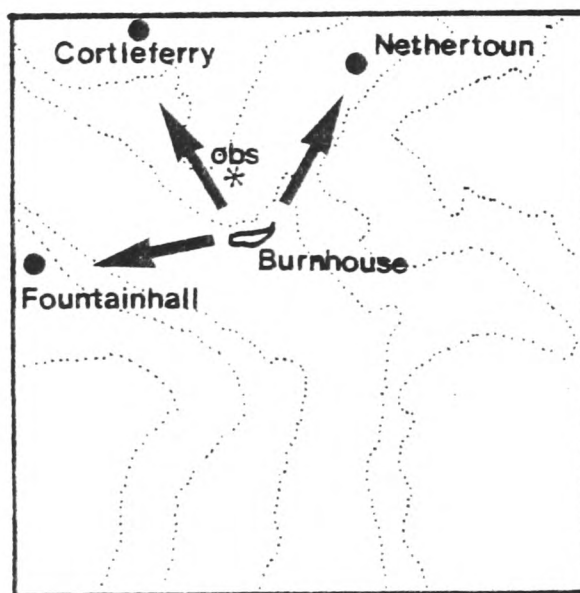
For departure data of the rookery, Burnhouse Mains was watched from a distance of 200m at the top of a bluff (Figure 5-3). Destinations could only be categorised into three directions due to the physical relief restricting flight lines. The rookery was watched for one hour

Figure 5-3

Flight paths used for analysis of inter departure intervals for
Burnhouse and Burnhouse Mains rookeries



1 km



on each of 6 days, between 14 April and 22 May 1980, and Burnhouse was watched on each of 3 days between 16 April and 23 May 1980, spanning a period from incubation through to the late nestling stage. All observations were made between the hours of 1000 and 1200.

In order to see how the Rooks of neighbouring nests may interact, during April and May 1980 one tree from each of Burnhouse and Burnhouse Mains rookeries were selected for more detailed observations. The trees were selected because they were easy to observe, with no obscuring branches, and because they were central, with other nesting trees to either side, back and front. The tree in Burnhouse contained 8 active nests, that in Burnhouse Mains 6. Each time a bird arrived at or departed from the tree the event was recorded. The aim of these observations was to reveal something of the nature of the cues used by Rooks when deciding whether to follow another individual from the colony.

To see whether birds were arriving in groups at the foraging site, two permanent pasture fields outside the study site were watched for a period of one hour each in 1978, and one similar field in the study area was watched for an hour on each of 7 and 9 April 1980. The time of arrival of each bird was noted, and the distribution of inter arrival intervals was tested for temporal clumping by the Shapiro and Wilk W statistic (section 5.1.2).

5.3.3 Results.

A. Clumping in departures from the rookery.

Details of observer location and flight paths are given in Figure 5-3. The significance levels of clumping for each flight path for each day are given in Table 5-2. In general, departure patterns from Burnhouse Mains are all extremely significantly clumped in time, with the exception of those going to Fountainhall, where they were only once. Table 5-3 shows that areas were used to varying extents, as judged by the number of flights to that area, on each day, a difference which is significant (Chi square = 79.6, d.f. = 10, $p < 0.001$).

TABLE 5-2

Significance levels for departure patterns from Burnhouse Mains
on different flight paths.

date	direction	P	W	N
14.4.80	N'toun	0.005	0.0021	183
	C'ferry	0.005	0.0090	53
	F'hall	0.077	0.0775	11
16.4.80	N'toun	0.005	0.0036	136
	C'ferry	0.005	0.0252	121
	F'hall	0.025	0.0252	18
08.5.80	N'toun	0.05	0.0111	67
	C'ferry	0.005	0.0130	30
	F'hall	-	-	0
14.5.80	N'toun	0.01	0.0085	67
	C'ferry	0.005	0.0120	29
	F'hall	-	-	0
20.5.80	N'toun	0.025	0.0113	55
	C'ferry	0.005	0.0063	68
	F'hall	0.005	0.0298	12
22.5.80	N'toun	0.005	0.0055	84
	C'ferry	0.005	0.0027	85
	F'hall	0.10	0.0907	8

P = significance level
W = Shapiro-Wilk statistic
N = Number of departure intervals

TABLE 5-3

Differential use of flight paths between days for birds
from Burnhouse Mains.

Day	N'toun	C'ferry	F'hall
1	183	53	11
2	136	121	18
3	67	30	0
4	67	29	0
5	55	68	12
6	84	85	8

Observations of the departure patterns for Burnhouse rookery also revealed significant clumping in time, as shown below in Table 5-4.

TABLE 5-4.

Significance levels for departure patterns from
Burnhouse rookery on different flight paths.

date	direction	P	W	N
16.4.80	F'hall	0.005	0.0045	83
	N'toun	0.005	0.0153	17
18.4.80	F'hall	0.01	0.0108	52
	N'toun	-	-	2
23.4.80	F'hall	0.01	0.0253	16
	N'toun	0.005	0.0018	175
	C'ferry	0.005	0.0034	119

The flight lines for Burnhouse rookery are shown in Figure 5-3.

B. Length of absence compared with subsequent stay at the nest.

The results from those nest observations where a departure was missed were eliminated from the analysis of the data. The 8 occasions when no departures were missed were observation periods of 2 hours, and all showed slightly positive but insignificant correlations between length of time spent away from the nest (probably foraging), and length of time spent at the nest before the subsequent foraging flight, as revealed in Table 5-5.

TABLE 5-5

Relationship between time spent away from the nest (presumably foraging), and subsequent time spent at the nest.

date	nest	rho	P	N
1.5.79	BHA4	+.56	NS	7
5.5.79	BM21	+.66	NS	6
	BM23	+.87	NS	5
	BM24	+.20	NS	4
7.5.79	BM21	+.42	NS	9
	BM23	+.40	NS	5
	BM24	+.44	NS	4
9.5.80	BM11	+.20	NS	5

The lumping together of all these data, for different birds on different days, revealed no trend ($\rho = -0.0487$, $N = 44$). It is possible that the non-significant trends were due to small sample sizes, and that individuals show consistent trends between days in the

relationship between time spent at the nest and away foraging. For this reason, observations made on the same bird on different days were lumped but these showed no significant trends either. The results are given in Table 5-6.

TABLE 5-6

Relationship between time spent away from the nest and subsequent time spent at the nest, lumping different days' observations.

nest	rho	N	P
BM21	+0.37	15	NS
BM23	+0.18	10	NS
BM24	-0.22	8	NS

However, that all correlations in Table 5-5 are positive is itself non-random (Runs Test, $p < 0.005$), suggesting a positive effect of time away and subsequent time at the nest, the non-significance of the individual results probably being a result of small sample size.

C. Clumped departures from particular trees.

Departure patterns from individual trees from each of Burnhouse and Burnhouse Mains rookeries were not found to be significantly clumped. These results are summarised in Table 5-7.

TABLE 5-7

Summary of results of departure patterns from individual trees.

tree	date	W	P	N
BHA	18.4.79	0.1522	NS	14
BM2	4.5.79	0.0542	NS	17
BM2	2.5.80	1.8761	NS	23
BM2	9.5.80	0.0917	NS	11

D. Clumping in arrivals at pasture fields.

Arrival patterns at permanent pasture fields are summarised in Table 5-8.

TABLE 5-8

Summary of results of arrival patterns on permanent pasture fields.

date	FS	W	N	P
5.5.78	9-53	0.0080	58	0.005
8.5.78	15-26	0.0125	37	0.005
7.4.80	5-19	0.0108	24	0.01
9.4.80	5-13	0.0120	39	0.005

All arrival patterns displayed an extremely clumped pattern. The data presented are only for flocks which maintain above 5 birds on the

field. In Chapter 4, this effect of birds being present on the field attracting others to land was greatest in the region between 1 - 4 birds, so fluctuations beneath this critical level could present an identical temporal clumping pattern. If a flock periodically fluctuated above and below the 4 birds, this flock would effectively be alternating between being attractive and non-attractive to birds flying overhead. This could give a similar temporal clumping of arrivals. All fields observed were in sight of the colony, and an interesting comparison for further study would be between in and out of sight fields and the effect of this on recruitment patterns (i.e. clumped or non-clumped).

E. Further evidence.

During two observation sessions of Burnhouse, further evidence of the importance of following others was obtained from the switching of direction of flights from the colony. During a routine departure pattern observation on 1 May 1979, Tree A was watched from 0844 until 1030 hrs. Until 0926, each of the 9 departures observed were to Nethertoun (Figure 5-3). Male 2 then flew out to Cortleferry at 0926 when males 7 and 8 were resting by their nests. The male of nest 8 flew out to Nethertoun, but thereafter also switched direction to Cortleferry at 1009, when males 2, 6 and 7 were resting by their nests. When male 6 departed at 1015, it switched its direction to Cortleferry, as did male 2 on his next departure at 1021. However, none of these birds left with other members of the same tree.

On 18 April 1980, departures from Burnhouse were observed from 1009 until 1120 hours. In the first 51 minutes there were 73 departures to

Cortleferry, but only 4 to Nethertoun. However, over the following 2 minutes, there were 8 departures to Nethertoun, and over the next 18 minutes a total of 15 to Nethertoun but only 8 to Cortleferry.

These two sets of observations suggest that birds are aware of where others are going, and sometimes act on this information. This suggests that apart from individuals following one another, information could be gathered from simple observation of common departure directions whilst resting at the nest. Unfortunately, the flight directions from all other trees were not recorded.

5.4 Discussion: colony departures

It is clear that most flights are socially facilitated, and a number of alternative hypotheses may account for this; residual anti-predator behaviour and the following of others to find food are two. Another may be that as females suffer from mass rape during incubation and early brooding, males may hang back until others leave in an effort to stop this. Testing the latter is difficult, for even if it could be shown that birds leaving in groups suffered less from interference, there would be no proven causal link.

The switching between areas between days and within days is also open to alternative explanation. An individual may discover a good food location and others may follow, or alternatively individuals could all have learned independently about temporal locations of the best food in their home range and be switching their feeding locations in response to this. One experiment which could test between these

two hypotheses would be to create a superior food source in an area infrequently used by Rooks and observe how the members of a colony recruit to it

The positive trend between time out feeding and time at the nest has several possible causes. After a long and unsuccessful food search, an individual may spend a long time in the colony to assess the predominant flight lines. However, if a long time out is a result of a series of fields being utilized but the last one was very good, this relationship would be weakened. These hypotheses could be tested by following an individual around, measuring feeding behaviour and subsequent behaviour at the nest. A further possibility is that after a long foraging bout a bird needs a longer period at the nest, for instance to relieve the female, to fight off nest encroachers or to preen.

That birds from specific trees were not clumped is probably an effect of small number of birds in the tree, resulting in a small number of departures. The general observation that birds followed others from elsewhere in the colony, that one bird leaving appears to precipitate other departures throughout the colony, and that individuals on surrounding fields lift and join outgoing groups, suggests that when local enhancement occurs, it is a colony-wide phenomenon, not restricted to within a tree.

Birds arriving together on a small sample of grass fields did so in groups. Again this could be the result of following behaviour, some kind of anti-predator activity, or the result of birds departing for some other reason in a group, and not splitting. Birds arriving in

groups support, but cannot prove the mechanism of local enhancement. Finally, the qualitative reports in (E) can be explained by individuals remembering what others in the tree are doing, by observations of what other birds in the colony are doing, or simply by a simultaneous but independent response to learned temporal variations in food availability in the home range.

In conclusion, all these findings suggest further work in order to test between various alternative causal mechanisms. The variety of measures taken complicate a synthesis of ideas presented in the thesis, but this is attempted in Chapter 6.

5-5 SUMMARY

1. Birds which left the colony on specific flight lines to various feeding grounds showed a significantly clumped distribution of departure patterns. Arrivals at grass fields were also temporally clumped. This is congruent with the idea that birds follow each other to new feeding locations, but can also be accounted for by other factors, including anti-predator behaviour.
2. The utilization of feeding grounds changes significantly from day to day.
3. It is suggested that a Rook may locate food by following others, and that its importance will vary depending on other cues available, such as the availability and need for food.

CHAPTER SIX

THE EVOLUTION OF COLONIALITY IN THE ROOK

6.1 INTRODUCTION

This chapter is speculative, and deals with the evolutionary ecology of the genus Corvus. By making interspecific comparisons of ecology and behaviour, I will attempt to reconstruct the selection pressures and intrageneric relationships which have given rise to the species characteristics within the genus. Special emphasis will be given to the Rook itself to account for its colonial nesting habit.

The genus Corvus contains 42 species, ranging in size from the Jackdaw (mean male weight 194g) to the Raven (mean male weight 1560g) (Coombs 1978). Its members are fairly similar, having an all black plumage, sometimes with areas of grey to white. The Corvus species share behavioural traits with other members of the family Corvidae. Such traits include prolonged courtship feeding, nest building and feeding of young by both sexes, incubation and brooding by the female only; breaking of food by the bill whilst held in the feet, burying of food, loud, harsh calls; omnivorous and more or less predatory feeding habits and a bold and inquisitive nature (Amadon 1944). Indigenous species are found throughout the world excepting New Zealand, South America and Antarctica, and in all types of habitat from arctic tundra to tropical forest. Some species are found in a range of habitats; the breeding range of the Raven stretches from the arctic with a continuous distribution to Central America. Amadon (1944) provides a succinct introduction to the genus,

"Corvus is the most advanced and successful genus of the Corvidae. Its large size and resilient, adaptable behaviour have enabled it to exploit many secondary habitats produced by human activities. It has spread to many areas not otherwise inhabited by the group and as a result has split into almost three times as many species as any other genus of the family."

Most of the 42 species defend a year-round, all purpose nesting and feeding territory (Type A, Hinde 1956). 24 of the 42 are confirmed as being territorial, with a further 8 probably being so (see Appendix 5). Of the remaining 10 species, 6 may be regarded as loosely colonial, so although nests are not normally found in the same tree, the defended area is small, and the feeding area is shared with others and is undefended (Type B, Hinde 1956). Of the four remaining species, 2 are the Jackdaw species (C. monedula and C. dauricus). Whether these two species breed in colonies depends on the dispersion of holes used as nesting sites. The holes may be aggregated, as in an old lime kiln, or they may be dispersed, as when using holes in trees. The only defended area is the nest hole, whilst the feeding area is undefended and shared with others. The remaining species are the Rook and Somali Crow. Very little is known about the latter, but in the Rook, pairs defend only a small area around their nest, and individuals share their feeding area with Rooks from the same and other colonies.

6.2 GEOGRAPHICAL GROUPS

Each continental landmass has its own group of Corvus species, several sometimes being sympatric. Western Europe has the Raven, Carrion/Hooded Crow, Rook and Jackdaw, which can all occur

sympatrically where ecological conditions allow. In North America there are 7 species, the Raven, the American White Necked Raven C. cryptoleucos, the Common Crow C. brachyrhynchus, Northwestern Crow C. caurinus, the Fish Crow C. ossifragus, Mexican Crow C. imparatus and the Sinaloan Crow C. sinaloae. Here only 3 species are normally sympatric, generally one raven, the Common Crow and one of the smaller crows (Northwestern or Fish). In Australasia too there are 5 indigenous species, the Australian Crow C. orru, the Little Crow C. benetti, the Australian Raven C. coronoides, the Little Raven C. mellori and the Forest Raven C. tasmanicus. Sympatric pairs of species exist, C. orru with C. benetti, and C. coronoides with C. mellori (Rowley 1973c).

The 7 species of Africa also form sympatric groups; the Pied Crow C. albus, the larger White Necked Raven C. albicollis, and the Black Crow C. capensis occurring together in many parts, whilst the arid areas are the domain of the larger ravens, C. crassirostris, C. rhipidurus, C. ruficollis and C. edithae.

