THE SOCIAL ORGANISATION OF ROOSTING IN ROOKS AND JACKDAWS.

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November chill blaws loud wi'
angry sugh;
The short'ning winter-day is near
a close;
The miry beasts retreating frae
the pleugh;
The black'ning trains o'crows
to their repose;

Verse II. 'The Cotter's Saturday Night'.

Robert Burns ⑱

Light thickens; and the
crow
Makes wing to the rooky wood:

Act 3, Scene 2 'Macbeth'

William Shakespeare

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CHAPTER 1

Introduction

Many birds, insects and mammals communally roost. Among the many birds, and in the Corvidae in particular, the roosting system is complex, orderly and precise. A number of hypotheses have been put forward to explain why communal, rather than solitary, roosting is so frequent.

This introduction consists of an outline of the autumn and winter roosting behaviour of the rook (*Corvus frugilegus L.*) and the jackdaw (*Corvus monedula L.*). A number of hypotheses intended to explain this behaviour are then considered, specifically in relation to rooks and jackdaws. Finally a plan is developed to approach and test one of the hypotheses.

The autumn and winter assembly system

Rooks spend most of their day feeding close to their own rookeries with some overlap with other rookeries (Patterson *et al.*, 1971) but in the early afternoon they assemble in the rookery trees. At this point (in my study area) they were frequently joined by jackdaws from neighbouring breeding colonies and possibly some rooks from smaller rookeries. The bird's behaviour varied; either they flew *en masse* to the next assembly or they arrived in small parties and departed again in larger parties. Within my study area there were numerous flocks composed entirely of jackdaws and consequently some smaller (primary) assembly points (e.g. a group of trees) were frequented by only jackdaws.

From the rookery or primary assembly, they progressed to a secondary assembly point, which could be a grass or cultivated field, nearer the roost, where they fed. They were joined by flocks from other secondary assemblies or rookeries and then moved on to the next secondary assembly where the same behaviour was repeated (seen by Gramet, 1956). This continued until the final assembly was formed just prior to entering the roost where the birds did not feed. Coombs (1961) did not observe this behaviour in Cornwall where birds flew directly from the rookery to the roost, (also seen by Brown, 1942, near Carlisle; Brian & Brian, 1948, in Hertfordshire). There were generally one, two or three secondary assemblies where birds congregated to feed (although Burns, 1957, only found one secondary assembly in his study area). The position of the secondary assembly changed slightly from day to day although some of them were near the location of summer nesting colonies. Philipson (1933), in Northumberland, found that peripheral areas of the roost "catchment area" were vacated by mid-day, and that some of the secondary assembly sites were not near rookeries but at the junction of flight lines. He concluded that rook flocks are attracted to each other and form these assemblies while Newton (1946)thinks they are simply habitual feeding places.

In bad weather (strong wind, fog, haar) these secondary assemblies would amalgamate or they might not even form, the birds flying directly to the final assembly without halting.

During the flight to the roost, jackdaws and rooks flew at the same pace. Flights with the wind, or on bright still days, seemed to be at a greater height than on days when flights were against the wind or when visibility was bad (heavy rain, fog, haar). On days of adverse winds, birds "hedge-hop" (Burns, 1957), presumably because wind speed at the surface (near the ground) was much less than at a height (gradient wind, Kimble, 1951); and at a height for flights with the wind. Brown (1942) believed an overcast sky with wind and rain brought the birds to the roost earlier (seen by Burns, 1957; Conroy, 1966) than usual, while clear skys delayed in the flights.

The final assembly and roost entry

The birds did not immediately enter the study roost on first arrival; instead they formed a final assembly some distance away. From November until March the position of this assembly did not vary greatly and was less than half a mile from the roost. But during early autumn when the roost was building up there could be several final assemblies close to the roost site but at different compass points; changes in final assembly position were also noticed by M'William (1924). Quite often flight lines into these assemblies have been mentioned which passed over the roost itself (Coombs, 1961; Conroy 1966) as they did in this winter roost. Final assemblies were generally situated in a field, but on arrival some birds landed in trees surrounding the assembly area (seen by Brown, 1942). Frequently, just before roost entry, the tree-perching birds would join the flock on the field. Feeding would sometimes occur but the birds generally just stood in silence without feeding (also seen by Dewer, 1933; Burns, 1957) only calling when other flocks arrived. The final assembly consisted of a large number of rooks and jackdaws standing close together on a small defined area. No inter- or intra-specific aggression was observed.

At a time, which appears dependent on light intensity (see Chapter 2) total silence would prevail (noticed also by Turner 1957) and the flock would rise *en masse* (seen by Burns 1957; Jackson 1964) and fly towards the roost. As they flew from the final assembly to the roost they would suddenly begin to call loudly (heard by Nelson 1907; Philipson 1933; Chislett 1952) and much aerial circling and diving would occur (seen by Brown 1942). On other occasions the birds at the back of the flock (in relation to the roost) would silently fly towards the roost and the others followed on in strict order giving a snake-like effect (sometimes birds at the back of the flock would fly to the front and thus the whole would "roll" into the roost). The former behaviour occurred most frequently before November and after February; and the latter behaviour was seen in the main roosting period of November, December and January (see by Munro, 1948).

On very rare occasions individuals or flocks entered and left the roost before final assembly; most often those birds which did, eventually joined the final assembly before roost entry proper occurred. However, when the weather was bad (strong winds, very low temperatures, heavy rain, haar, fog), roost entry was directly from the rookery (not seen by Bedford S.N.H.S. 1951 or Coombs, 1961).

As birds were flying over the roost-trees before settling for the night I have frequently seen the whole flock of birds "zig-zagging" up and down the wood by gliding rather than active flying. Turner (1957) described the first arrivals alighting just inside the fringe of the roost-wood and the following birds gradually perching further and further towards the centre of the wood. It is possible that this behaviour was a result of the wind direction at the time i.e. birds prefer the leeward part of a roost (see Chapter 3).

Inside the roost wood

Roosts can be composed of many species of fairly dense trees generally with an undergrowth (e.g. Brian and Brian, 1948). The Bedford

School N.H.S. (1951) studied a main roost which was a narrow spinney of ash with some oaks and poplars. The trees were about 13 m. high. They found the whole spinney was used when the maximum number of birds were present with a preference for the ash at the North end of the belt. (Conroy, 1966, also noticed a preference for part of a roost wood). Only the higher branches of the trees were used (noticed by M'William, 1924; Burns, 1957; Conroy, 1966) with the birds being quite closely packed in the roost (seen by Brian and Brian, 1948). (This was not seen in this study). Coombs (loc. cit.) also found that the rooks preferred the taller trees (mixed coniferous and deciduous) while the jackdaws went to roost in the lower dense plantation of conifers. He considered that the relative positions with the taller to the south-west and the fact that prevailing winds were also from the south-west, meant that the combined flocks usually came over the jackdaw roosting area first (i.e. into the wind). From this he inferred that as this area was often filling up before the rooks settled, the jackdaws were not forced to take the lower trees. However this is a particular instance and in my study roost rooks and jackdaws roosted together and not in separate parts of the roost. Anticipating Chapter 3 it is worth noting that adult rooks forced younger rooks and jackdaws to roost lower down in the tree canopy. Coombs (1961) ignores the fact that the rooks preference for the taller trees might exclude the jackdaws from roosting in them when they are 'full' of rooks. He noticed little aggression when other members of the Corvidae, such as carrion crows and ravens, roosted with the rooks and jackdaws. Pairs of rooks roosted close together or in contact although the branches were not full, frequently having only one pair or an individual on each (seen by Bedford S.N.H.S. 1951). Conroy (1966) quoted data from the ARC Rook Unit, Aberdeen University, that birds do not remain on the top branches, but move to lower branches after dark (see Chapter 3). Coombs (1961) assuming that rooks and jackdaws could not see in the dark, postulated that the noisy calling while roosting is simply a means of pairs regaining contact in the melee and consequently the noise ceases once all pairs are perched together.

Segregation within the roost may occur according to the feeding areas used by individuals. Jackson (1964) studying a main roost in Leeds found two woods at the site, birds from one mostly fed towards the south-west while those in the other used the east. From calculations of breeding population size he inferred that only one of the woods contained a small percentage of immigrant birds.

Departure from the winter roost in the morning

Not all birds awoke at the same time and most preened before any local movement within the roost occurred. On most occasions small groups of rooks left the roost in twos (seen by Stewart, 1924) returning directly to their respective rookeries, i.e. the primary assembly point the night before, where they dispersed to feed. In the roost studied in this investigation, a rookery was located within its boundaries (Figure 1). Although no roosting occurred in the nest-trees the first movement of most pairs each morning was to fly to the rookery before going to the fields to feed(also seen by Coombs, 1961).

Light intensity and weather may be effective in determining the time of departure (Burns, 1957; Lundin, 1962; Coombs, 1961; Griffiths, 1955). Jackson (1964) found that rooks arrived at a rookery earlier in the morning the colder it was, and a delay if the temperature increased;

headwinds caused earlier departure and tailwinds delayed departure. However, Brown (1942) suggested that clear skies with no wind caused early departure and overcast sky with wind and rain delayed departure.

Some birds visited the final assembly site(s) before leaving for their rookeries. In these instances a larger group of birds formed and eventually left in one direction. Philipson (1933) noticed this in Northumberland, and also that groups of individuals may stop briefly in rookeries departing when a following group arrived.