Details of the general breeding and feeding biology of species are known for the European group but are lacking for the African, American, Australasian and other species groups. However, the ecological niches of sympatric species are similar for each geographical group. Apart from the arid regions, which tend to favour the larger ravens, there normally co-exist a raven, large-bodied with massive tearing bill, a smaller crow with a general purpose bill, and a smaller, slender billed crow with a more specialised diet, i.e. less carrion and vertebrate food with greater reliance upon invertebrates. In Australia, the sympatric species are reduced to two groups of two,

a larger extremely generalist feeder and a smaller, more specialized feeder (Rowley 1973a).

All crows are characteristically omnivorous and will eat most types of food presented. The implication that a Corvus species is a specialist is at variance with the idea of omnivory, and evidence of specialization will come from a study of the preferred food types of species co-existing in the same habitat. Investigation of the problem is hindered by the change of habitats caused mainly by man since the species evolved. One approach is to look at the food given to nestlings. In Corvus species, the food taken by adults for much of the year has an artificial component, generally in the form of grain or processed 'cake' fed to livestock, freely available in large quantities.. This is generally a low grade vegetable protein fed to herbivores for conversion into high grade muscle protein. As it is left on the surface of the ground or in troughs, the food is equally available to all Corvus species present, and overlap in the diets of the species is therefore artificially increased. However, when feeding their growing young, the adults must select a diet which is rich in animal protein, due to the rapid growth of the nestlings. To meet these requirements, the adults are restricted to collecting naturally occurring high protein food, so long as this is sufficiently abundant (Lockie 1959). Man's main effect here has been the artificial increase of certain invertebrates, due to an increase of soil fertility, and of field types affecting the availability of these prey items (e.g. increased supply of short grass). So the natural food now available may not be precisely the same as that available during the evolution of the species. At this stage of the annual life cycle the overlap in species diets will be smallest and differences

most easily discerned, for example by the relative proportions of different feeding actions used, especially when different species are utilizing the same habitat.

6.3 THE COMPARATIVE APPROACH

Crook's (1965) analysis of avian social organization revealed that only 6.3% of families were both colonial nesters and flock feeders, a small proportion are colonial nesters with defended feeding areas, the remainder holding all purpose nesting and feeding territories at least during the breeding season. All Corvus species exhibit gregarious phases; they form communal winter roosts, and those individuals of territorial species which are excluded from breeding habitats form roaming flocks whilst the others breed. As only 4 of 42 (9.5%) of Corvus species are colonial, it is possible that territoriality, rather than coloniality, is the ancestral social pattern in the genus, and coloniality a more recently evolved one. More important are the ecological correlates of social organization. To understand why coloniality may have evolved, a comparison of those aspects which might cause coloniality should be made between sympatric congeners, for here is a result of evolution working on the same raw material (hypothetical proto-Corvus) in various ecological conditions. There are problems with this method; apparent adaptations may be artefacts of post hoc reasoning, there may be confounding variables of associated conditions, and adaptation may have taken alternative paths to the same end. However, even the most rigorous of comparative studies suggest that the main ecological pressures affecting elements of social organization are the abundance and distribution of food and

predators (Clutton Brock and Harvey 1979). As discussed in Chapter 1, the possible influences considered here are access to mates or another limiting resource and the distribution and abundance of food and predators. Sufficient data for all continental groups are missing, so only the British species will be considered, but where differences have been studied in other sympatric groups, these will be introduced.

6.3.1 Mates

Emlen and Oring (1977) argue that where one sex has the opportunity to monopolise additional members of the other, the fitness of those individuals which succeed in doing so will be elevated. Acquisition of extra mates could be achieved by direct defence of a harem, or by monopolising a resource required by members of the opposite sex. As monogamy is the mating system in 90% of avian species, it is possible that the cost of attempting to acquire more mates is too great, perhaps because large amounts of parental care are required from both parents just to raise one brood. In other words, the costs incurred by the parent as a result of withholding care from one set of offspring whilst acquiring another mate may be greater than the benefits. In Rooks, a pair rarely manages to fledge all its hatchlings, nearly always losing some by starvation, unless the brood is small (1-2). Mean losses by starvation are 41% in broods of over 5 (Lockie 1955). A male would probably be stretched to raise two broods successfully, and this is confirmed from all reports of attempted bigamy seen in this genus (Rowley 1973, Green 1982). In addition, Davis (1976 and refs therein), has shown that for many long lived birds, mate fidelity leads to a demonstrable increase in reproductive success.

The future condition of the mate is therefore important, so that fitness may be maximised by equalising the burden of reproduction and sharing parental care. Evidence of mate fidelity in Corvus is scant. Studies on individually marked Ravens are non-existent, and no statement exists for the Carrion Crow, although here mate fidelity seems likely as only mated pairs seem able to retain their territory from year to year (Charles 1972). In Rooks and Jackdaws, year to year fidelity has been confirmed (Coombs 1960, Roell 1978).

To summarise, all four species are single brooded, the eggs are continually guarded, and in each species the male collects all the food for his female whilst she incubates, and during the first two weeks of nestling life. The opportunity for the female to successfully raise more than one brood is low since the male does not incubate. Although males in the genus have been reported to support two females (Rowley 1973, Green 1982), no male has ever been reported as rearing two broods, perhaps because of his inability to collect sufficient food. In conclusion, differences in social organization are unlikely to have evolved as a consequence of differences in mating systems, for the opportunity of departure from monogamy seems to be very restricted.

6.3.2. Access to another limiting resource.

In Chapter 1 it was noted that groups may form in order to defend a limiting resource from other groups. One case was that of the Acorn Woodpecker, which forms groups to defend 'granary' trees, in which winter and spring food supplies are held. Without such a tree,

breeding does not occur (Koenig 1981b). It could be argued that nest sites are limited and clumped for the Rook and Jackdaw, and that group formation is to defend these against other groups. In the Rook, there is no evidence that groups of nesting trees are defended against other groups of Rooks. The main piece of evidence ^{which} suggests group defence of the colony is not important in the evolution of group living in the Rook comes from the lack of inter-group encounters. The peaceful co-existence of birds from different colonies on the same feeding field (Chapter 3), and a lack of a defended feeding area also supports this conclusion. A similar absence of inter-group encounters over a scarce resource suggests that this is true for the Jackdaw also, even though nest sites may be limiting for this species.

6.3.3 Predation and Harassment

Assessing the effects of predation upon species is problematic: observations of predatory acts are rare and therefore difficult to quantify. Clearly the smaller the species, the larger the range of potential predators it has, and so Jackdaws have a larger number of predators than Ravens. Interestingly, it is the smaller species of each group of Corvus species which are colonial or semi-colonial. There is no evidence of differential predation on the British species, although due to the relatively predator free environment, this is not surprising.

Another explanation which regularly occurs for gregariousness is harassment from larger congeners (Rowley 1973c, Bossema et al 1974, Roell 1978). A size related interspecific dominance hierarchy has

been confirmed in the British species (Lockie 1956b, Coombs 1960b), and between Australian species pairs (Rowley 1973d). So the occurrence of a smaller species in either a nesting or feeding range of a dominant species puts ^{the smaller one} under threat.

6.3.3.1 Harassment at the nest

The assertion that Carrion Crows can cause desertion of rookeries by harassment was investigated and rejected by Green and Flintoff (1939-40). Their observations include several rookeries containing breeding Carrion Crows without any apparent ill effect. Coombs (1960b) and Roskaft (1980) report that Carrion Crows within a colony evoke a variable response, they may be expelled or apparently ignored. Given that the principal cause of egg and chick loss in some Carrion Crow populations is intra-specific predation by non-breeding flock birds (Charles 1972) as opposed to breeding pairs, it is arguable that the chance of a solitary, open nest of a Rook or Jackdaw surviving the attention of Carrion Crows would be low. Lone Rook nests, classified as being over 100m from the nearest nest, have been observed by Spencer (1951), Roell (1978) and myself. Roell reports that 6 of 8 nests he observed were harassed by Carrion Crows and eventually abandoned. Spencer did not observe the final demise of his nest, but found remains of it, including the young, but no lining material. He concluded that other Rooks had ransacked the nest and removed the lining material. This was only possible because the female was forced to leave due to infrequent visits by the male. The observations I made in two years on an isolated nest, suggested that it seemed to be infrequently visited by the male, who, in both cases, was often observed displaying in the main part of the colony. Perhaps isolated

nests do not survive well because of the attractiveness of the main part of the colony to the male, and it is possible that such observations result from poor nest site selection by inexperienced birds. The frequently evoked explanation of harassment by Carrion Crows may then be the result of 'easy pickings' caused by the female being forced to leave for food. There are no reports of a Carrion Crow attacking a lone nest of a Rook, forcing its inhabitants to leave, and then destroying the contents. Jackdaws gain protection from potential harassment by their hole nesting habit.

6.3.3.2 Harassment whilst feeding

When feeding within the territory of a Carrion Crow, Jackdaws appear to gain advantage by forming flocks (Roell 1978). Given the choice between two artificial feeding sites within the territory of a Carrion Crow, Jackdaws show a preference for that site at which other Jackdaws or Rooks are feeding. If there are Carrion Crows present at the site, Jackdaws show neither preference nor avoidance of that site, unless the territorial male Carrion Crow is present, in which case the site is avoided. Carrion Crows, on the other hand, prefer to land where Jackdaws are feeding, and at the same time, the Jackdaw feeding flock is less likely to be flushed by a harassing territorial male Carrion Crow the greater their number. Roell (1978) concludes that flock feeding in Jackdaws enables them to withstand attacks from Carrion Crows and that the vigour of the territorial defence of Carrion Crows contributes to their flocking habits. Flocking as a means of resistance to territorial attacks from a congener can be observed in non-breeding populations of Carrion (Charles 1972) and Australian (Rowley 1973) Crows. When using a feeding site within the

territory of a member of the same or a larger, dominant species, feeding is less likely to be interrupted as the number of individuals in the flock increases, although this is not to say that this is the main causal factor for flocking. In terms of the cost-benefit analysis of Chapter 1, the territorials are assumed to gain more by joining these intruders and feeding with them than trying to drive them away.

During their breeding season, the smaller of each of the Australian sympatric species pairs is often forced to breed within the large, all purpose territory of its dominant congener, normally as a result of lack of suitable nesting sites. Feeding by the subordinate species normally occurs in undefended treeless areas away from territory of the dominant species. However, the flock feeding habit of the subordinate species also provides a means of exploiting food within the territory of the dominant species when a rich food source occurs there (for instance the seeding or ploughing of a paddock). One advantage of flocking appears therefore to come from the inability of the territorial species to flush such a large number of birds (Rowley 1973).

However, individuals in the feeding flocks of the subordinate species may also gain from local enhancement to food patches, although this has not been studied (Rowley 1973). In section 1.4 and Chapter 5 it was suggested that colonial nesting may extend the local enhancement effect to birds who together utilize a large feeding range (Ward 1965). It is possible that if the semi-colonial Australian and North American species do gain a food finding advantage from flocking and do not defend an all purpose territory, then progressively closer

spacing of nests may occur in the future. They may be at an early stage in the evolution of coloniality.

There is no evidence for direct inter-specific aggression between other European species. So speculations, for instance on Raven-Carrion Crow interactions, cannot be made.

6.3.4 Food

More is known about the diets of the European species of the genus Corvus than other aspects of their biology. Such studies are easier than equivalent studies on predation and they are more likely to be funded as a result of the commercial impact of the Corvus species on farming practices, and their findings are illuminating because the three smaller species commonly occur together, having the same kinds of food present in their environment. In the west of Britain all four species occur together, often with other genera of the Corvidae. The food available to each species will be restricted by micro-habitat preferences and physical attributes of the birds themselves e.g. size (agility) and bill characteristics. It seems likely that habitat overlap between species is greater now than in the past, due partly to the greater homogeneity caused by farming practice, but also to the supply of artificial food which can be used by all species.

The food of the Raven is least well studied, and ^{data} is only available in the form of percentage of castings containing the remains of a particular food type (Ratcliffe 1962, Marquis, Newton and Ratcliffe 1978). Such data are only useful in a very general qualitative

comparison, and are also affected by the artificially imposed habitat restriction of this species. Important in the food are the following; sheep carrion, lagomorphs, rodents, birds and their eggs, reptiles, amphibians, insects and a large range of vegetable food. This represents a good sample of all the foods available, revealing the diet of an extreme generalist.

When comparing diets, differences between Corvus species are more likely to be realistic when comparing the foods given to the nestlings of different species, as discussed in section 6.2. A further useful feature of using nestling food is that it should reveal differences between specialists and generalists, thus generalists should show greater variation between areas than specialists, due to their ability to cash in on local abundances. This is apparent when considering the results of studies on the nestling diet of the smaller species. The variability of the predominant prey species, depending on the location of the study, is very obvious (Lockie 1959, Holyoak 1968, Yom Tov 1975, Picozzi 1975, Houston 1977). Lockie's (1954) study analysed the nestling diet of all 3 species in the same habitat in Oxfordshire. 20-30% by volume of the diet of nestling Carrion Crows is not found in Rooks or Jackdaws, and consists of carrion, small mammals and nestling birds. About 40% of the diet is Lumbricids, mainly in the form of Lumbricus terrestris, a species with permanent burrows which often grazes on the surface (Edwards and Lofty 1972). The remainder consists mainly of grassland coleopterans, dipterans, arachnids and lepidopterans.

Rooks on the other hand, are more reliant on earthworms, which account for up to 80% of nestling intake in some rookeries, but with

Lumbricus terrestris forming a smaller proportion, more being taken from the turf root mat (Lockie 1959, Waite 1981). Tipulid larvae are the second most important, whilst surface invertebrates form a much less important component. In one cold spring in Oxford, earthworms were scarce, Tipulidae failed to increase in biomass, and Rooks tried to compensate by taking one species of larval lepidopteran from the surface. Rooks will also feed on defoliating caterpillars (Feare 1978).

Jackdaws at Oxford did the unexpected by collecting 60% of their food from the woodland canopy in the form of lepidopteran larvae, with grassland coleoptera, lepidoptera, diptera and arachnids making up the bulk of the remainder. The more typical pattern found by Lockie (1959) in Edinburgh, and by Richford (1978) was that these surface invertebrates of grassland normally form the bulk of the diet.

Two trends emerge from this review of foods. One is the great variation between populations of the proportions of each prey type given to nestling Jackdaws and Carrion Crows, which may reflect local availability of each type. The second trend is the precise micro-habitat from which each species collects the main items of its diet when sharing the same habitat of grassland. Thus a Jackdaw's and Carrion Crow's food consists of items which live on the surface, a Rook's of those items found below the surface. Differences in aspects of food seems to occur in two other dimensions. Lockie (1956) has shown that those prey species shared by the Jackdaw and Carrion Crow are separated on a size dimension, so the surface invertebrates taken by Jackdaws are smaller than those taken by Carrion Crows. The size of items given to ^{nestling} Jackdaws at Oxford is similar to that reported from

Skomer by Richford (1978). Rooks and Carrion Crows, however, select broadly similar sizes of surface invertebrates, but as mentioned above show a difference in where most of the food is obtained, i.e. above or below the soil surface.

The third trend was revealed by another angle of attack to discover species feeding differences, not utilizing nestling food. This concerns the relative proportions of various feeding actions used by each species, as each will give access to prey not available by other techniques. Lockie (1956) compared the relative use of 7 feeding methods in Rooks and Jackdaws on grassland, and Holyoak (1970) used the same categories for the Carrion Crow on the same habitat type. The findings are that Rooks direct their feeding actions to objects beneath the surface about half the time, Jackdaws very rarely, and on those occasions when Rooks take more surface invertebrates in early autumn, the Jackdaws are taking more items by jumping for aerial insects, at which they are better, being more agile. Carrion Crows, on the other hand, take virtually all their food (over 80%) from the surface by picking or probing about the surface, and very little (a mean of 4% of feeding actions) by probing beneath the surface.

In summary, where the three species occur on the same habitat, there is separation in the utilization of resources. Jackdaws and Carrion Crows take predominantly similar food types but separate out on food size, and Rooks, which take similar sizes of invertebrates as Carrion Crows, concentrate on sub surface invertebrates. In addition, Carrion Crows utilize a greater range of habitats, and take small mammals, eggs, nestling and adult birds, whilst Jackdaws can utilize arboreal insects. The Raven may fit into this picture by taking

different food sizes from the Carrion Crow, although no data for this exist. Ravens are also able to penetrate the tough skin of dead sheep, something Carrion Crows and the other species are unable to do (Houston 1977b). Relative utilization of different micro habitats within the same area is probably part of the reason for the differences in diets of the different species.

Evidence for food differences between sympatric species in other Corvus groups is rare. In the Australian group the three large species show a preference for flesh, in C. coronoides in the winter over 50% by volume of stomach contents is flesh, the smaller, nomadic species specialise on insects, and they are often to be found with insect irruptions (Rowley and Vestjens 1973). In Africa, the Pied Crow fills the niche of the Carrion Crow, taking small mammals, reptiles, bird eggs and young, carrion, insects and other invertebrates, whilst the Black Crow takes much of its food by digging beneath the surface for invertebrates (Skead 1952). Ravens take similar kinds of food as the Pied Crow, but there is no detail on the sizes of items chosen, or preferred habitat differences.

The largest differences between all purpose territorial and colonial nesting species appears to be in the food. The relevance of food distribution was discussed in Chapter 1. Briefly, feeding by local enhancement is the best means of exploiting a cryptic, unpredictable and clumped food supply. The food of nestling Rooks fulfils these conditions (section 1.6). Local enhancement may act at a number of levels; by directing individuals to an area of their home range by following others from a colony; to a particular field (by attraction to a flock); and to areas within the

field (by approaching a successful bird). However, the influence of sympatric territorial congeners on social feeding and nesting should not be overlooked, especially in the case of the Jackdaw with respect to flock feeding.

6.4 COLONIAL NESTING AND THE INFORMATION CENTRE HYPOTHESIS

6.4.1 Introduction

Local enhancement on the coarse scale had been formalized as the 'Information Centre Hypothesis' (henceforth ICH) for colonial nesting and communal roosting behaviour (Fisher 1954, Ward 1964). Tests of the model to date have emphasised one component and left the other assumptions untested. Mock (in press) has finally dissected the model into a number of component parts, each of which can be tested and falsified. Clearly, if the ICH cannot be falsified it is not a useful hypothesis. However, it is possible that the ICH is important only at certain critical periods of extreme localization of food; it may have evolved as an 'insurance policy' for such times. So testing the model may prove negative except at certain times, but the behavioural components on which it is based may still occur during 'non-active' periods. The components and their relevance to the current study are therefore considered below.

6.4.2 Components

Philopatry

Birds which discover a good site must return to it. This fundamental assumption has rarely been tested. Black-headed Gulls utilizing an artificial food source (Andersson et al 1981) apparently do, and the data presented in Chapters 3 and 4 show that Rooks return only to a very good food source. However, reasons for not returning to a site may be other than poor food quality (e.g. different prey type required, Tinbergen 1981).

Variability in feeding success

To show that one individual follows another for the purpose of locating a better feeding place, site-dependent differential feeding success should be demonstrated. If this does not occur, no advantage would be gained by following. Such a demonstration would require that all sources of food be monitored, or super-abundant supplies, better than any naturally occurring one, be given in an experiment, and Anderssons's study did this by supplying fish on a floating raft. In this Rook study, a ploughed field is known to give the highest ingestion rate of any field type, so differential success must occur as some birds would still be feeding on poorer grass fields when a ploughed field becomes available.

Detection

For transfer of information, a bird must be able to detect when another has done well. It is therefore necessary to show that successful individuals differ in their behaviour when they return to the colony, and that others can, and sometimes do, detect and use

these cues. Candidates include prominence of pouch or crop, turn around time at the nest, and the sounds of the young, yet no worker has convincingly shown such detection to occur. I was unable to identify such a cue in Rooks.

Synchrony

If some birds use others to find food, it is arguable that they should leave the colony in temporally clumped groups. This is the most commonly quoted congruent evidence for the IC H, (Krebs 1974, Andersson 1981, this study), yet it is open to alternative explanations. Furthermore, it is also necessary to show that the birds which follow have had recent poor feeding success.

Following

Having established synchronous departures by successful and unsuccessful birds, it is then necessary to show that the birds which depart together actually go to the same feeding location. In this Rook study, the arrival of new recruits at a field with the return of a bird which has taken food to the rookery (Section 4.3), is indirect evidence for this.

Toleration

If one bird follows another, the 'leader' must tolerate the follower, i.e. the food resource is not defensible or the finder does not wish to defend it. In Rooks this is clear not only from the review of foods (Sections 1.3.2 and 1.3.3), where patches are relatively short lived and prey items within them at a very high density, but also from the absence of any reported attempt of birds trying to drive off followers.

Payoff

Any cost incurred by the follower, for instance from delay in leaving the colony, should be met with at least an equal benefit, for example, by an elevated food intake, and this has not been systematically studied.

6.4.3 Conclusion

Of these seven points, five occur in Rooks; detection, payoff and proof that followers have been unsuccessful remain to be ^{investigated}. However, even if each individual step is proven for one species, a number of confounding variables remain: each step is open to alternative explanations and experiments would need to be done to exclude such possibilities.

One way forward in this problem lies in the techniques of Tinbergen (1981), and will involve the interaction between sampling of different feeding areas, feeding success and the incidence of following. By focal animal sampling using radio telemetry, a complete record could be kept of feeding success, prey density of areas visited, subsequent behaviour at the nest, details of flights (whether following or followed) and the reaction to flocks, together with measures of the range of food densities available.

Another way forward to test the ICH would be to control all these variables, which could be achieved only in a laboratory situation. However, one variable, visibility, could be controlled for in the field situation. There are valleys in Scotland inhabited by Rooks

only between spring and autumn (McKilligan 1980). One experiment, not requiring marked birds, would utilise a colony at the end of such a valley, where there are various fields in and out of sight of the colony. When such fields were being ploughed, one would predict an exponential recruitment rate to an out of sight field once discovered, and a steady recruitment rate to the in-sight field, if the ICH was operating. Some attempt would need to be made to control for the food quality of the fields. All this discussion assumes that the observer will be gathering data whilst the ICH is operating. Whilst independent behavioural components of the ICH can be shown to operate, only in one laboratory example have naive birds been shown to use knowledgeable birds to locate food (de Groot 1980). Perhaps the best time to gather data required to test the ICH in Rooks would be early in the morning after heavy overnight snow, during the early nestling period. Such extreme localization of food, which could easily be supplemented by manipulation of food supplies would be most likely to *prove* the ICH.

6.5 INTER-SPECIFIC COMPETITION AND SPECIATION.

That up to 4 similar congeners co-exist in the same habitat, potentially competing for the same food, poses some problems for niche theory. However, the evidence reviewed in section 6.3.4 shows that competition is not so great since the species separate on a number of niche dimensions. Traditionally, these niche differences between sympatric congeners have been viewed as a result of competition between co-evolving congeners (Lack 1945, Cody 1974, Diamond 1978).

More recently, the systematic analysis of the assumptions of these models, and the lack of empirical evidence supporting them, has questioned their general applicability (Connell 1980). A new idea is that species may have evolved separately and became adapted to different sets of conditions, and that co-existence is made possible by the pre-adaptations to different resources or parts of the habitat. Competition is viewed in this framework as keeping the closely related species apart, either through exploitation or interference competition. In the former, resources of species A are depleted by species B, restricting the distribution of the former. In interference competition, one species directly restricts the distribution of the other, for instance by inter-specific territoriality or, in the extreme, by predation.

Some interesting results of competition can be seen where ranges of Corvus species are expanding or a species is artificially introduced into the range of another. For example, in the S.E.Asian group of Corvus species, the Jungle Crow C. macrorhynchos occurs in wooded areas, with Carrion Crows and Ravens utilizing the more open areas (Goodwin 1976, Higuchi 1979). However, in areas where the Jungle Crow overlaps with the Slender Billed Crow, C. enca, it is to be found in the open spaces, whilst the Slender Billed Crow becomes the crow of the forest (Goodwin 1976). Complete exclusion is occurring on the east coast of Kenya, where the House Crow has been successfully introduced from India, and is displacing the indigenous Pied Crow (pers. obs.). Both appear to fill the same niche as medium sized generalists in their native areas, and for some reason the Indian bird is more successful. In both cases, it would be interesting to observe whether the habitat shift or exclusion is caused by exploitation or

interference competition. In the one case where inter-specific competition has been studied in this family (Hogstedt 1980) Magpies were shown to suffer from competition with Jackdaws because of both interference and exploitation.

As Rooks are well adapted to open ground, only needing a few trees in which to nest and roost, and have become emancipated from the forest edge and the wide variety of foods contained therein, it is possible that the Rook evolved from an ancestral species, exploiting a novel steppe habitat in S.E. Europe. The Rook has become specialised on sub-surface invertebrates, and nowhere in its range does it nest in the centre of large areas of woodland; this is probably because of its requirement for grassland feeding. It is possible that by specializing on sub-surface food, individuals gained by observing others to help them sample for good food patches, and hence the colonial habit may have evolved.

There is a chicken and egg relationship between colonial nesting and flock feeding with the specialization on sub-surface invertebrates. Did territoriality break down for some other reason, thus enabling flock feeding and its advantages when feeding on sub-surface invertebrates, or did such specialization on sub-surface invertebrates lead to a breakdown of territoriality? Waite (1981) observed that the biggest difference in food intake rates in Rook flocks occurs at small flock sizes, that is, between flock sizes 1-5, thereafter the rate of improvement with increasing flock size declined markedly. He concludes that the most important difference for Rooks between the territorial and the gregarious habit is in terms of food finding. Rooks which choose to forage permanently on their own or in

pairs would be at a disadvantage in terms of food resource exploitation when compared with those which exploit the flock system, as discussed in Chapter 5. By the very nature of their specialisation on sub-surface invertebrates, they create the need for feeding by local enhancement given what is known about their prey distribution (section 1.6), but it is impossible to tease out which came first.

Further adaptations to being a feeder on sub-surface invertebrates include an earlier breeding season to coincide with the earlier flush of earthworms (Figure 1-1) which occurs before the later insect flush. The later insect flush has associated with it the breeding season of most of the insectivorous passerines. The Carrion Crow's breeding season appears to be synchronized with both the insect flush and the associated appearance of eggs and young of the majority of other passerines, which feature in its diet (Lack 1968). The Jackdaw's breeding season coincides with that of the Carrion Crow, suggesting that the Jackdaw and Carrion Crow may be linked to different sections of the same food source. The origins and advantages of non-territoriality in the Jackdaw would clearly repay study. By defending an all purpose territory, and by having an extremely varied diet, Carrion Crows in most habitats ensure a year round food supply. Forgetting the problems of maintaining a territory in the same habitat as a territorial dominant species, a more specialised species like the Rook, relying on sub-surface food during the breeding season, may not be able to ensure a constant food supply in what is a relatively small area (when compared to its range as a colonial breeder). It sometimes requires the help of others to locate good patches, as its food supply does not represent a defensible resource (Brown 1975). So by becoming specialised, the Rook is obliged not to defend an all purpose

territory. Because Rooks in flocks have higher intake rates, they are better off sharing a large area with others, utilizing the better sampling and food finding abilities of the flock. This argument suffers from the depletion effect of tolerating others. Clearly the feeding of others will deplete the patch (Bengtsson 1976) but this is offset by the huge densities of worms (up to 500/m²) and the relatively short life of the patch. The many factors affecting earthworm densities in the short term (e.g. temperature, humidity, predation; references in section 1.3.3) makes this difficult to quantify.

6.6 CONCLUSIONS

In Chapter 1, the problem of why Rooks nested in colonies was discussed in the light of other studies on the social organization of animals, and a review of the evidence suggested that food was probably most important since the Rook and the Carrion Crow are found in broadly overlapping habitats, and share most environmental conditions. Chapter 2 revealed that neither individual nor colony defence of a feeding range occurs, and some birds transfer between colonies between years; the aggregation into groups to defend trees as a scarce resource is not supported. During the breeding season, males often find it difficult to feed all their nestlings, and are constantly sampling their environment by a variety of mechanisms, to find the highest prey densities. Chapter 3 revealed that only higher prey densities were revisited on consecutive foraging trips. Flocks of Rooks tend to form on higher food densities, and individual Rooks probably use this as an indication of good feeding locations. Especially in hilly terrain, the good food may occur out of sight of

the colony. As birds often leave the colony in groups (Chapter 5) it is possible that some individuals follow others, who are flying faster or more directly to their own feeding ground, in order to decrease their food searching time. Data for arrivals at one out of sight field giving high intake rates support this idea. Individuals therefore seem to exploit the results of others' sampling, made possible in this colonial nesting system.

However, even after reviewing all the evidence, whether colonial nesting actually evolved because of its food finding advantages is difficult to say. It may have been a secondary adaptation after the breakdown of a defended, exclusive feeding area due to the constraints imposed by feeding on sub-surface invertebrates and the sampling problems involved. Colonial nesting does not need to occur in a flock feeding species, as can be seen from the North American and Australian semi-colonials (Bent 1946, Rowley 1973d), but colonial nesting does increase the potential sampling benefits of the flock feeding habit. The common occurrence of the breakdown of the defended feeding area in an all-purpose territory species when artificial situations create abnormal food distributions (e.g. C. splendens, C. corone), suggests that food dispersion patterns have an important influence on the nesting patterns of Corvus spp. The change in food distribution consequent upon the change in the feeding habitat therefore seems the most likely explanation of coloniality in the Kook.

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APPENDIX ONE

Al.1 Introduction

The aim of this appendix is to record characteristics of the birds caught for the field study, and the methods used to catch them. A certain amount of analysis of the size data has been done, and a method for sexing adult Rooks by measurements devised. A few relevant peripheral ideas are briefly discussed.

The Rooks considered here are taken from the study area described in detail in Chapter Three. The population is from the Borders Region of Southern Scotland, 20 miles south of Edinburgh, centred at $55^{\circ}44'N$, $2^{\circ}54'W$.

Al.2 Traps and trapping

Parts of this section have been published as a paper entitled "Some results from trapping Rooks", Ringing and Migration, 3 (4):203-212, 1981.

Al.2.1 Trap types

All traps were basically cages with ground entrance tunnels as described by Hollom and Brownlow (1955). In 1978 a cylindrical trap of 1.25m height and 1.5m diameter was tried, built to the design of

Allsager et al (1972). It was made from 20mm x 40 mm rigid mesh as it was required to be portable. This failed to catch any birds, and observation revealed that Rooks and Jackdaws could leave the trap through the entrance tunnel. Addition of a trap door sprung by the entering bird later achieved a few catches of individual birds.

Three traps were built in 1979. Trap 1 was a portable rectangular box 2m x 1.5m and 1.5m tall, made of the same rigid mesh, with one entrance tunnel at ground level on each of the long sides. Trap 2 was a 2m square 1m tall cage with two ground tunnels, all made of 25mm mesh 'chicken' wire netting. Trap 3 was a 4m square and 2m tall variant of trap 2, built to a plan supplied by Dr. Ian Patterson (pers. comm.). A sketch of traps 2 and 3, which are built on site, is given in Figure A1-1.