Conclusion

Regional variations of roosting behaviour are to be expected. The roosting behaviour where numbers are augmented in winter by immigrants from Continental Europe may differ from say, the extreme south west of England, where this does not appear to occur. For instance main roosts can become established from August to November and mid-winter changes in roost site have been recorded.

Likewise the changeable summer roosting described by some authors may not occur in areas containing few suitable roosting sites (Patterson *et al.*, 1971). However, regardless of such variations of roosting behaviour, a complex, disciplined and synchronised system is evident.

Published hypotheses as explanations of communal roosting by Corvidae

The hypothesis of the "transfer of information relating to the location of food".

Ward (1965) suggested that the function of the communal roost is to act as an information centre and thus extend the benefits of social feeding. Philipson (1933) proposed a similar hypothesis.

Ward's study on *Quelea quelea* suggested that birds which lack good feeding places follow other birds, which know of good feeding sites. He proposed that roost sites need not be permanent and that this pattern is found in communally-roosting and socially-feeding birds which have an irregularly distributed food source. His idea results from (a) the behaviour of Quelea quelea when the birds leave the roost in the morning (b) roosts increasing in size when food is in short supply and (c) the constant shifting of the roost site dictated by the unevenly (inferred) distributed food supply.

Many authors (Wynne-Edwards on starlings, 1962; Moffat on pied wagtails, 1931; Immelman on weaver finches, 1965; Ward see above) have put forward the view that when food supplies deteriorate, and its distribution becomes uneven, birds tend to form large communal roosts. Dunnet and Patterson (1968) suggested that rooks had difficulty in obtaining food in the summer and consequently one would expect them to have an established roost in the area. Patterson et al. (1971) did in fact describe a permanent summer rook roost in the same area used by Dunnet and Patterson (loc. cit.). However, other observers have reported erratic or nomadic roosting by rooks in summer (e.g. Coombs, 1961). Nevertheless, although this hypothesis may be applicable to the summer roosting behaviour of rooks the behaviour of rooks in winter is different.

In winter, several rookeries may have a common feeding ground and other rookeries in the same roost system may share a different feeding area. Little mixing occurs between the different rookery groups during the day, but mixing within each group happens often, with birds being seen in each other's rookeries (Patterson et al., 1971). Thus during winter Ward's hypothesis cannot be sustained because groups of rooks feed as separate communities and so information on food location, which might be passed on at a large roost composed of many communities, cannot be acted on to any large extent.

How far is this segregation of rook communities taken in the roost? To my knowledge only one author (Jackson 1964) has claimed observations of segregation between individuals from different feeding areas in a rook and jackdaw winter roost. His winter roost contained two separate, but adjacent, woods from which he observed birds leaving in the morning, or arriving in the evening, from opposite directions; birds that fed in the west roosted in one wood and birds from the east in the other. His observations, however, are unreliable as none of his birds were marked, he did not describe whether they mixed in the final (pre-roost) assembly and he did not follow the departing flocks to their feeding areas.

In conclusion it is apparent that in autumn and winter during the main roosting period, adult and young rooks mostly feed within their own rookery feeding areas (Patterson _et_ _al_. 1971). Thus there is no need for rooks to come to a large roost in order to follow members of the same community to a food source.

The hypothesis of epideictic behaviour.

Wynne-Edwards (1962) proposed that the primary function of the roost is to bring the members of the population-unit together, so that information can be gained on the state of the population when conditions of population size and food supply require it, and the need for some form of regulation of numbers can be transmitted to the members. The fact that the birds roost together afterwards becomes of secondary importance. The "epideictic demonstrations" he mentioned are the aerial circling and diving on entering the roost.

Wynne-Edwards stated four conditions that must be met for his hypothesis to apply. Firstly, there must be only one winter roost for a particular "catchment area" of rookeries, with no overlap of other areas. Secondly, the roost must persist at the same site for some years. Thirdly, flights to and from the roost must be synchronous; and lastly the "epideictic demonstrations" must occur after the breeding season, i.e. breeding behaviour and roosting behaviour are essentially different activities. Although the behaviour of rooks and jackdaws meets these four conditions and supports Wynne-Edward's contention, the ultimate validity of the latter must remain in doubt until supported by experimental data.

Anti-predator hypothesis.

The orthodox view of the mode of operation of natural selection suggests that there must be an advantage to each individual in roosting with others.

A suggestion to explain communal roosting is that the increased awareness of the approach of enemies confers some protection to members of the group. Nevertheless, communal roosts are extremely conspicuous particularly when the same site is used year after year (as it is in the rook and jackdaw). Zahavi (1971a), in his study on white and pied wagtails (Motacilla a. alba and Motacilla a. yarrellii), found that a large flock was more difficult to approach than a small flock or scattered individuals; as in a large flock one or another of the birds would be awake and raise the alarm while smaller groups were generally less attentive. However, Gurr (1968) on the basis of observations on a communal roost of Australasian harriers (Circus approximans) found a roosting individual could be approached closely before it alone moved, leaving the remainder undisturbed.

Zahavi (1971a) considered that there would be an increase in predation pressure as a result of the aggregation of birds, although the chance of an individual succumbing to a predator is less in a large flock than in a smaller flock. Birds that roost singly or in pairs would not be as attentive as some individuals in a rook and jackdaw communal roost, but at the same time their position would be less conspicuous to a potential predator.

Secondary benefits would accrue from the aggregation of birds. The reduction in attentiveness each bird would have to exert in order to watch for intruders (i.e. a reduction in energy expenditure) would be one such benefit. Conversely Darling (1952) stated that continual disturbances, brought on by small groups in a large roost, may result in greater activity and allow the birds to endure the long winter night. However, this would cause a higher metabolic rate which would deplete energy reserves faster than a resting bird.

In a communal roost the birds most likely to be caught by a predator will be those on the periphery. If competition for the "best" perches does occur, then those on the periphery may well be low status birds. Jumber (1956) gave evidence that suggested that individual starlings roosted in the same places each night.

Rooks and jackdaws have no serious predators except man and communal roosting is not very effective against him, although some of the birds are alert and will warn others of any approaching 'enemy'. However I find it difficult to believe that such large winter rook roosts are necessary for any anti-predator function to be effective, particularly as the same function could be carried out by a much smaller aggregation of rooks from a few small rookeries.

Increased warmth or shelter.

It has been suggested that a communal roost could offer two energetic advantages: (i) closely packed birds could form a heat unit of high thermal capacity with reduced heat losses; or (ii) the number of available woods or roosting places offering shelter might be limited and in consequence communal roosting occurs.

Solitary feeders sometimes congregate into communal roosts. Tree creepers, *Certhia* spp. (Lohrl, 1955) and the wren,(*Troglodytes troglodytes*) (Armstrong, 1955) sometimes roost clumped together on cold winter nights probably to conserve heat. Broekhuyson (1960) noted in the European swallow (*Hirundo rustica*) that clustering was more noticeable in periods of starvation and low temperature. Stonehouse (1956) suggested a survival value in close huddles or aggregations of the emperor penguin (*Aptenodytes forsteri*) and Prevost and Bourliere (1957) found that emperors by roosting together, used half as much energy as those roosting solitarily.

Conroy (1966) stated that decreased heat losses could explain why rooks changed from smaller to larger communal roosts as the winter progresses. He also stated that this would account for the birds' appearing to drop to the lower branches in the roost thereby decreasing surface area and space between individuals. What I believe he means is that birds by dropping to lower branches reduce the area of their bodies exposed to heat loss by radiation (for more detail refer to the discussion in Chapter 3). Birds in this study maintained quite large individual distances (although pairs were close) throughout the winter in the roost and although birds did progress down the trees as weather deteriorated little change in individual distance was noticed.

To anticipate later Chapters, I consider it unlikely since rooks and jackdaws do not huddle, that they gain any energetic advantage by roosting together, although pairs will roost touching each other (also seen by Coombs, 1961) which may be of some advantage. It must be mentioned that Brenner (1965), during his work on starlings observed a lower individual metabolic rate (i.e. heat loss) among grouped birds than in single birds in dark "roosting" conditions. This reduction in heat loss by grouped birds increased their survival time. In casual observation of roosting starlings on a building I noticed that they roosted quite close to each other and it is possible that Brenner's observations are the result of a reduction in heat loss because the birds were close together, rather than reduction in heat loss by each bird hearing the other individuals and thereby feeling 'calmed'.

Patterson et al. (1971) questioned why rooks should roost with individuals from other rookeries in summer when they could roost in their own rookeries. They put forward the idea that nesting woods are not suitable for roosting, and that the birds' requirements for a roost become more exacting later in the winter (explaining the seasonal cycle of roosting) leading to a concentration into a very few sites by mid-winter; they did not think that this was because of more shelter in a winter than in a summer roost. Nevertheless they did not specify in what way the birds' requirements might become "more exacting". Several authors (M'William, 1924; Brian and Brian, 1948; Burns, 1957) considered shelter to be paramount in the rooks choice of roost sites. Brian and Brian (1948) studied rook roosts which were on southerly sides of woods, the trees being young and dense and Burns (1957) noticed that when a strong wind blew rooks and jackdaws chose the sheltered side of the wood to roost.

Most, if not all, of the statements on the topic of roosts and shelter are inferences or opinions. Only by measurement of the weather inside a roost, and detailed observations of the changes in the distribution of the birds in the wood, can any firm conclusion as to the relationship between weather and bird roosting behaviour be made.