All traps had ground tunnels constructed according to the instructions in Hollom and Brownlow (1955) scaled to give an entrance of 500mm span and 250mm height, tapering to give an inner arch of 150mm span and 250mm height (Figure A1-1). The tunnels projected about 500mm into the trap cavity. An important innovation fitted to all three traps in 1979 was a trap door fitted to the inner of the tunnel. This was constructed of 3.5mm gauge wire for the frame, covered by 25mm mesh wire netting, and of such a size as to be slightly larger than the inner end of the tunnel. Being hinged to the top of the inner end of the tunnel it formed a one way trap door. When the trap was set, these doors were propped open by means of a piece of wire secured to the door by a piece of Blu-Tack, a proprietary adhesive putty. As a result, a number of birds entered the trap before the wires supporting the trap doors were knocked away.

Those birds inside were prevented from leaving by the closed doors and this attracted other birds down which, as observations proved, entered by pushing open the doors from the outside. It is likely that a number of Rooks in the cage provides a strong attraction which encourages others to enter (see Chapter 4, also Waite 1981).

Trap 1 is fairly expensive to build as the cost of the mesh is high, and it is also a difficult material to work, but it does provide a durable trap which is usable from year to year and is portable. Trap 3, a fairly traditional design, is expensive to build because of the large amount of netting and substantial corner poles required, which can be difficult to drive into the ground. Trap 2, on the other hand, is very cheap and simple to build, being smaller. It can be built by one person in less than three hours and will give long maintenance free service.

All three traps were in simultaneous use during 1979, so that their comparative effectiveness could be assessed. They were spaced 50m apart, out of sight of each other at ground level and all within 100m of the same rookery, and all were baited with bread and bruised oats. Trap 2 is by far the most effective design, see Figure A1-2, catching just 11% fewer birds than the large trap 3 despite being only one third the volume. Trap 1 was only half as big as trap 2 and the catch was reduced by 50%, and so trap 2 is by far the most cost effective design.

Figure A1-1

Trap design with detail of entrance tunnel.

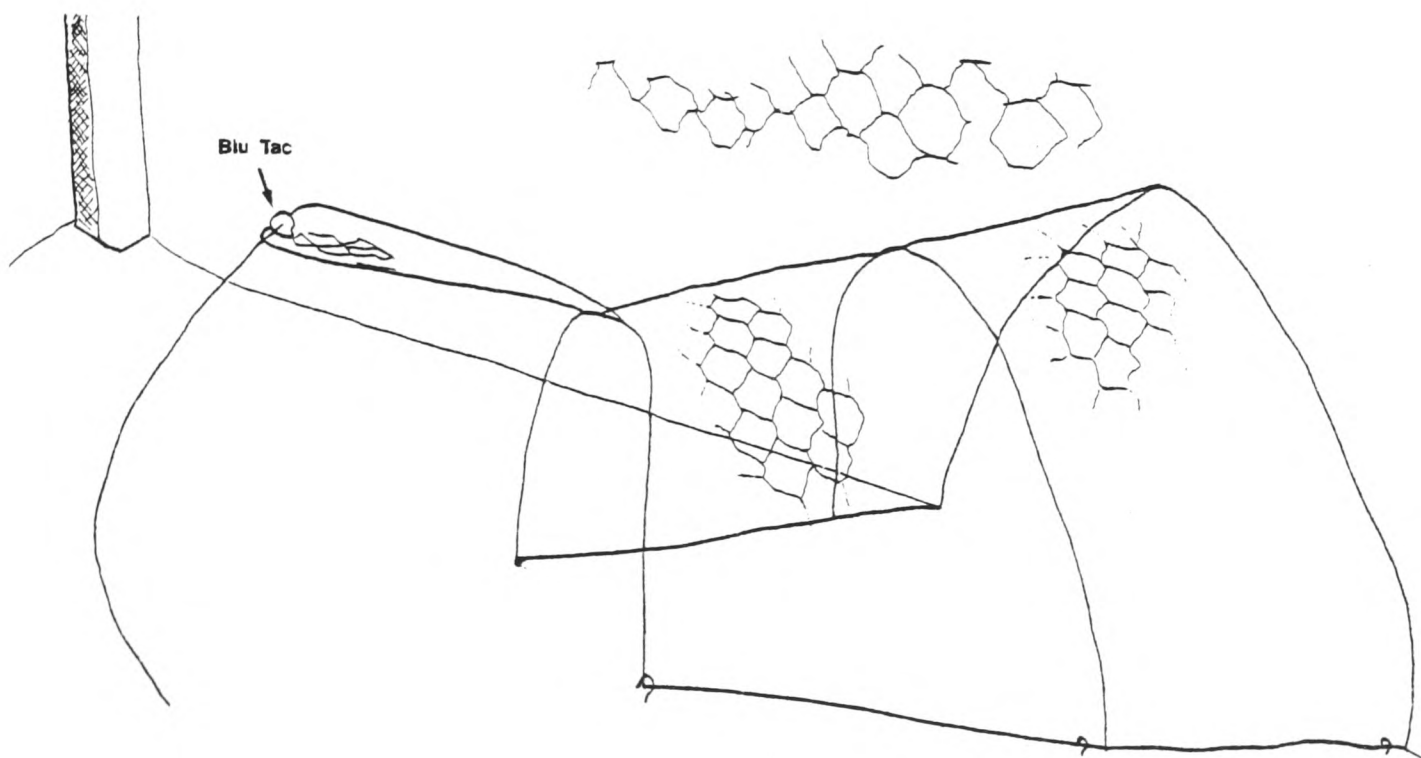
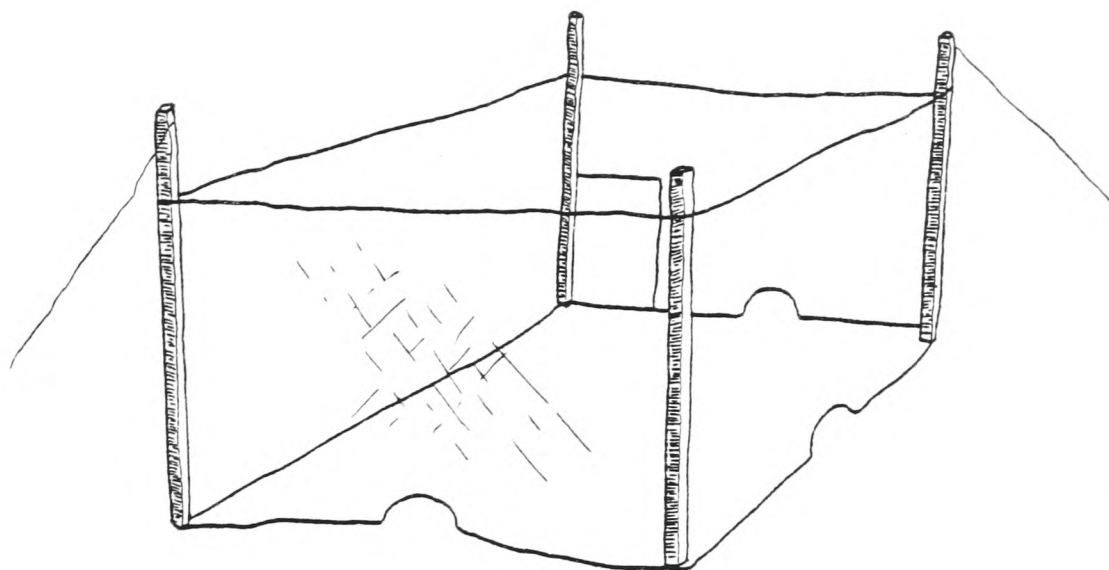
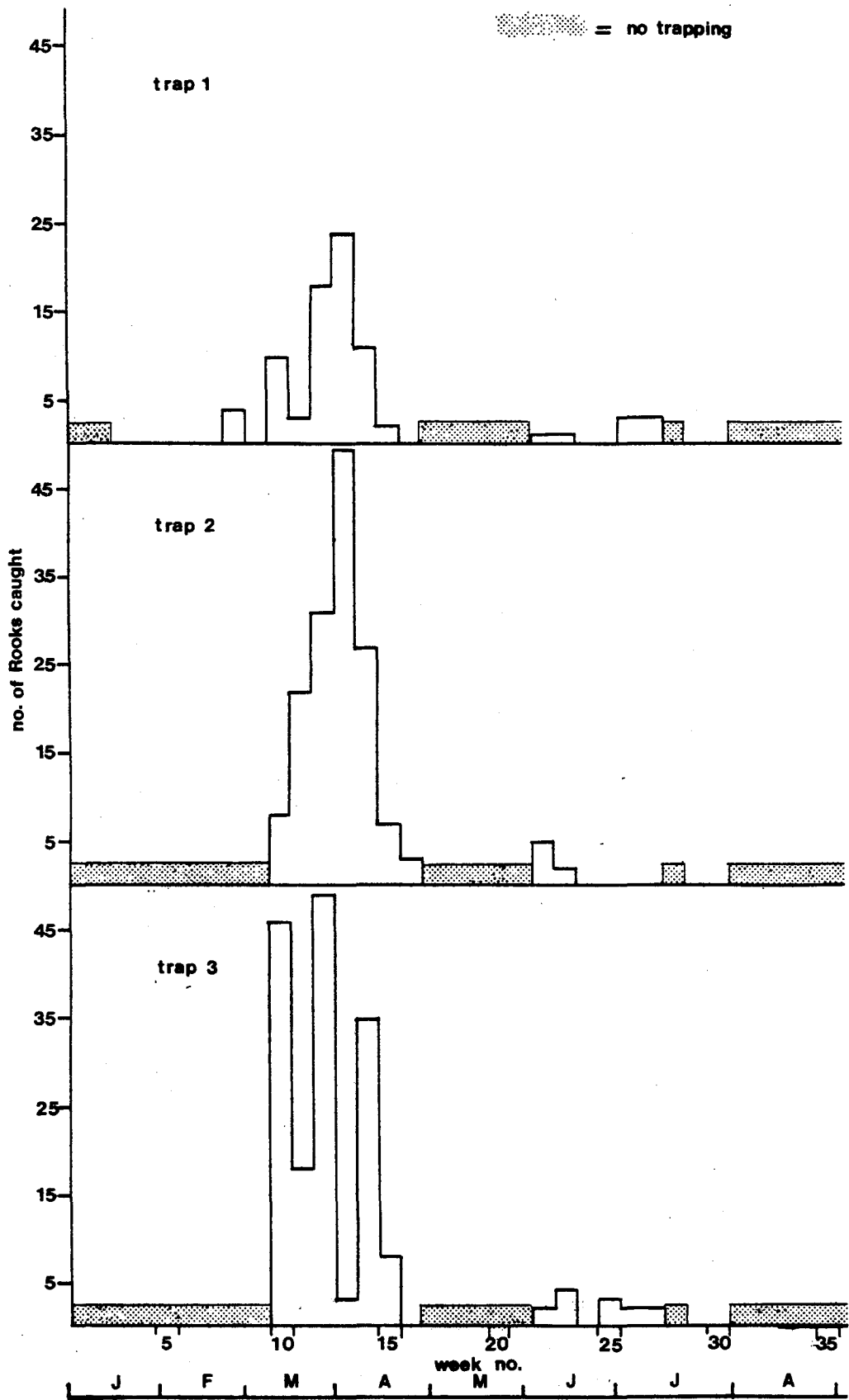


Figure A1-2

Comparative catching success of trap types during 1979.



Al.2.2 Trap construction

The sides and roof of the trap are constructed from wire mesh, 5cm mesh chicken wire for cheapness, but 2.5cm mesh for strength and preference. All joins are made with 1mm binding wire. The corner poles may be varied to suit the size of trap; 2cm diameter bamboo poles are sufficient for a 2m x 2m x 1m trap, 7cm x 7cm stakes for a 4m x 4m x 2m trap, and 10cm x 10cm stakes for a 4m x 6m x 2m trap. 3.5mm gauge straining wire is suitable for hanging sides from and as guy wires in the larger traps, 1mm wire for the small trap. The weakest point in the construction proved to be the junction between the tunnels and the trap walls, especially prone to damage when large birds such as Pheasants Phasianus colchicus or Herring Gulls Larus argentatus enter. The answer is to strengthen the tunnel at both ends and in the centre by semi-circles of 3.5mm straining wire, bound to the tunnel. Great care must be taken to bind the tunnel to the wall of the trap, extra time spent in construction is repaid later as repairs are time consuming, and lost catches annoying.

Al.2.3 Trapping success

Al.2.3.1 Background

Patterson (pers. comm.) found that in N.E.Scotland Rooks could be caught only during spring and again in early summer (but see Al.2.3.3). In this study, trapping was attempted with the automatic cage traps between January and August 1979, and again from November 1979 until July 1980, using bruised oats and bread as bait, although

other items were tried as will be described.

Rooks could be caught only from mid-March, with a peak during April falling throughout May to zero in July, see Figure A1-3. Jackdaws could be caught from June onwards with a peak during July and August. Factors which might affect trapping success include weather, food availability and trap location, and these are discussed below.

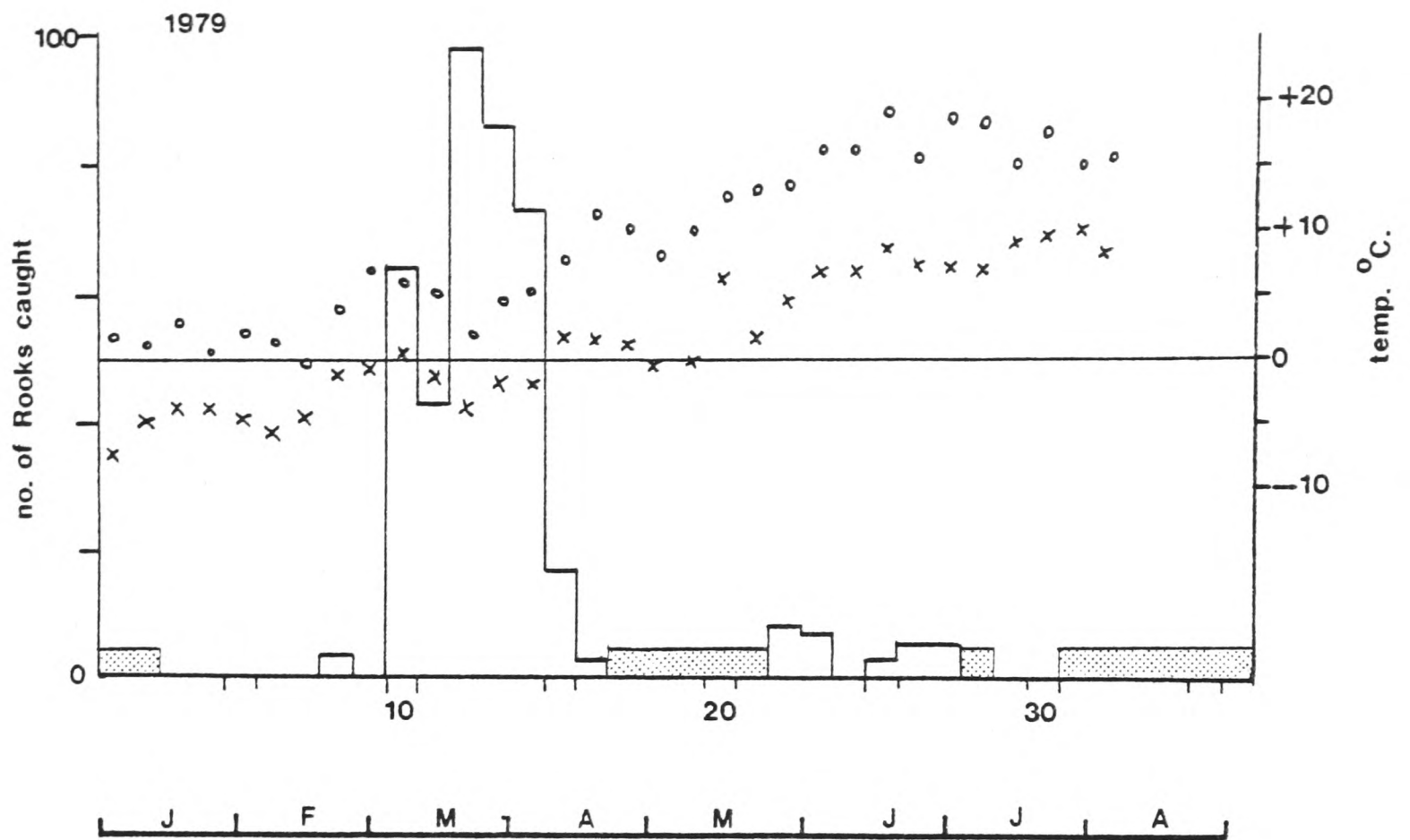
A1.2.3.2 Weather

Considered in relation to meteorological data, supplied by Galashiels Meteorological Station situated 7 miles south of the study area, no clear trend emerges with differences between the two years (Figures A1-3 and A1-4). The good trapping period of 1980 was shorter than that of 1979, beginning two weeks later and ending two weeks earlier. Considering temperature first (Figure A1-3), in 1979 Rooks were caught during a period when the minimum temperature was below zero, and numbers caught decreased rapidly as the minimum temperature rose above zero. Possibly on such days, feeding on invertebrates early in the day may have been inhibited due to inactivity of the prey until the temperature rose, and as a result the Rooks took grain from the trap to feed their young and sitting females. A glance at the 1980 figure, however, shows that Rooks did not begin to enter the traps until after the minimum temperature stopped falling below zero.

Considering the influence of precipitation, see Figure A1-4, 1979's trapping success occurred when this was high. This is contrary to expectation except for the weeks of snow cover, as high rainfall would increase the numbers of earthworms in the surface layers of soil

Figure A1-3

Number of Rooks caught in traps in relation to temperature
during 1979 and 1980.



week no.1 = January 1-7

o o o o o = mean max. temp. for week

x x x x x = mean min. temp. for week

stippled = no trapping

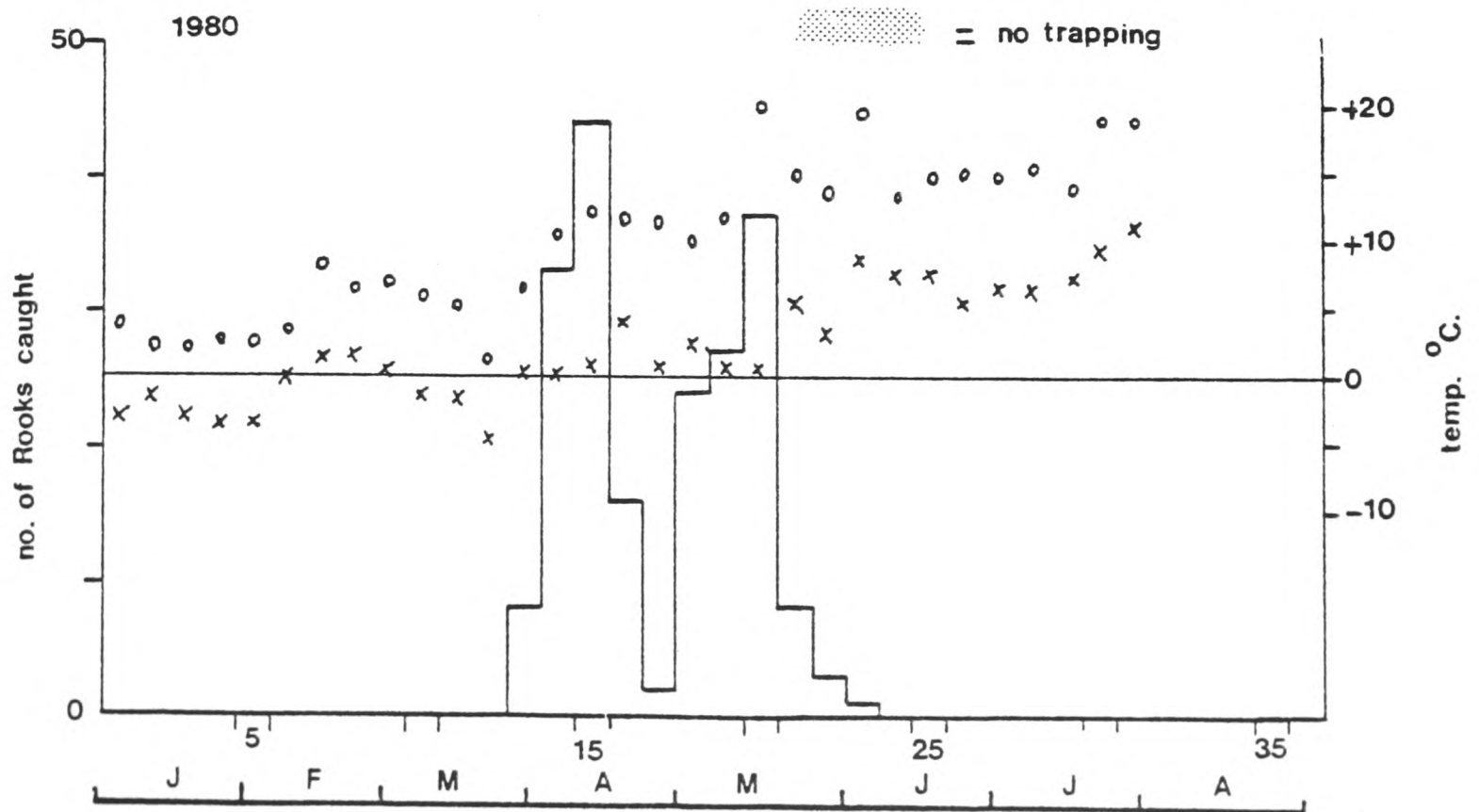
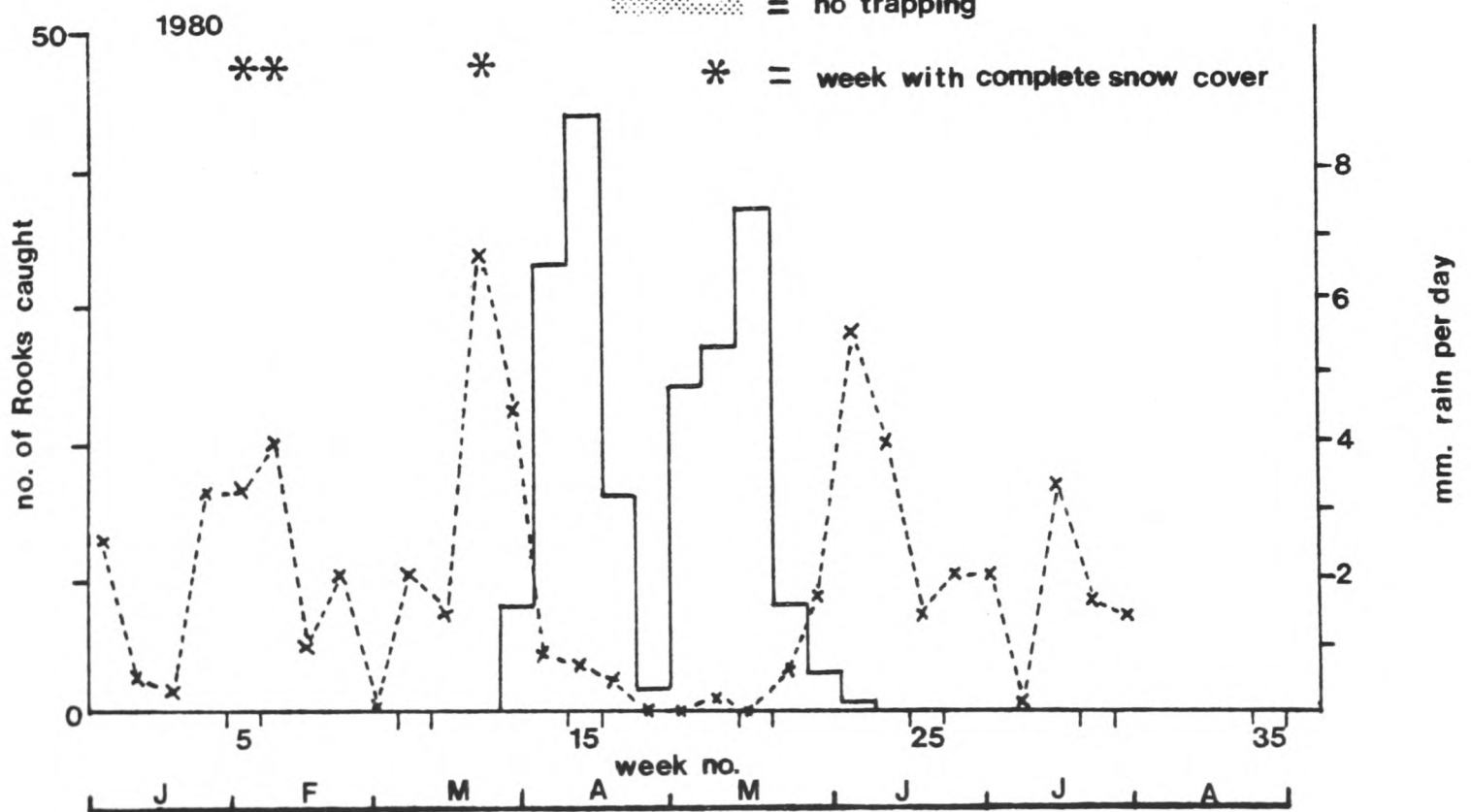
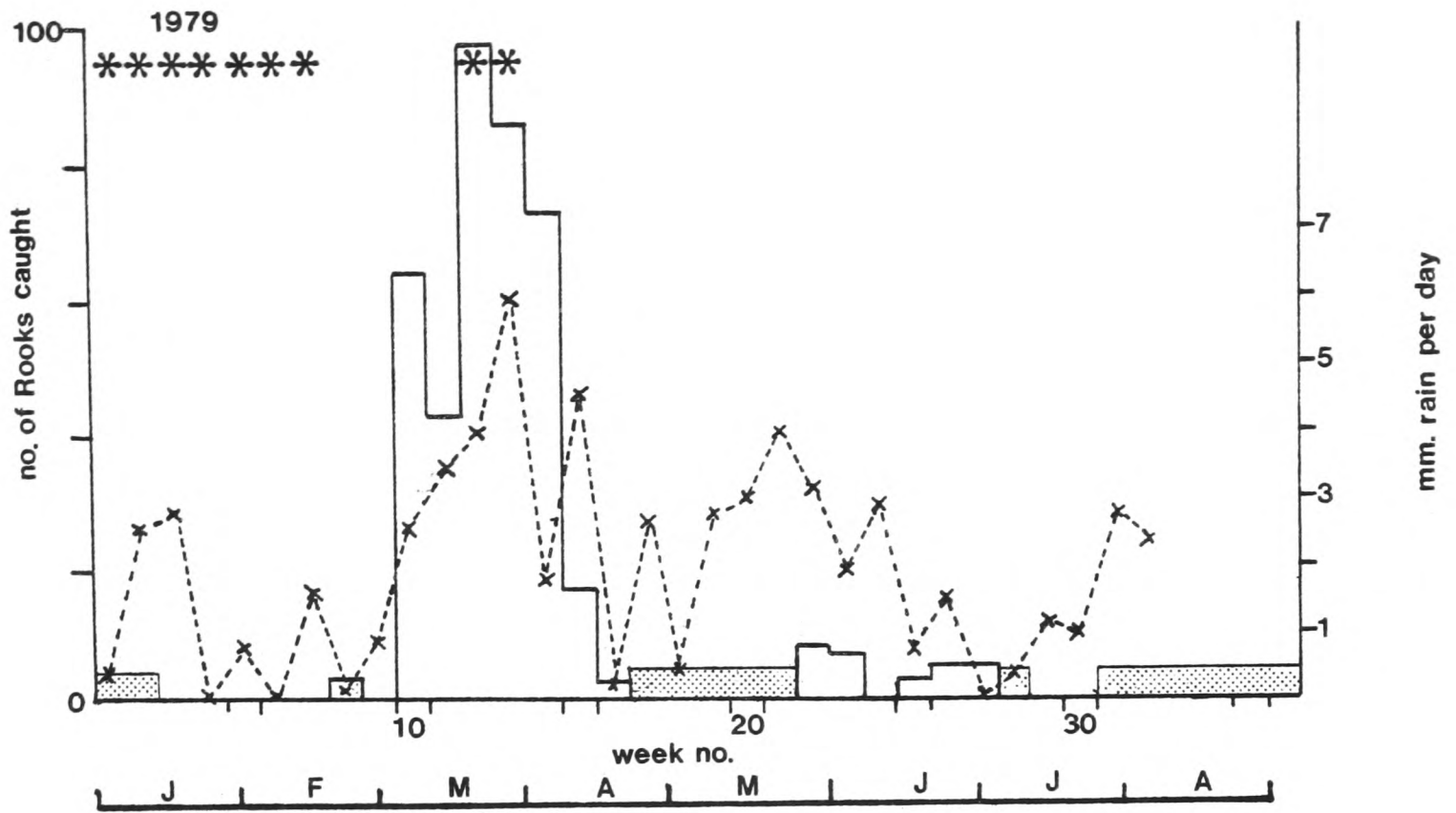


Figure A1-4

Number of Rooks caught in traps in relation to precipitation
during 1979 and 1980.



(Gerard 1967). 1980's figures show the reverse trend which could be predicted, as earthworms burrow or become inactive during dry periods.

Combining the two figures for each year shows that in 1979 trapping success was good during a period of low temperature and high precipitation, some of which was snow, and in 1980 success was good during a period of high temperature and low precipitation. The two years' figures are clearly different but no clear trend emerges. A multivariate approach to this problem is needed for accurate predictions, which would involve factors such as temperature, rainfall, measures of food requirements and availability (see below).

Al.2.3.3 Trap location

Trap location may have affected trapping success. All Rooks were caught near rookeries during the breeding season. As association with the rookery decreases during the summer (Patterson, Dunnet and Fordham 1971), it is possible that traps located on the higher grass pastures where Rooks fed in the summer may have been more successful. Where concentrated artificial food sources are available during the moult, traps may catch well if located near these (e.g. piggeries in Aberdeenshire, Patterson pers. comm).

Al.2.3.4 Food availability

Trapping success may have been a reflection of the availability of the Rooks' natural food. During the spring and early summer, Rooks feed mainly on earthworms, which peak in availability in April, and leatherjackets which reach peak biomass in May (Tinbergen 1981).

Earthworms may become unavailable in spring during periods of cold weather when they burrow deeply, and again in dry periods of the summer. The latter period coincides with emergence of leatherjackets as winged adults, and are therefore no longer available as grubs obtained by probing. These events could all lead to potential food shortages and could arguably cause Rooks to enter traps. Whereas the cold induced shortage, which coincides with a high food demand of the growing young, resulted in successful trapping, that resulting from dry, warm weather, which coincides with an increase in food demand due to the onset of moult (Feare, Dunnet and Patterson 1974), did not induce Rooks to enter the traps. This is in spite of evidence of a food shortage, lack of rain and higher temperatures resulting in a predictable gathering of Rooks into large flocks on a few damp fields (Chapter 5). In both years, Rooks were caught during the breeding season when food demand is high. Trapping during the post breeding moult, which lasts from late May until September, did not occur. This is in spite of a food shortage, caused by aestivation of earthworms, emergence of leatherjackets and absence of grain, coupled with measures of poor body condition (Beshir 1970, Feare, Dunnet and Patterson 1974).