The study plan.

The four hypotheses (food location, epideictic display, anti-predator and increased warmth) may have, in varying degrees, something to offer in explaining the known facts of communal roosting in rooks and jackdaws. However, some present difficulties if not insuperable problems, of attack. I therefore decided to investigate the social organisation of a winter communal roost and the manner in which shelter might be of advantage to the birds as these aspects were measurable. Work performed in the winter 1969/70, on an urban starling roost suggested certain worthwhile avenues of investigation. Two questions were posed:

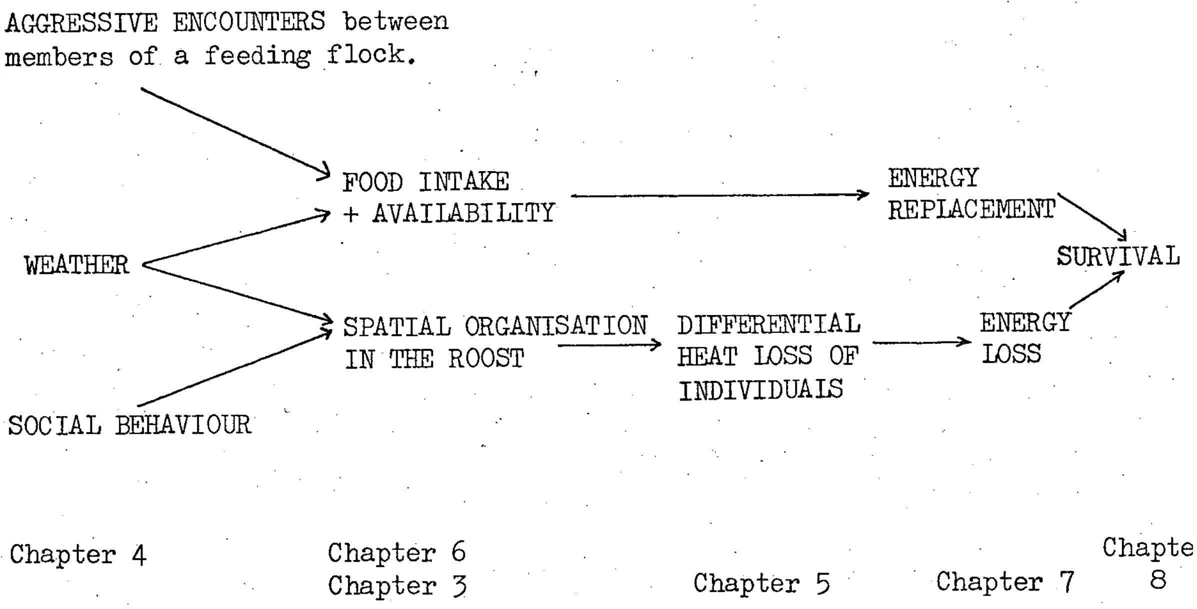
(1) Does the behaviour of rooks and jackdaws in a communal roost reduce the rate of loss of heat energy?

(2) Is the net loss in energy reserves variable between individuals and could it be critical to some for survival?

The work is divided into three interconnecting parts; behaviour, physiology and climate. The social organisation of a winter communal roost of rooks and jackdaws was studied for two winters (1970/71 and 1971/72) with particular reference to the weather and climatological characteristics of the roost. Observations on the field behaviour were compared with the behaviour of a captive group of birds. Measurements of the rate of heat loss in a controlled laboratory environment were made in a variety of conditions so as to ascertain the energetic stress on individual birds under conditions that birds would be exposed to in a roost. An investigation (in captivity) of the effect of weather and competition on food consumption was done to shed light on what factors contributed to energy replacement; and samples of birds taken just before going to roost were analysed for fat and stored food.

By knowing the effect of climate and weather on roosting organisation; by knowing the effect weather variables have on the rate of loss of heat by individuals and pairs; and by knowing the energy reserves available, a statement as to the potential value of such behaviour can be made.

A flow diagram representing the study plan is shown below.



The main winter roost studied was situated at Stevenson Wood, 3 km. east of Haddington, East Lothian.

All experiments on captive birds were done between October and February unless otherwise stated, and they were held in climatic conditions similar to those occurring in the field.

In order to avoid dislocating the flow of the narrative I have relegated descriptions of additional work to the appendix. All of the raw data is stored on tape in the Edinburgh Regional Computer Centre or on output in the library of the Department of Forestry and Natural Resources, but an indication of the number of observations are given where relevant.

All analyses were processed by an IBM 360/50, 370/155 or 4/75 computer using Fortran IV and S.P.S.S. (Nie, Bent and Hull, 1970) and the statistics used in this study are briefly described in Appendix 5.

East Lothian and the general climate.

A sketch map of the area is shown in Figure 1. The most northerly section of East Lothian, is approximately triangular. The coastal plain of East Lothian is roughly triangular and is at an altitude of up to 77 m. The Lothian Plain lies immediately to the southward, with the terrain rising slowly toward the 154 m. level in the Lothian Platform, which extends east to St. Abb's Head. The Lammermuir Hills occupy the central and southwestern sections of the area. These Hills rise to above 388 m. and run from WSW to ENE with the north face rising rather sharply. North of the Lammermuirs the only drainage system is that of the River Tyne flowing through Haddington to the sea, across the Plain.

The S to SW winds, which develop with the advance of depressions, are funnelled through the Clyde-Forth valley to East Lothian. A more detailed analysis shows that WSW winds predominate. The shelterbelts inland tend

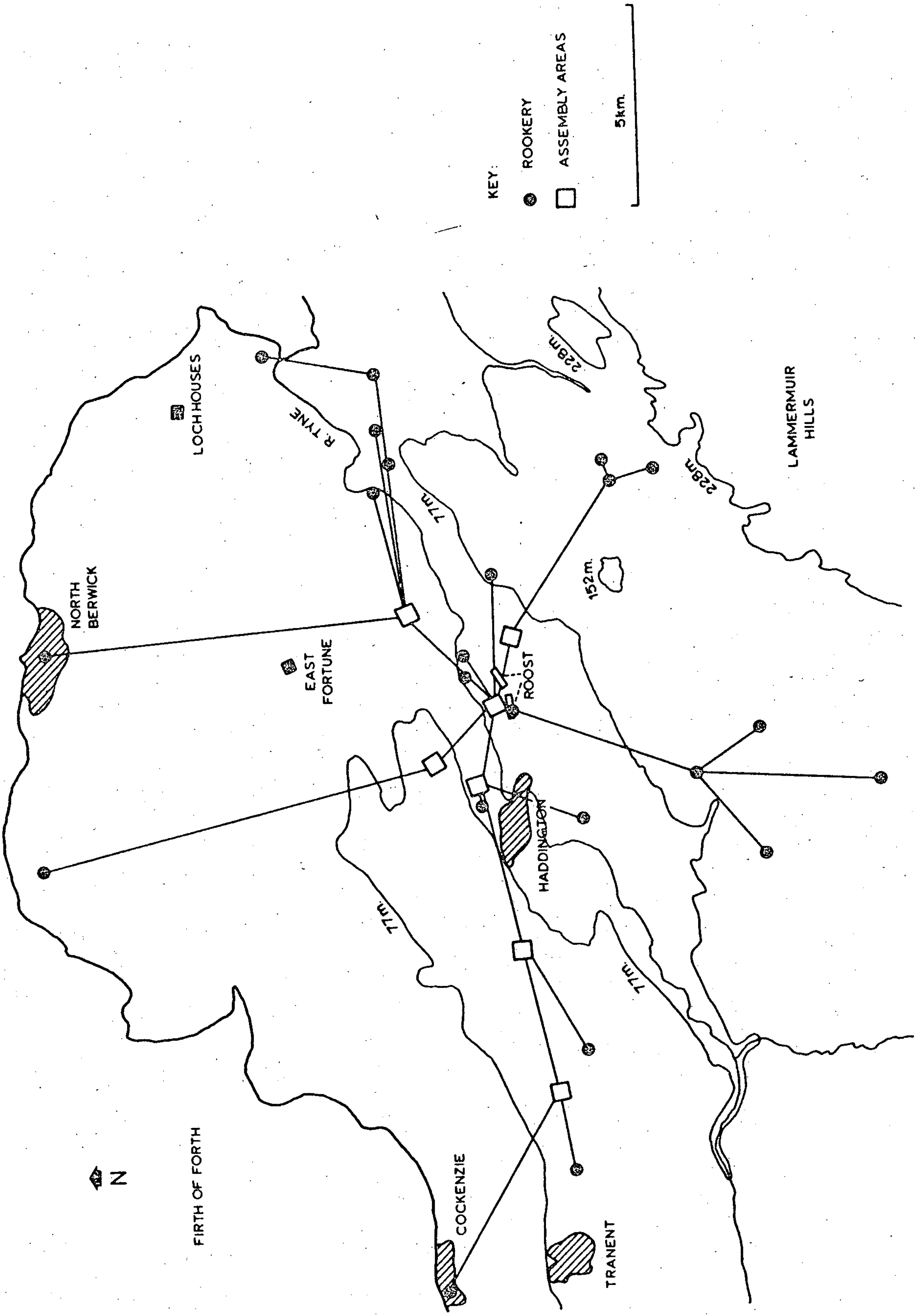


Figure 1 Rookeries, assembly areas, flyways and main roost in the East Lothian.

to decrease the wind velocity which is high from the funnelling effect. In Figure 2 the annual rose for the East Fortune airfield, an open exposure in the Lothian Plain demonstrates the major wind directions. Autumn to early winter is the principal period for gales, which normally come from the WSW and WNW.

East Lothian has a low annual rainfall of 66 cm. The coastal plain of East Lothian has a potential water deficit of 7.4 cm. which suggests that it is liable to suffer from annual droughts (McVean & Lockie 1969 from Green 1964). In the coastal plain, the annual range of average daily mean temperatures is some 11°C increasing from about 3.3°C in the coldest month, January, to nearly 15°C in July. The coastal zone is a little warmer especially in winter but the difference is small. The effect of altitude is noticeable for as one ascends above the Lothian Plain at about 154 m. the mean temperature at the coldest part of the year is about 1°C lower than in the coastal plain. At 246 m. in the Lammermuirs the average night minimum temperature in January and February is well below that at 154 m. or 92 m. The terrain of the Lammermuirs favours the cold night air and it accumulates in pools where, almost certainly, the coldest winter nights occur. (Compiled with the use of meteorology office data, a report by F.H. Dight, "The Climate of the East Lothian and North Berwickshire" Met. Office. Climatological Memo. 49 and personal communication with Mr. Armour, Met. Office, Edinburgh).

The roost (NT 5445 7415):

The roost is situated 3 km. due east from Haddington, East Lothian, in a mixed deciduous and coniferous wood called Stevenson Wood. This wood is divided into two parts (Figure 3) which henceforth will be

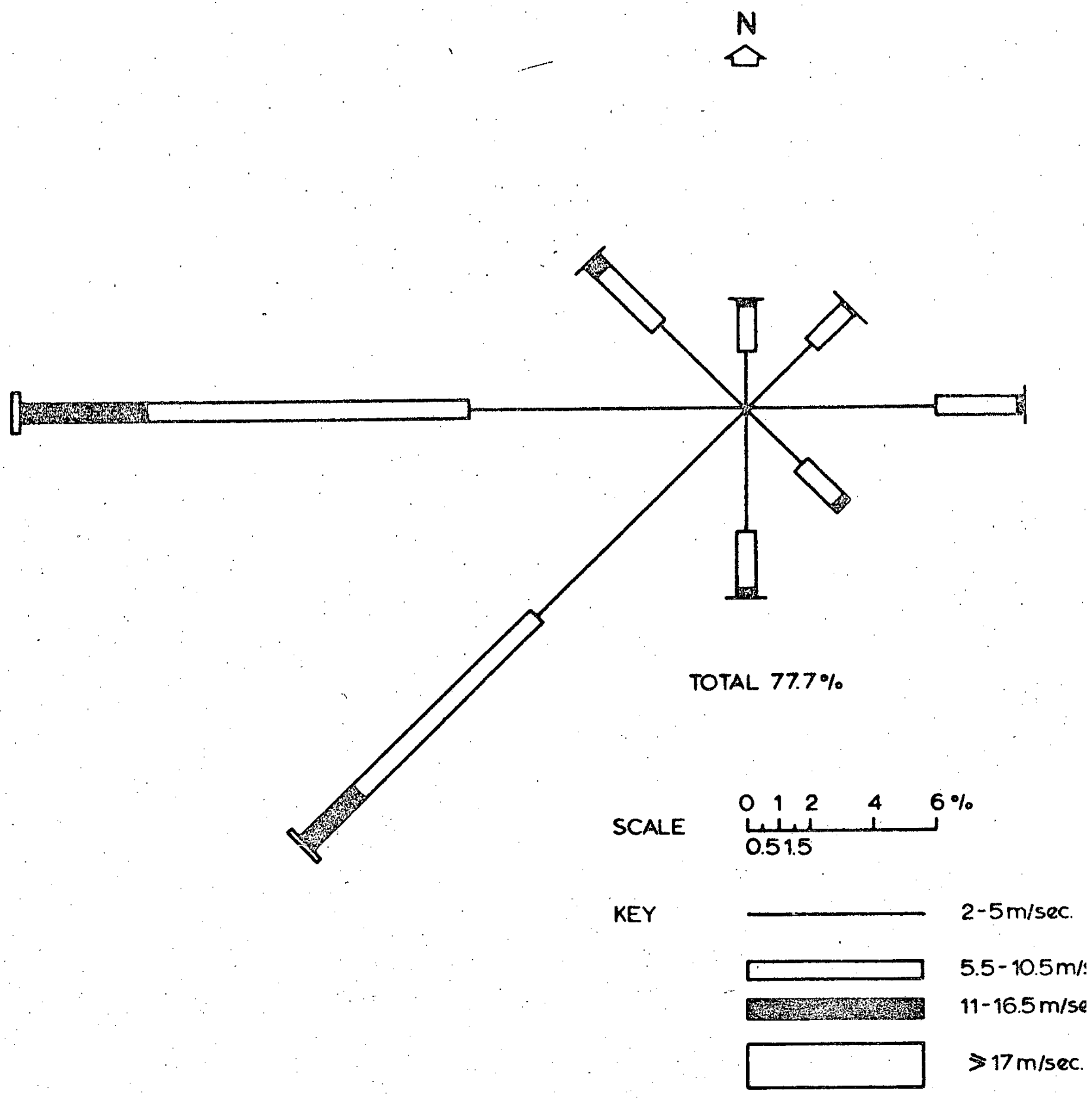


Figure 2 Annual wind direction rose for East Fortune Airfield.

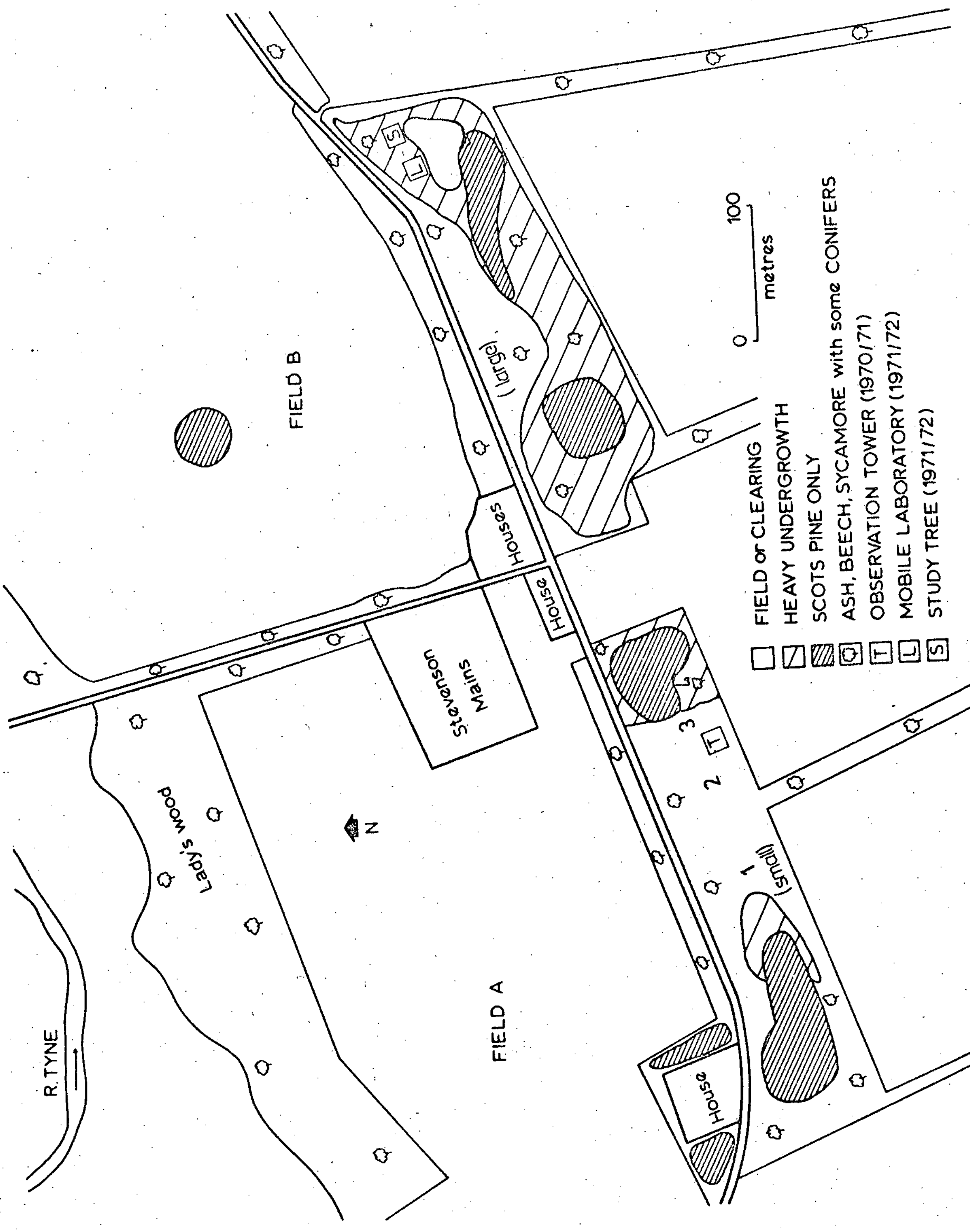


Figure 3

Plan of the roost and the surrounding area, showing position of study trees.

described as the small and large wood. The axis of the roost wood lies approximately SW by W (255^{o}) by NE by E (75^{o}) and in consequence the majority of the winds blow straight up the wood. Shelter belts protrude from the southerly edge of the wood running SE by S. An aerial photograph Figure 4, although taken in April 1962, gives a general view of the present day situation.