As Rooks were often seen feeding in the fields surrounding the traps during this period, this can probably be explained by food quality. Amino acid requirements for feather growth are very specific, and the requisite ones are acquired from thinly dispersed invertebrate prey, and not from the grain put down as bait in the traps (Newton 1968). Acquisition of the amino acid cystine is important during moult; it is about the fifth most common amino acid of feathers, but one of the four least common in most other animal

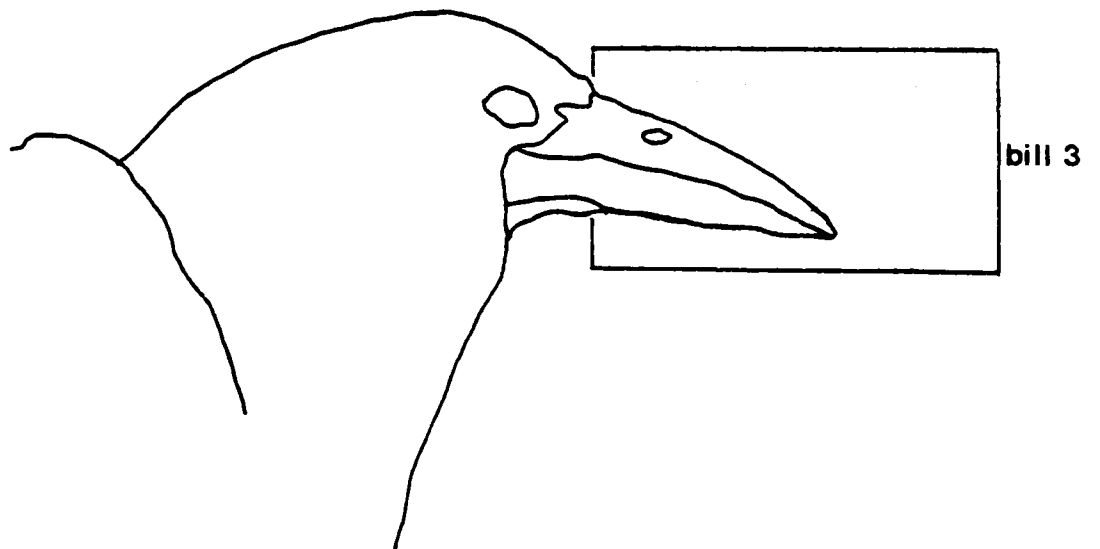
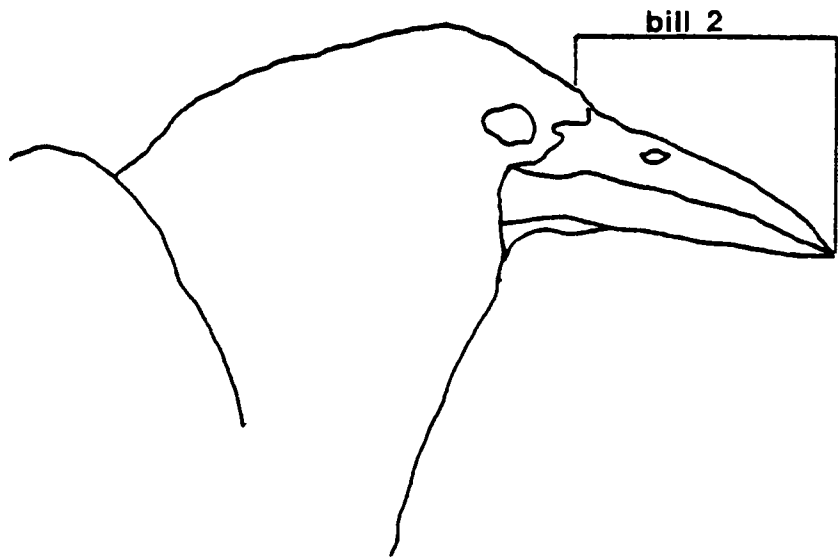
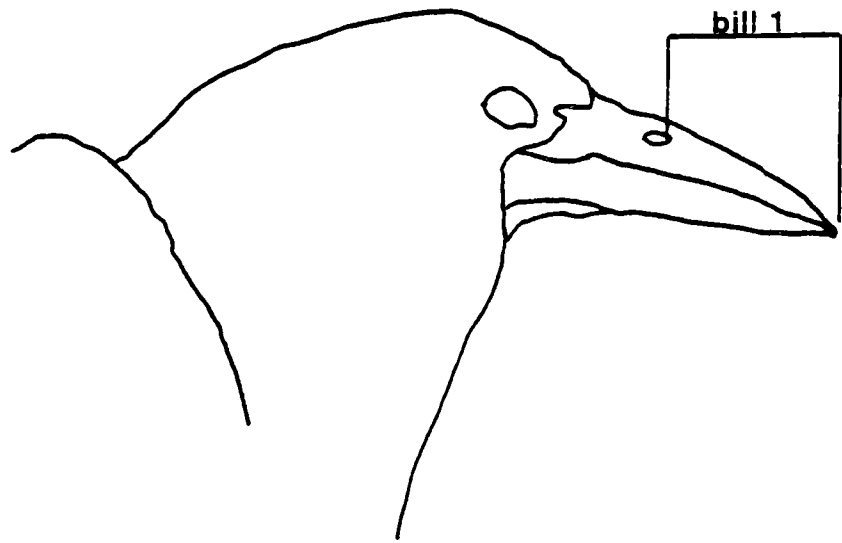
proteins. Thus much protein has to be gathered in order to concentrate the amounts required for new feathers (Newton, 1968). Adult mortality during the summer is not high (Holyoak 1971) and it would appear that Rooks are not at risk from starvation at this period. As cystine is 15 times more common in animal-derived food than in grains such as oats and barley (HMSO Bull. no 174, 1974) it is probable that Rooks in moult are more selective in their food intake and therefore not tempted into the traps. This trend was anticipated, and mealworms were offered as an alternative bait. However, Rooks appeared not to recognize the mealworms as food, and were not eaten by the Rooks until the end of the study. Other high protein food was tried, such as eggs and raw meat, but this met with little success.

A1.3 PROCESSING THE BIRDS

In total, 419 individual Rooks were caught, 2 in 1978, 311 in 1979 and 106 in 1980. In addition, 25 were retrapped on average 3.7 times (s.d. = 1.8, range 2-10). All birds were processed in a standard manner. Each was weighed using a 1000g 'Pesola' spring balance and three bill measures were taken with dial callipers as shown in figure A1-5. The bill was measured from the anterior of the nostril to the tip of the upper mandible (bill 1), from the nasal-frontal hinge to the tip of the top mandible (bill 2) and the bill depth with the callipers against the nasal-frontal hinge (bill 3). The wing was measured with a stopped 500mm steel rule using the maximum chord technique (Svensson 1976) and in 1980 the tarsus was measured, also using Svensson's technique.

Figure A1-5

Bill measures taken of all Rooks caught in tunnel traps.



Each Rook caught was fitted with two patagial wing tags as detailed in Anderson (1963), one on each wing. Each bird had a unique combination of tag base colour and painted letter-digit combination. 'Humbrol' enamel and polyurethane varnish were used for the letters and digits, which did not prove satisfactory as some tags quickly became worn as a result of preening actions by the wearer. Acrylic paint is recommended for this purpose (Patterson pers. comm.). On the reverse side of the tags a strip of sellotape bearing the laboratory's address was attached prior to the varnishing stage in an attempt to ensure the return of tags found on dead birds. In late 1979 and all of 1980, BTO rings were also attached.

Al.4 SEXING ROOKS BY DISCRIMINANT ANALYSIS

This section has been accepted for publication as a paper entitled "Sexing Rooks by discriminant function analysis", to appear in Ibis 124, 1982.

Al.4.1 Introduction

From external appearances, Rooks are sexually monomorphic. Although males are generally larger than females, there is considerable overlap between the sexes in all aspects of size, as can be seen from Table Al-1.

TABLE A1-1.

Measurements of Rooks used in the
Discriminant Function Analysis.

measure	sex	mean	S.D.	range	N
wing	male	321.6	6.7	299-338	102
mm	female	300.8	7.7	280-314	54
bill 1	male	41.7	2.6	36.3-48.3	102
	female	37.2	2.1	32.9-41.4	54
bill 2	male	61.3	2.5	57.8-68.4	102
mm	female	56.5	2.3	51.0-60.8	54
bill 3	male	21.3	1.15	18.7-26.3	102
	female	19.5	1.05	17.3-21.9	54
tarsus	male	55.2	2.0	49.2-58.9	31
mm	female	52.2	1.2	50.0-53.8	15
weight	male	494.0	26.7	445-560	102
g	female	417.0	30.0	325-475	54

Discriminant function analysis can be applied to such measures and used to determine the sex of individual birds, as has already been done for Fulmars Fulmarus glacialis (Dunnet and Anderson 1961) and Moorhens Gallinula chloropus (Anderson 1975). The technique is described in detail here as no straightforward guide for its use by biologists exists.

Of the 419 Rooks caught by the methods described, 156 were sexed subsequently by behaviour, mainly by behaviour at the nest, although 15 were found dead and sexed by dissection. The female does all the incubating of eggs, closely brooding the newly hatched young and is

fed at or near the nest by the male (Coombs 1978). Thus females could be sexed by being fed, and males by feeding an incubating or brooding bird. Each individual was sexed at least three times by behavioural means before being included in the analysis and in practice most were sexed on a far greater number of occasions, often in excess of twenty. As checks on these determinations, 43 of 48 behaviourally determined females had brood patches whereas none of the 94 behaviorally determined males had. A further check for 34 birds came from 17 mated pairs in which both birds were tagged. All measures are for adult birds (2 years and older), trapped between the months of March and June.

A1.4.2 Method

The basic problem solved by discriminant analysis concerns the differentiation between two groups, be they species, populations or sexes. If a character is selected and measured, the means for the two groups may differ significantly (e.g. Lincoln, Racey, Sharp and Klandorf 1980) but their distributions may overlap so that from this one measure it would not be possible to assign an individual of unknown membership to either class with any degree of accuracy. A second character may differentiate in a similar way (e.g. Corkhill 1972, and Harris & Hope-Jones 1969). Discriminant function analysis computes a new variable which is a linear function of the first two (or more) variables which serves to differentiate the two groups. For a further introduction to the technique and a simple example see Sokal and Rohlf (1969) which also contains further references.

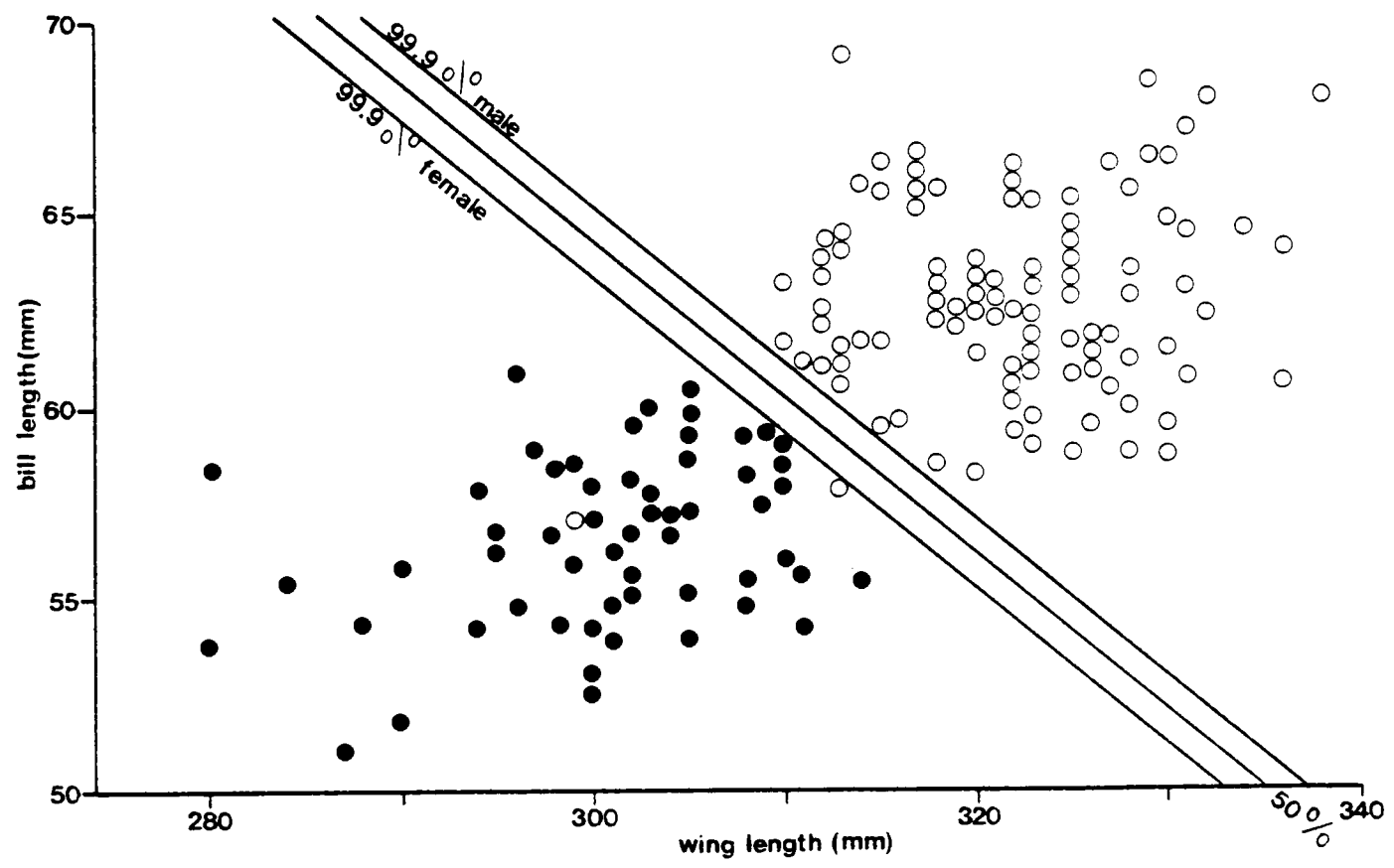
In the analysis described here, wing length (maximum chord, see Svensson 1976) and maximum bill length (bill 2 of Figure A1-5) were used. Weight is not used due its known variability (Beshir 1970) and insufficient tarsus length measurements were taken, although preliminary analysis suggest that this measure would be suitable. The data were analysed using the SPSS programme "Discriminant" (Nie et al 1975).

A1.4.3 Results

Analysis showed that the discriminant function based on the measures of 156 Rooks of known sex correctly classified 98.7% of them. Two small males were classified as females (see Figure A1-6). The discriminant function is based on birds of known sex and its value to the field worker lies in its use for assigning future unknowns as male or female. The rest of this section is therefore devoted to how to calculate a table of probabilities of membership to classes, and how to construct from this a graph with probability contours such as Figure A1-6.

Figure A1-6

Discriminant line with 99.9% confidence contours, for adult
male and female Rooks using wing and bill measures.