The smaller wood is about 75 m. in width and 400 m. in length. The larger wood is on average 100 m. wide and 350 m. long. Most of the small wood has no undergrowth although at the easterly end the undergrowth is heavy and grows to the bottom of the canopy; in the large wood undergrowth is generally prevalent. Figure 3 shows the general distribution of tree species, most of which are between 19m. and 22 m. high.

Lady's Wood, immediately to the north of the small wood, is primarily deciduous and the small circular wood in the middle of the field to the north of the large wood is Scots pine. The trees in the grounds of Stevenson House are oak. The River Tyne flows east just north of Lady's Wood. Field A and B (Figure 3) are either bare (ploughed) or grass during the winter. Rookeries are positioned at the west and east ends of the small wood in Scots pines.

This roost was probably known in 1794 (George Buchan-Hepburn: General View of the Agriculture of East Lothian) at Tyningham but subsequently moved to Stevenson (Munro, 1948), and was possibly in use as a roost by 1945.

East Lothian consists of mixed farmland with pasture and arable fields. There are few woods of any size and the majority of these are in the south-west part of the county.

Figure 4 Aerial photograph of the roost and the surrounding area (April 1962).

CHAPTER 2

The influence of light intensity on the roosting times of the rook (Corvus frugilegus L.) and the jackdaw (Corvus monedula L.)

Introduction.

The rhythm of roosting of rooks and jackdaws is distinct and precise. Each afternoon in winter both species cease feeding and congregate at or near their nesting places. From there they proceed in stages to a roosting wood which may hold thousands of birds and which they enter just before dark.

Other birds have a similar rhythm and the means by which this behaviour is triggered has been the subject of many studies (review by Davis 1955; also studies by Jumber 1956, Delvingt 1963, Swinebroad 1964, Meanley 1965). Most agree that light intensity is involved, but correlations of arrival at the roost with light intensity are not good. This led Davis (1955) to suggest, because of the variation in light intensity when starlings (Sturnus vulgaris L.) actually enter the roost, that observations earlier during the sequence of assembly before roosting would be needed in order to establish the nature of the relationship between light intensity and roosting. Subsequently, Davis and Lussenhop (1970) demonstrated the effect of light intensity at different times in relation to civil twilight, on the sequence of events leading to roosting by starlings.

Little work has been done on the Corvidae which roost communally. Haase (1963) and Jackson and Fiedler (1969) studied the winter roosting behaviour of the American common crow (Corvus brachyrhynchos Brehm) and presented evidence showing that light intensity influenced (a) the time at which roosting occurred and (b) the rate at which birds entered the roost. Analyses of the effects of light intensity on the nightly roosting rhythms of rooks (Corvus frugilegus L.) and jackdaw (Corvus monedula L.) have not been published to my knowledge.

This Chapter describes the effects of light intensity and time in relation to civil twilight on the arrival and departure of rooks and jackdaws from a large roost at Haddington, East Lothian, South East Scotland, from November 1970 to February 1971.

Method.

Each morning rooks and jackdaws leave the roost and fly in parties almost directly to their rookeries and nesting places and thence to their feeding areas. Patterson, Dunnet and Fordham (1971) have in winter shown that young and adult rooks mostly feed within their own rookery feeding areas. In the early afternoon the rooks will stop feeding and reassemble at the rookery while jackdaws may join the rooks or form their own small group. I have called this early afternoon gathering, just before birds fly nearer to the roost, the primary assembly. After some time the birds will move to secondary assembly areas (positions of which change slightly from day to day) to be joined by flight lines from other primary areas. There may be several successive secondary areas. From these they move to a final assembly area (which is generally quite close to the roost) before entering the roost just before dark, this final phase being named roost entry. The position of the assembly areas and the roost in the study area can be seen in Figure 5. (Most secondary and final assembly areas are on the ground and not on trees.)

Observations of the departure of birds from a primary assembly point

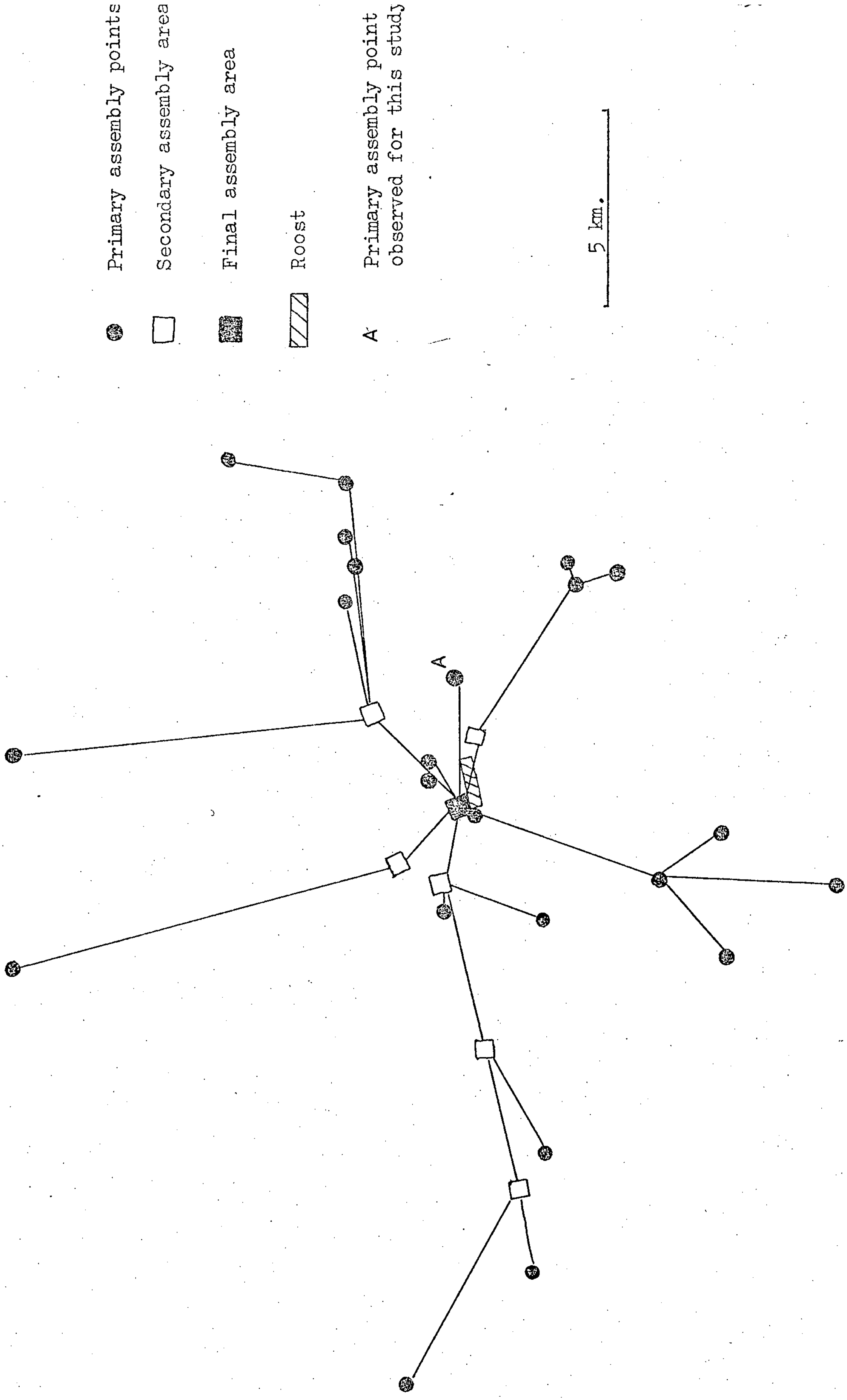


Figure 5. The position of primary, secondary and final assembly areas showing the flight lines of rooks and jackdaws to the roost.

were made on seventeen occasions and the arrival of the roosting population at the final assembly on nine occasions. Thirty-three observations of roost entry were made and twenty-five observations of the morning departure of birds from the roost. All measurements of light intensity (±1 ft-c.) were made with an Evans photo-electric light meter directed towards the zenith.

The thirty birds usually congregating at the primary assembly point (A - Figure 5) tended to move as a group. Where there were more birds, as occurred at primary assembly points, birds usually left in small parties, one after the other.

So as to calculate the time at which fifty per cent of the birds had arrived at the final assembly, sequential ground level photographs were taken of the flock on the field, these being paralleled by recordings of light intensity. The final assembly field was slightly below the observer's position and photographs could be taken at an angle sufficient to allow accurate measurements of flock area. The oblique-view negative was rectified by focusing the image through a photographic enlarger on to a map of the area which was tilted until the boundaries of the final assembly area (on the negative) coincided with the same points on the map. This image was then printed and by using a planimeter the area of the flock was measured. From the rectified prints of the flocks it appeared that the density of birds in the final assembly changed little as the birds maintained approximately the same distances between each other regardless of numbers. Thus, the area of the flock was a measure of the numbers of birds in it.

In the laboratory, the final area of the flock was measured from the last photograph and the photograph showing fifty per cent of the final flock area was identified, it being possible to determine when the photograph was taken and also to associate with light intensity. Some birds assembled in the trees surrounding the final assembly area. However, the birds in the first two or three incoming flocks would divide themselves between the trees and the ground assembly (in a ratio of roughly 1:10). The subsequent much larger number of incoming flocks would settle only on the ground. The entire roosting population would be present at the final assembly area, the vast majority on the ground, thus the birds assembling in the trees had a small effect on the time fifty per cent of the population had arrived.

Observations on the morning departure of the birds from the roost were more subjective, as not all the birds leaving the roost could be counted. Counts of birds leaving a clearly visible segment of the roost were by means of a standardised sampling method whereby, each morning, starting with the sighting of the first birds seen to leave, a continuous record of bird numbers, light intensity and time of day was taken. For periods of five minutes I counted the birds seen leaving the roost and at the end of each count I immediately took readings of light intensity and time. Since meter and watch were hung at eye level the taking of the readings did not interfere with the almost continuous counting. Any variations in the total count of the sample segment of the roost were probably due to variations in the use of the roost by the birds. As the total roost population was not known I have assumed that the birds in the part of the wood under observation behaved in the same fashion as all the birds in the roost. Thus I was able, retrospectively, to determine the time of day, the light intensity at that time and the number of birds still occupying the segment of the roost that I watched.

Results.

At the same time (in terms of GMT) each day the light intensity may vary considerably for two reasons - the effect of (a) weather and (b) the gradually changing season. For the latter reason the times and changing light intensities were related to civil twilight at the roost (from Brown's Nautical Almanac 1970, 1971).

A regression line of light intensity on departure time from the primary assembly point was fitted to the data (Figure 6, line A). The slope of the line is significantly greater than zero at the 0.01 per cent level ($F = 179.8$) indicating a relationship between light intensity and the time the birds left this primary assembly point for the final assembly. Most of the variance in departure time is explained by light intensity ($r^2 = 0.909$). Likewise the time of arrival of fifty per cent of birds at the final assembly was related to light intensity (Figure 6, line B) ($F = 13.0$, $p = 0.005$), but the variance in arrival time explained by the light intensity is less than that in the preceding analysis ($r^2 = 0.660$). This suggests that variables other than light intensity may be influencing the time of arrival or that errors in dealing with the larger flock-size at the final assembly are greater. However, the slopes for departure time from the primary assembly, and arrival time at the final assembly, against light intensity were not significantly different from each other.

The implication from these two analyses is that birds will depart from the feeding area and fifty per cent of the total population will arrive earlier at lower light intensities and later at higher light intensities. The mean time of departure from the primary assembly point was 25.9 minutes before civil twilight and arrival of fifty per cent of all the birds at the final assembly was 16.4 minutes before civil twilight.

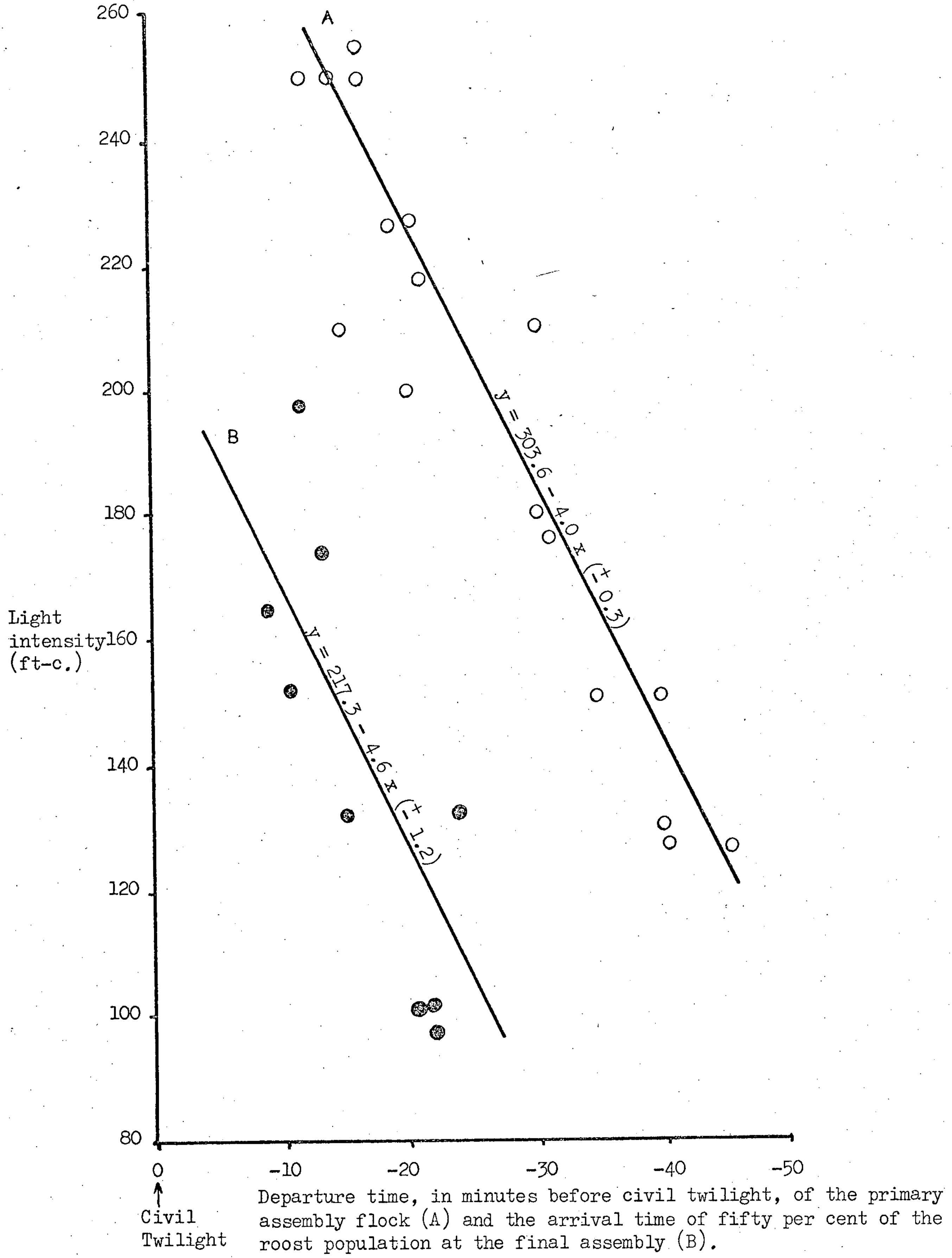
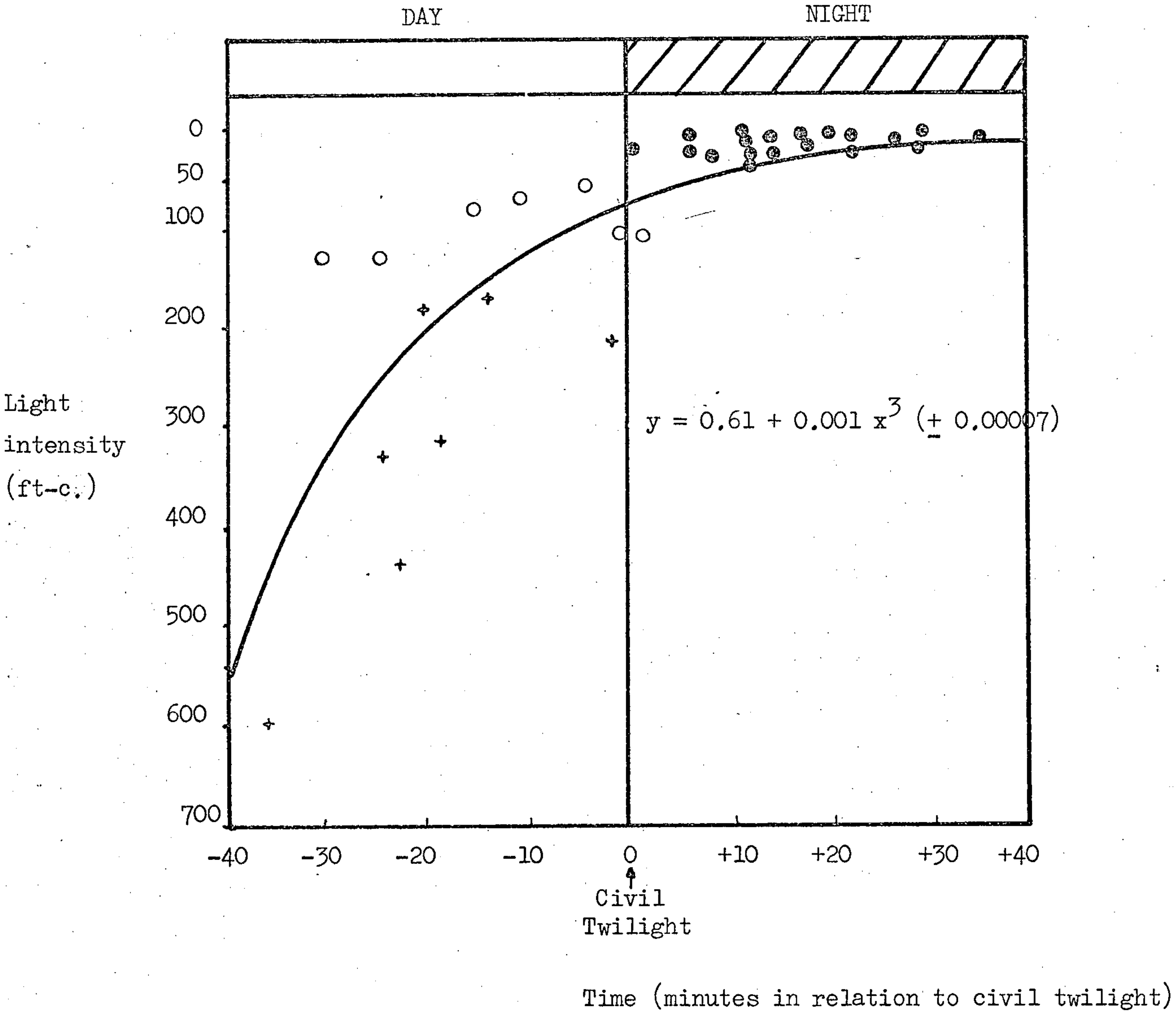


Figure 6. Relation between light intensity and time before civil twilight when a rook and jackdaw flock (A) left a primary assembly point; and (B) when fifty per cent of the roosting population had arrived at the final assembly area.