● = female

○ = male

Al.4.4 Construction of table of probability of group membership

These calculations, which result in Table Al-2, involve the use of a number of values calculated by the computer. These are the unstandardised discriminant function coefficients (UDFC) of the measures used (here, those of wing and bill-length, their associated constants, and the means of the the discriminant scores of males and females. Table Al-2 is constructed by solving Equation 1.

$$Z = \frac{S_a + S_b}{2} - \frac{Y V(S)}{S_a - S_b} \quad \text{Equation 1.}$$

where

Z = zone for confidence limit

S_a = mean discriminant score for males

S_b = mean discriminant score for females

Y = logit for chosen confidence limit
(from logit tables)

V(S) = pooled variance of scores S within each sample

V(S) is calculated from Equation 2.

$$V(S) = \frac{\frac{V(w)}{(n_a-1)} + \frac{V(b)}{(n_b-1)}}{(n_a-1) + (n_b-1)} \quad \text{Equation 2}$$

where

V(W) = variance of wing measure

V(b) = variance of bill measures

Solving Equation 1 for both positive and negative values for each

value of Y will give probabilities of membership to male and female groups respectively. The results for this set of calculations are given in Table A1-2.

TABLE A1-2.

Probability of group membership and associated discriminant scores.

Probability of misclassification	discriminant score	
	male	female
per cent		
50 - 25	-.277 to -.275	-.277 to -.280
25 - 10	-.275 to -.273	-.280 to -.282
10 - 5	-.273 to -.272	-.282 to -.283
5 - 0.1	-.272 to -.176	-.283 to -.378

Using Table A1-2 it is possible to assign an unsexed bird to a group by calculating its discriminant score and seeing where this falls among the range of values. The discriminant score of an unsexed bird can be calculated from Equation 3.

$$DS = UW(Wa) + UB(Ba) + K \quad \text{Equation 3.}$$

where

UW = UDFC for wing measure

UB = UDFC for bill measures

K = constant

(these three from programme output)

Wa = actual wing measure of unsexed bird

Ba = actual bill measure of unsexed bird

In practice, however, it is more convenient to construct a graph with probability contours either side of the discriminant 50% line, see Figure A1-6. This is done by solving Equation 4, using three wing measures for each probability. Figure A1-6 has only three contours due to the closeness of the intermediate ones.

$$B = \frac{DS(p) - (UW \times Wa) - K}{UB} \quad \text{Equation 4}$$

where

B = bill measure to plot against the chosen wing
measure

DS(p) = discriminant score for chosen probability from Table A1-2

UW = UDFC wing

UB = UDFC bill

K = constant

Wa = actual wing measure

Wb = actual bill measure

By way of example, for the 50% probability line the DS for the chosen probability would be -.277 (from Table A1-2), the two discriminant functions and the constant are extracted from the

programme output. Three wing measures chosen will solve for three bill measures which will give give the 50% plot on Figure Al-6.

Al.4.5 Application

This method is being successfully applied to two other species, the Dunlin Calidris alpina by Nigel Clark, and the Osprey Pandion haliaetus by Yves Prevost. Discriminant functions can be computed using a greater number of characters than two, as used here. On classes difficult to discriminate, several measures would be taken, the discriminant function computed and applied to a table such as Table Al-2. Where several measures have been taken and a graph such as Figure Al-6 is required, the programme will indicate that pair of measures which discriminate best between the two classes. Alternatively, in classes difficult to differentiate, several measures could be used to compute the discriminant function. In this case, the field worker would replace his graph with a calculator, and the known equation, key in the measures for a particular bird and apply the result to a table such as Table Al-2. The utility of the method is to introduce more than two axes on the discrimination graph, and to use this in the field. In the example cited, where only two axes are used, it allows a figure to be placed on the probability of an individual being one sex or another, which is not possible by simply eyeballing the data as in figure Al-6.

A very obvious application of being able to sex birds in this manner is in marking schemes. The computed sex of an individual could be incorporated into the variants of a marking scheme, be it wing

tagging, colour ringing, radio tagging or whatever. Sexual differences in behaviour may then be revealed, previously impossible to realise in what are to us sexually monomorphic species.

Al.5 SEXUAL DIFFERENCES

The following two sections have been published as part of a paper entitled "Some results from trapping Rooks", Ringing and Migration, 3 (4): 202-212, 1981.

Al.5.1 Data for size differences

Using the discriminant function, the basic statistics for both sexes based on 99.9% discrimination of all adults caught from this population are given in Table Al-3, together with those from other studies.

Comparison of these measures with those of other populations has not been successful. Several other accounts of weights are given (e.g. Lockie 1954, Beshir 1970, Swingland 1977, Lincoln et al 1980) but weight has been shown to vary much with season (Lockie 1954, Beshir 1970). Beshir's weights are for shot birds, a different sampling procedure, and the weights he gives are about 50g above my own for each class. No measures of wings, bills or tarsi could be traced in the literature.

The frequency distributions for wing and bill measures are given in

Figure A1-7

Frequency distribution for each sex of wing and bill measures
of adult Rooks from the study population.

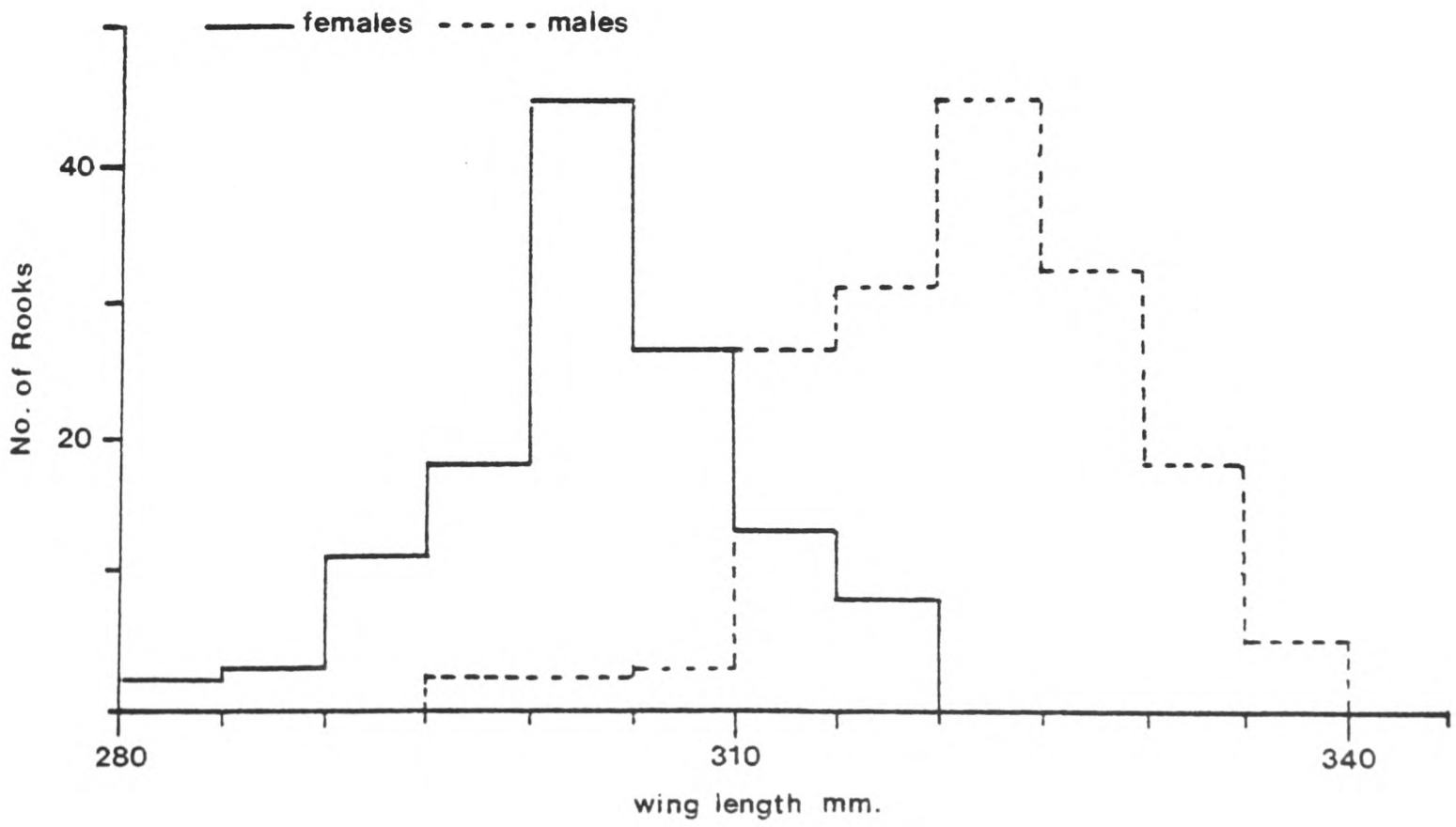
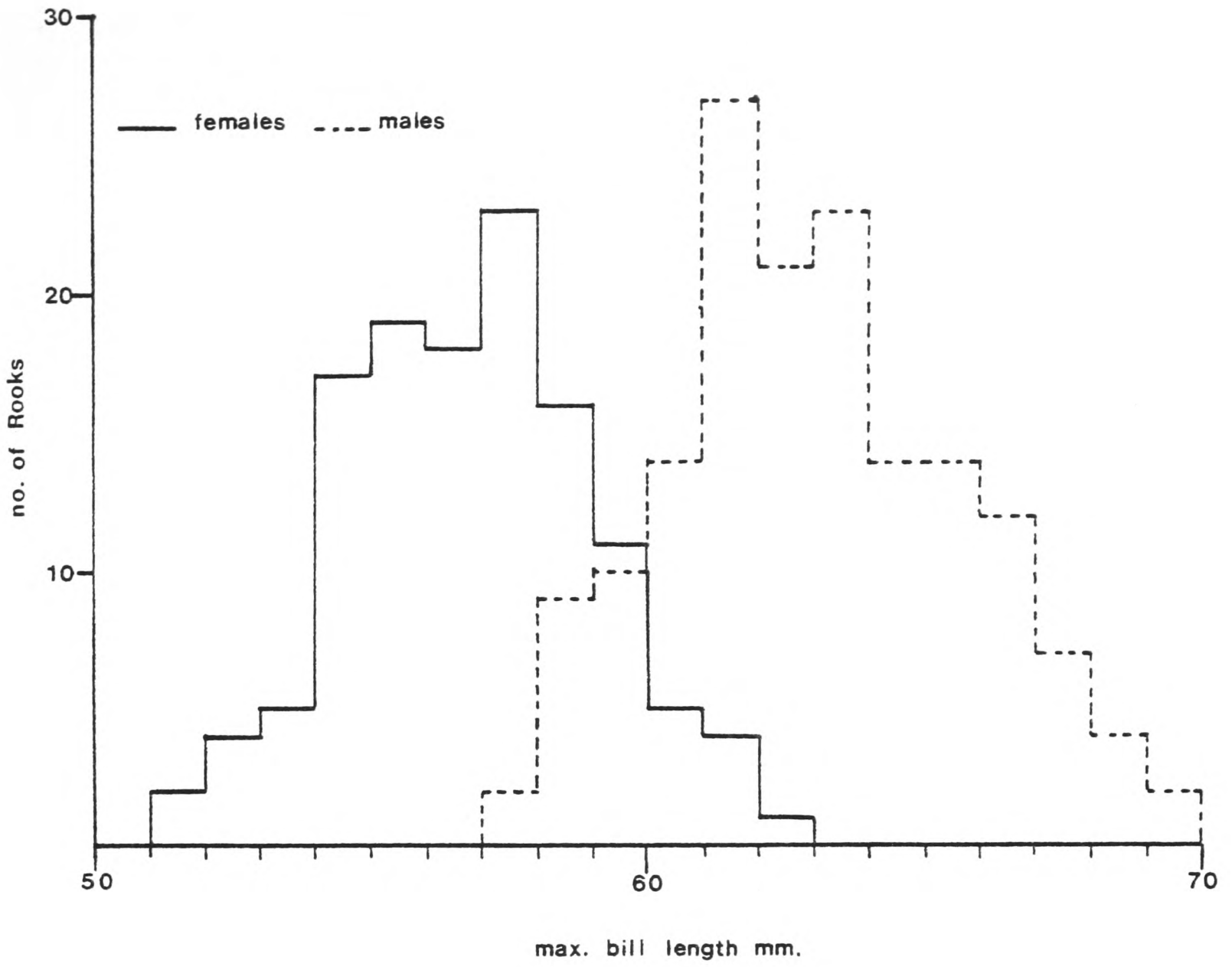


Figure A1-7. The differences between the sexes are significant for both the wing and the bill measure (T test; bill, $t = 20.3$, $d.f. = 285$, $p < 0.001$; wing, $t = 241.2$, $d.f. = 287$, $p < 0.001$). The mean sex difference in size for all skeletal measures taken is 8.3%, with an overlap of the ranges of 51% for the long bill measure, and 64% for the wing measure. The degree of sex difference in size is similar to that found in the Carrion Crow, for which Holyoak (1970) showed the difference to be 8.05%, and Picozzi (1975) 7.6%, expressed as the mean sexual difference using various measures, Table A1-4.

A1.5.2 Causes of sexual dimorphism

Many factors exist which may have caused this difference in size between the sexes. Sexual dimorphism results from the different selection pressures acting upon each sex, and their relative sizes will depend upon the sum of all pressures acting both to increase and to decrease size (Ralls 1976).

Various aspects of competition may be important. Increase in male size may result from male-male competition for females, selection favouring those traits which aid in winning fights (intra sexual selection) and hence females. Thus males increase in size over a number of generations, as does the prominence of those features used in display. This is supported by evidence derived from looking across a spectrum of species, as male rivalry is more important in those species with polygamous mating systems, where the relative pay off for winner and loser of male-male competition is much greater. Polygamous species show much greater sexual dimorphism (Brown 1974).

TABLE A1-3

Basic statistics of adult Rooks in the study
and other populations.

sex	measure	mean	S.D.	range	N
M	weight	489	30.24	405-560	162
F	weight	418	34.52	325-525	126
M	bill 1	41.7	2.7	36.3-49.5	162
F	bill 1	37.64	2.0	32.9-44.4	126
M	bill 2	62.87	2.74	56.5-70.0	161
F	bill 2	56.78	2.25	51.5-62.2	126
M	bill 3	21.23	1.14	18.6-26.3	161
F	bill 3	19.81	1.02	17.3-22.6	126
M	wing	320.8	7.67	299-338	162
F	wing	302.5	7.6	280-326	125
M	tarsus	421.4	115	303-579	103
F	tarsus	386	109	288-556	77
M	*weight	525	28.5		62
F	*weight	458.2	39.2		59
M	**weight	500	35.0	460-578	13
F	**weight	431	21.0	410-466	5
M	***weight	490	41.5	390-548	27
F	***weight	423	34.5	340-465	21

* Data from Beshir (1970) for Rooks shot between March-June.

**Data from Lockie (1954) for Rooks shot between March-June.

***Data from Coombs cited in Lockie (1954) for Rooks shot between March-June.

All measures in millimetres except weights, in grammes.

In the Carrion Crow, bill size is a good predictor of success in all types of competitive encounters. Charles (1972) found a strong

positive relationship (correlation >0.9) between all aspects of bill size and success at encounters between males. This is important when defending a territory, for only territorial Carrion Crows can breed, with the male the most active in maintaining the territory. In times of critical food shortage, success at encounters is important again; Houston (1977) and Picozzi (1975) have noted a predictable male bias in winter flocks, possibly a result of this.