KEY:
+ Arrival of first flock at final assembly
○ Final assembly complete
● Entry into roost of first birds

Figure 7: The chronological sequence of events, when rooks and jackdaws go to roost, related to the time of day (± minutes before civil twilight) and light intensity.

NOTE: For the purposes of calculating the regression equation the x-axis was labelled from 80 (≡ -40) to 0 (≡ +40). This is because a computer cannot handle an axis that proceeds from zero in a positive and a negative direction. Since Civil twilight is the base line of observation of time, Figures 7 and 8 have therefore been redrawn as shown.

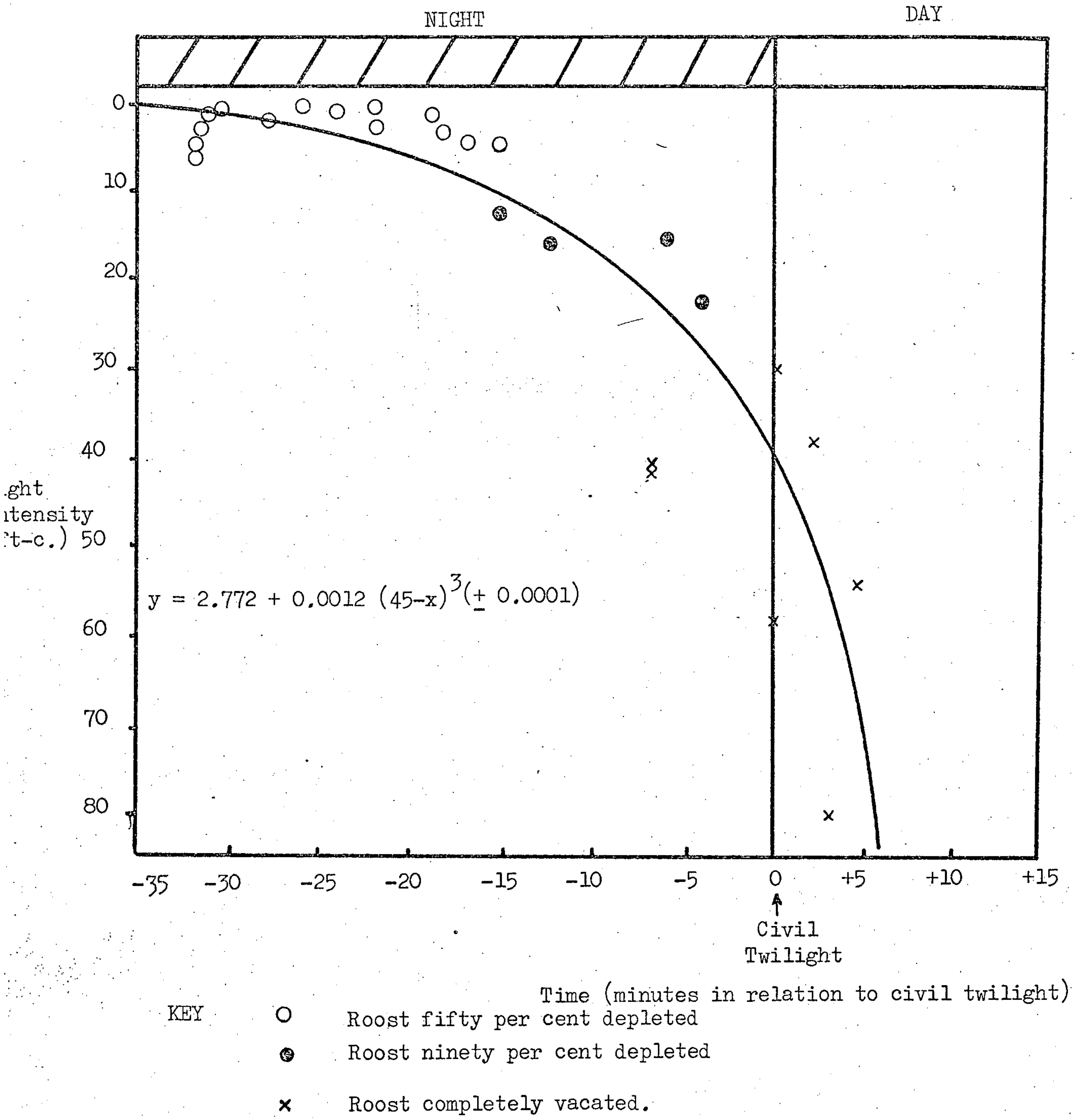


Figure 8. The chronological sequence of events when rooks and jackdaws depart from a roost, related to the time of day (± minutes before civil twilight) and light intensity.

NOTE: For the purposes of calculating the regression equation the x-axis was labelled from 50 (≡ -35) to 0 (≡ +15), see note in Figure 7 for explanation.

The mean light intensities were 198.5 ft-c. and 142.2 ft-c. respectively.

For each phase of the roost entry a regression analysis (Figure 7) of light intensity on time in relation to civil twilight showed that a significant relationship exists ($F = 213.7$, $p < 0.0001$) as also exists for morning departure (Figure 8) ($F = 95.7$, $p < 0.0001$). The variance in the time of each phase of roost entry explained by light intensity (r^2) is 0.829, whereas in morning departures light intensity explains 0.799 of the variance. The mean time of going to roost was about 4 minutes before civil twilight and the mean time of departure in the morning was about 15 minutes before civil twilight.

Discussion.

Departure time from one primary assembly point is determined by light intensity in relation to the time of day. The fact that the regression lines of the primary assembly departure time, and the final assembly arrival time, against light intensity are parallel (i.e. the slopes are not significantly different) suggests that the birds fly directly to the final assembly without being affected by other factors. Conversely, although the relationship between bird departure, and bird arrival, and light intensity are similar (i.e. the relationship can be expressed by almost the same equation), the fit of the arrival time regression line is not as good as that for the departure time. The resultant lower value for the variance explained by light intensity in the arrival time at the final assembly may indicate that other factors do influence the rhythm of roosting. The birds at the primary assembly point, which was studied, used no secondary assembly areas. Consequently the relationship between light intensity and departure time from a primary assembly point further from the roost might be different from that observed.

Some birds at primary assemblies more distant from the roost than the one studied, would arrive later at the roost if they left at the same time as those nearer. Adverse wind might affect the rate of progress of birds coming from some directions and as it has been suggested that rooks navigate to the roost by sight (Coombs 1961) the difficulties associated with the rapid onset of darkness, or low visibility, while still flying to the roost would also be avoided by earlier departure. In fact rooks do seem to vacate peripheral areas of the roost catchment area earlier than birds nearer the roost (Philipson 1933). All observations of completed final assemblies occurred on or before civil twilight. However some primary assembly points are up to five times further from the roost than the one studied (which departed on average 25.9 minutes before civil twilight). If we allow five minutes for the birds from the primary assembly (A, Figure 5) to get to the roost, then birds five times further away would need at least 25 minutes; if we assume they do not stop at secondary assembly areas and that birds left all primary assembly points at the same time then those five times further away would only just get to the roost before civil twilight. If the wind was against them, or some other adverse condition was present, they would arrive after civil twilight which I have never observed.

Variation in light intensity throughout the day might cause aberrant responses by the birds if the element of time was absent from the assembly behaviour. Very low light intensities in the middle of the day do not cause the birds to fly towards the roost, although the same low light levels later in the afternoon seem to stimulate the birds to move from a primary assembly point. (Moreover departure time and arrival time are earlier at lower light intensities and later at higher light intensities).

Thus birds frequenting a particular rookery feeding area must 'know' when to leave in order to arrive at the secondary assembly area before the other birds have left. It is suggested that either rooks and jackdaws must be able to integrate distance with time (measured by light intensity) or that birds belonging to particular feeding area are conditioned by experience to react to a particular light level. The birds using more distant feeding areas cease feeding before those in areas nearer the roost, but continue to feed en route at secondary assembly areas which differ slightly in location from day to day.

There is a big difference between the light intensities encompassing the phases of roost entry (0-600 ft-c.) and those of roost departure in the morning (0-80 ft-c.). The difference between morning and evening behaviour may result from a distinct function, other than simply flying to the roost, involved in the evening assembly sequence which is absent in the morning departure. However, the more prolonged evening assembly sequence may be due to the more serious effect of rapidly deteriorating weather conditions on evening flights than on morning flights, which can more easily be delayed.