TABLE A1-4

Size differences between sexes in the Rook
and the Carrion Crow.

species	derivation	measure	p.c.diff.	N	authority
Rook	mean all	bill length	10.8	288	Green
"	mated pairs	bill length	8.2	14	(this study)
"	mean all	bill depth	7.2	288	"
"	mated pairs	bill depth	6.8	14	"
"	mean all	wing length	6.0	288	"
"	mated pairs	wing length	5.9	14	"
"	mean all	tarsus	9.0	180	"
Carrion Crow	mean all	bill length	8.2	219	Holyoak
"	mated pairs	bill length	9.6	18	(1972)
"	mean all	bill depth	8.1	219	"
"	mated pairs	bill depth	9.3	18	"
"	mean all	wing	4.0	219	"
"	mated pairs	wing	9.1	18	"
"	mean all	bill length	10.8	43	Picozzi
"	mean all	wing length	4.3	44	(1975)

So a large bill, or a factor accompanying it, is advantageous to a Carrion Crow. My own data suggest that this is not true for Rooks. Although twelve of fifteen encounters observed between marked birds over a food item on grassland during spring resulted in a win for the bird with the larger bill (Appendix 2), this was probably just an effect of sex, with males dominating females. 6 of the encounters were between males, and in half the winner had the larger bill, and half the smaller. In those conflicts where the male with the smaller bill won, the winner was a breeding adult, the loser a non-breeding adult. Being a colonial breeder, the pay off from encounters at the nest is not so large for a Rook. Defeat of a Carrion Crow may mean inability to breed in that year, but this is not so for a Rook, for it could build elsewhere in the colony and breed successfully. However, the costs incurred in rebuilding may take the form of delayed laying of the clutch, and these later laid clutches have a lower successful output (Owen 1959). Pressures for increase in size may not have been so large for a Rook as they were in the Carrion Crow, but this is not reflected by a smaller sexual difference in size in the Rook, see Table A1-4.

A bird with a larger body size will have a proportionally larger bill, which may in turn affect the size of food items taken. Differences in food size taken by each sex have been variously interpreted as being a side effect of a sex specific change in size for some other reason, or as a reason in itself. Given the many other means of reducing inter-sexual feeding competition which have been demonstrated, e.g. various aspects of niche displacement and allopatry outside the breeding season, then it is possible that selection has caused divergence in size as a result of the advantages accrued from

feeding niche differentiation (Selander 1966, 1972). Only in cases where bill size alone is dimorphic is the situation clear, as is so in some species of woodpecker (Centurus striatus, C. herminieri, Melanerpes partoricensis) and the extinct Huia, Heteralocha acutirostris. In those species, such as the Rook, where the feeding apparatus is dimorphic as a result of body size differences it is a matter of conjecture as to whether niche displacement is the primary advantage or merely an incidental one.

Whereas crows of the genus Corvus are sexually monomorphic for plumage characteristics (except for the Jackdaw, see Voipio 1968) in all aspects of body size there is a difference of around 8%, with males the larger sex. The effect of this upon the size of food items has been shown by Holyoak (1970) for the Carrion Crow. Invertebrates fed to the young by the male averaged 63% longer than those given by the female, where the difference in bill size is around 10%. The sexes also differed in the proportions of different feeding actions used. This bill size difference may be of importance in reducing competition between the sexes for food, but it may, on the other hand, be only a by product of another pressure which gave rise to sex dimorphism in overall size.

Bioenergetics may be another important factor when considering reasons for sexual dimorphism. The mass of an animal influences the rate at which it uses energy, so that such measures as resting metabolism, energetic cost of flight, egg weight, heart rate, and conductance per unit mass decrease exponentially as total body mass increases, whereas storage capacity, digestive ability and lipid reserves decrease linearly (Downhower 1976). These relationships will

affect the ability of a bird to respond to conditions of deprivation and surfeit. A large bird can survive for a longer period on its reserves than a small one, but also takes longer to replenish them. Such relationships affect birds differently depending on their life history pattern. Thus for a bird resident in its breeding range which has a greater reproductive output the earlier in the season it starts to breed, small size would be beneficial to females who can come into reproductive condition rapidly with the spring flush of food (e.g. Great Tit, Jones 1973), although this is at the cost of greater risk of death during the cold winter months. Larger size in females would be beneficial in those species where eggs are produced from reserves laid down before migration to the breeding grounds, and here females are generally the larger sex (e.g. Dunlin Calidris alpina, Downhower 1976). Other factors may override this, for instance in lekking species such as the Ruff Philomachus pugnax, Buff-Breasted Sandpiper Tryngites subruficollis and the Pectoral Sandpiper Calidris melanotos, sexual selection appears to have led to males being the larger sex in species which migrate to their breeding grounds (Pitelka, Holmes and MacLean 1974). In a resident Swedish population of the Hooded Crow however, larger females breed first (Loman 1980), yet females are still smaller than males. The competitive advantage gained by males is probably a stronger evolutionary force.

Al.5.3 Mated pairs

By the end of the study there were 19 mated pairs of birds in which both members were tagged. In 15 of these pairs, both members were adults. Of the remaining 4, in 2 of the pairs a male had taken a 2nd

(calendar) year female as its mate, in one case the situation was reversed and the remaining pair had mated as 2nd year birds.

Despite the overlap in ranges between the sexes in adult Rooks in all aspects of size, in all mated pairs the male was always larger.

This has led at least one author (Holyoak 1968) to suggest that mates are selected on the basis of size. From my data on the sizes of mated pairs of Rooks, the size dimorphism between mated pairs does not differ significantly from that predicted by taking male and females at random from the population (t-test; $t = 0.5618$, d.f. = 140, $p > 0.2$). Although Table A1-4 suggests that mated pairs of Carrion Crows show greater size dimorphism than that of the population means, it is possible that this difference would not be significant if the data were analysed in the same way above as for Rooks. Size dimorphism is expressed as how much the larger member of a pair (the male) exceeds the smaller on any measure.

A1.6 CHANGES OVER TIME

Retrapping of marked birds enabled an assessment of changes over time in aspects of size of birds. A total of 24 birds were caught on more than one occasion (mean 3.7 times, S.D. 1.8, range 2-10) all but 3 being males.

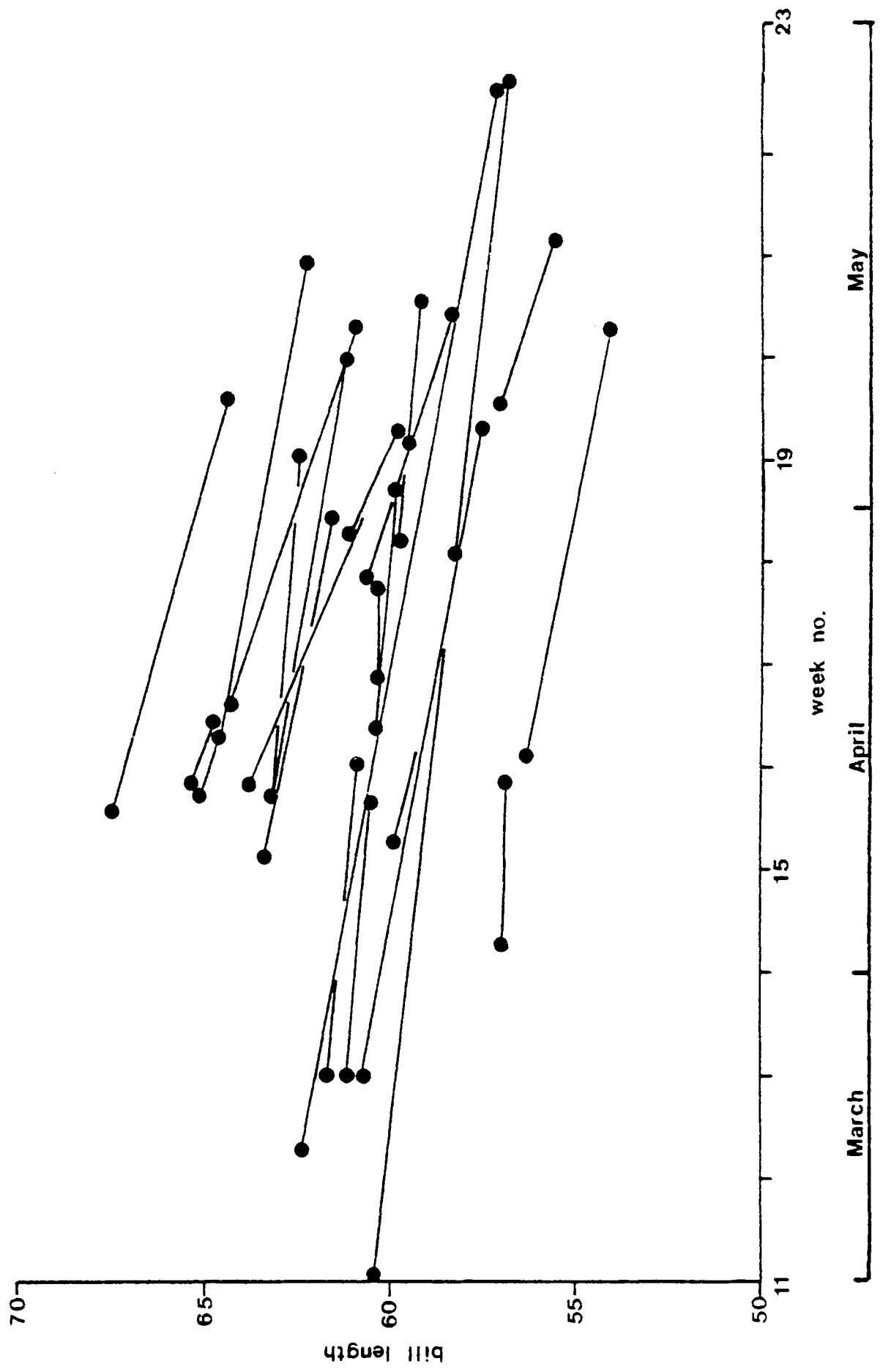
To reveal whether a trend of increase or decrease in certain measures occurred with time, the sign test (Siegel 1956) was applied. Measures of tarsi showed no trend, and wing length showed no significant trend, although twice as many birds showed an apparent

decrease than showed an increase. Abrasions of flight feathers in trapped birds would account for that variation not attributable to measuring errors (Pienkowski and Minton 1973). Weight changes have been discussed by Lockie (1954) and at length by Beshir (1970). The few retraps I have do not conform to the trend of decrease during this period, which these authors show. Beshir obtained his samples by shooting, my birds were taken from a trap, well fed with bait, perhaps obscuring any trends apparent.

Both measures of bill length in males showed a significant decrease over time ($p < 0.001$) as revealed in Figure A1-8, a mean decrease of 0.1% per day. The only two birds to show an increase in bill length were two females, known to have bred successfully, and who were incubating and brooding during the inter-trap period. The decrease in length occurred in the distal part of the bill, as the short bill measure (see Figure A1-5) also decreased. The distal portion of the top mandible is of cartilage which appears to be continually growing, and the many reports of malformed Rook bills (e.g. King et al 1968) in the literature and from my own observations, appear to result from the crossing over or overgrowth of the top mandible, although some growth of the bottom mandible occurs also. Wear is therefore prevented, and unchecked growth follows. I would suggest that the decrease in bill length at this time occurs because wear on the bill tip exceeds growth. This is further supported by the fact that Rooks probe for earthworms and leatherjackets (Lockie 1954), often digging with a pick-axe motion, at the time of year that the measures were taken. Large amounts of food are collected by the males, since they are collecting for themselves, their mate and their growing young and so the bill suffers a large amount of wear. After the breeding period

Figure A1-8

Decrease in bill length with time of adult male Rooks during 1979.



Rooks spend more of their feeding time on field types where probing is far less frequent, for instance stubble fields, livestock troughs etc., where presumably wear is much less. In live zoological collections, where Rooks and other corvids are unable to perform such bill wearing activities, the incidence of overgrowth of the top mandible is very common.

APPENDIX 2

Wing and bill size (mm) of victors and losers of conflicts over food
on grassland during March - June 1979 and 1980.

	victor		loser	
	bill	wing	bill	wing
M	61.4	505	M 64.6	495
M	60.9	515	F 54.3	395
M	64.9	515	F 58.1	430
F	58.1	430	F 55.6	420
M	59.4	500	M 63.8	495
M	61.7	495	M 62.7	530
M	65.6	515	M 61.6	510
M	61.7	485	F 57.6	465
M	63.2	505	F 58.6	375
M	61.3	430	F 58.0	355
M	65.3	480	F 58.0	410
M	64.6	515	F 57.5	480
M	67.8	430	M 62.4	510
M	59.9	490	F 52.9	385
M	67.9	500	M 62.7	530
<hr/>				
Mean	62.9	483.7	59.2	452.3

APPENDIX 3

Dates of circuits undertaken for home range analysis.

78 circuits were carried out from a vehicle as per Figure 2-2 on the following dates.

April 1979 - 10,11,17,18,19,20,23,24,25,26,27,30

May 1979 - 1,2,3,4,7,8,9,10,14,15,17

July 1979 - 17,20

October 1979 - 18,24,31

November 1979 - 1,2,8,12,14,19,21,26,27,29

December 1979 - 12,13

January 1980 - 10,14,17,23,30

February 1980 - 4,6,7,11,13,14,18,20,27,28

March 1980 - 3,5,6,12,24,25,27

April 1980 - 4,5,8,10,11,14,23

May 1980 - 1,3,5,7,8,12,15,20,22

The small number of circuits during summer 1979 was a result of few birds being present in the study area, those seen were a long way from roads on upland pasture, which with heat haze made identification difficult.

APPENDIX 4

Breeding records for Rooks of the study area.

In 1979, 311 birds were wing tagged

85 were breeders 56 adult males, 5 second year males
 24 adult females

135 were non breeders 45 adult males
 44 adult females
 46 second years

61 of these were not seen again in 1979

5 first year
31 second years
9 adult males
15 adult females

Of these 61, 21 adults returned during 1980,

11 as non-breeders (9 male, 2 female)
7 bred at Symington (6 male, 1 female)
1 male bred at Burnhouse Mains

13 were found dead 1 first year, 3 second years
 6 adults (6 males, 3 females)

16 were tagged too late in season to assess their status.

Of these 85 birds which bred in 1979, in 1980:

14 failed to breed but were present in the study area (16%)

10 absent (12%)

61 bred for two years running (72%)

of which 49 (57% of all breeders) bred in the same rookery

and 12 (19% of all breeders) bred in a different rookery.

31 adults bred in 1980 who were present in the study area as non-breeding adults in 1979.

APPENDIX 5

Social organization of breeding individuals of the genus Corvus.

Species	Nesting pattern
monedula	nest site dependant
dauricus	nest site dependant
frugilegus	colonial
brachyrhynchus	territorial, colonial reported
caurinus	loosely colonial
ossifragus	loosely colonial
sinaloae	loosely colonial
imparatus	loosely colonial
leucognaphalus	territorial
nasiscus	territorial?
jamaicensis	terrterritorial?
palmarum	territorial?
splendens	territorial, colonial reported
macrorhynchus	territorial
enca	territorial
typicus	territorial
unicolour	territorial
florensis	territorial?
validus	territorial?
orru	territorial
benetti	loosely colonial

coronoides	territorial
mellori	loosly colonial
tasmanicus	territorial
woodfordi	territorial
fuscicapellus	territorial
tristis	territorial?
kubaryi	territorial?
moneduloides	territorial
tropicus	territorial
corone	territorial, colonial reported
cornix	territorial
torquatus	territorial
capensis	territorial
albus	territorial
ruficollis	territorial
edithae	colonial
cryptoleucos	territorial, colonial reported
corax	territorial
hipidurus	territorial
albicollis	territorial
crassirostris	territorial.

Data taken from Bent (1946), Goodwin (1976), and the National Museum of Kenya, Nairobi.

"Nest-site dependant" means that the nesting distribution is dependant upon the distributon of nest sites.