CHAPTER 3

The social organisation of birds and the weather in the roost

Introduction

The events leading up to roost entry are orderly and there is no reason to suppose that entry into the roost and the disposition of the roosting birds is not done systematically.

This Chapter describes the horizontal and vertical distribution of roosting birds, and also the effect of weather upon their distribution.

I define the terms used thus:

'Weather' is used as the collective noun for all the night-to-night changes, or combinations, of windspeed, temperature, wind direction, cloud cover and rainfall duration.

'Climate' is used as the collective noun to describe the characteristics of a region (e.g. Southeast Scotland) or place (e.g. at the top or bottom of a tree, or in a wood) in terms of windspeed, temperature, wind direction cloud cover and rainfall duration.

The questions posed in this investigation were:

1) Is one part of the roost wood, or part of a roost tree, generally warmer (i.e. higher temperature or less windy) than another?
2) Do the birds congregate more in one part of the roost wood, or part of a roost tree, than another?
3) Does there appear to be a relationship between the changes in distribution of birds and changes in the weather in the roost?

Method

Experimental design

To study the horizontal distribution of the birds within the roost I selected four deciduous trees in the small wood (Figure 9) for reasons of (a) practicality, (b) the finite length of the cables to the weather sensors and (c) because, in contrast to the large wood, the small wood, being clearer of undergrowth, was more suitable for unobstructed observation of the lower crown. Moreover it was easy to see the birds in the particular deciduous trees chosen and there was no evidence to show that the birds preferred these trees to any other deciduous trees (see later); coniferous trees were not usually chosen for roosting. Additionally there happened to be a track down the centre of the small wood on which a tower was built and along which the four trees were visible.

These trees were labelled 1 to 4 where 1 was nearest the west end of the wood and 4 at the east end of the wood. S.G.B. Ltd. kindly loaned a 20 m. high scaffold free of charge which I erected in the eastern half of the wood, so that I could clearly see (with 7 x 50 binoculars) the four trees representing the roost wood. The four trees were deciduous and of the same height and size. On each of the deciduous trees (1, 2, 3, 4) I maintained a temperature and wind sensor 1 metre below the top of the tree and half way between the periphery of the crown and the trunk. The sensors were positioned so that the anemometer was exposed to winds from all points of the compass and not shaded or sheltered by a branch from winds from a particular direction (see Appendix 6 for description of weather sensing system).

The temperature and the mean windspeed for the preceding hour, were recorded in each tree, and Turnhouse Meteorological Station data were

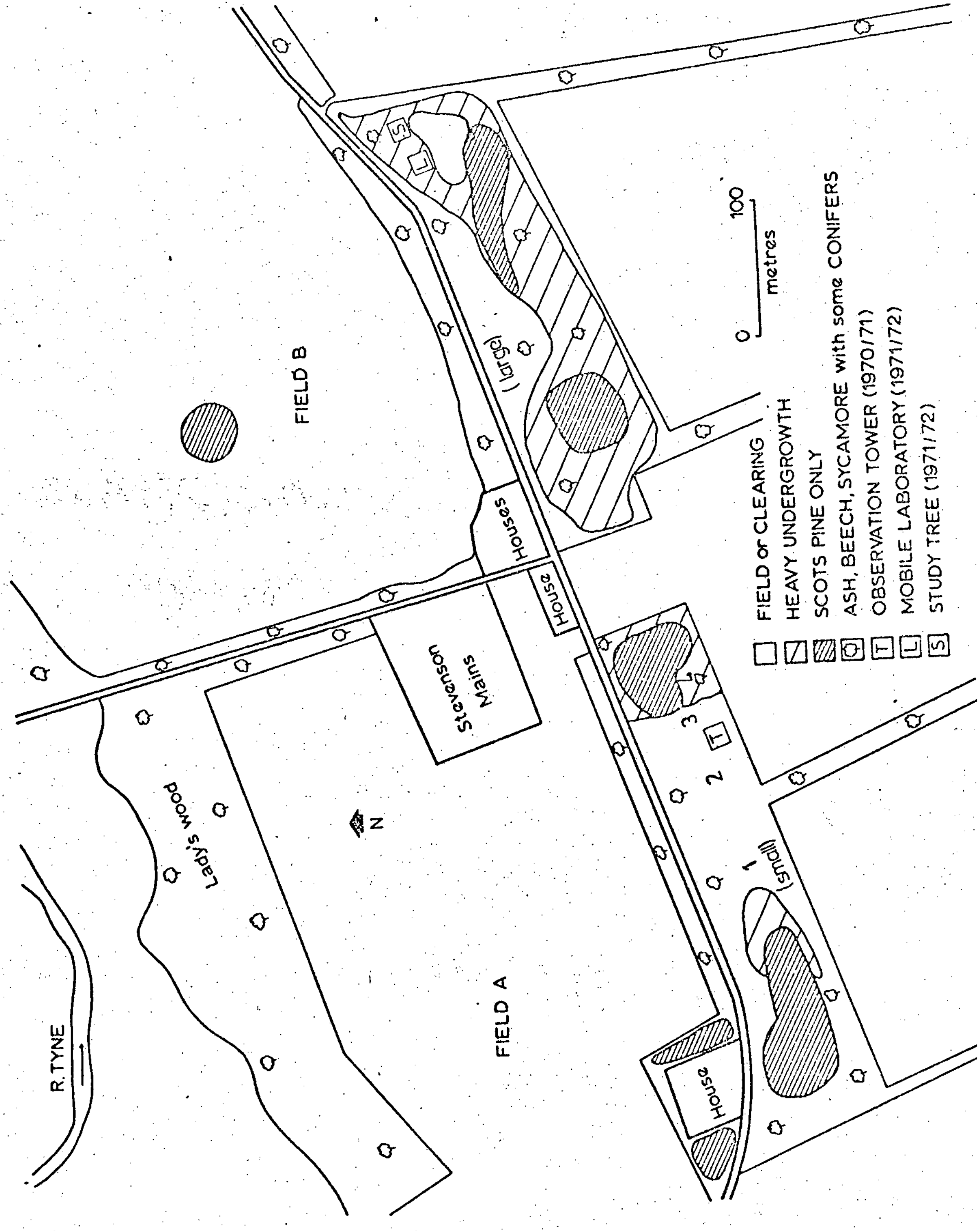


Figure 9
Plan of the roost and the surrounding area, showing position of study trees.

collected and transcribed, for each hour of the night. Turnhouse data included temperature, windspeed, cloud cover (octas), rain duration (tenths of an hour) and wind direction (degrees of compass). (The suitability of using Turnhouse data is discussed in Appendix 7).

Temperature, windspeed, rainfall amount and wind direction data were also collected from Haddington Meteorological Station but unfortunately this information was only measured at 0900 hrs. each morning.

Counts of the number of birds were made every three hours from the time the first birds alighted until the beginning of morning departure, with a period of five minutes spent viewing each tree.

The thirty-eight nights on which counts of the numbers of birds and weather measurements were made were as follows:-

1970 November	13, 22-26
1970 December	8-21, 23, 25, 26
1971 January	3-8, 19-21, 26
1971 February	15, 18, 19, 23, 25

On all nights that count were made the birds could be clearly seen. The binoculars used to observe the furthermost trees (1 and 4) had good light gathering properties and there was enough light present to discern the outline of each bird. The top of the tower was slightly below the top of the trees and so the top one-third of the deciduous trees had a background of sky which facilitated counting.

An investigation of the vertical distribution of adult rooks, young rooks and jackdaws was made on a single deciduous tree (S in Figure 9; 15 m high) in the study roost. A mobile laboratory (L on Figure 9) was set up near to the deciduous study tree. Counts of the numbers of birds were taken through a laboratory window which was marked with a grid delineating the tree crown into four positions (see Figure 10). Position A included the crown top; Position B, the eastern portion of the tree crown from the bottom of position A down 2 m., and from the trunk to the crown's eastern periphery; Position C, the same as position B but the western portion; Position D, from the bottom of positions B and C down.

Figure 10.

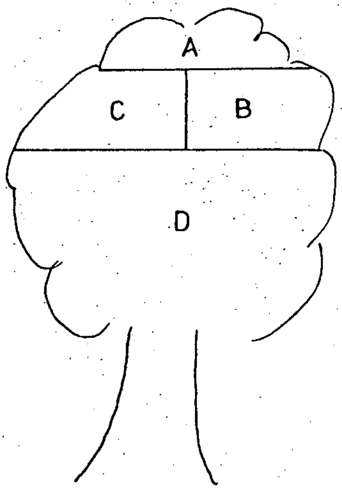


Diagram of deciduous study tree showing the four tree positions.

A small wood clearing (area 400 m.) stretched approximately south from the main study tree and mobile laboratory. The clearing was enclosed on all sides by dense tree growth.

The following counts were made from the time the first birds alighted in the tree until the beginning of morning departure: the number of adult rooks, the number of young rooks and the number of jackdaws. Counts were made over a five minute period (devoted to each tree position) every third hour of numbers of birds found in the differing tree positions.

Weather measurements on mean hourly windspeeds and hourly temperatures were recorded at each position, and data regarding hourly rainfall duration, hourly cloud cover and hourly wind direction were gathered from Turnhouse. (The suitability of using Turnhouse data is discussed in Appendix 7.)

The anemometers and temperature sensors (description Appendix 6) were positioned as follows:

Position A. 0.5 m. from the top of the deciduous tree immediately above the centre of the tree i.e. exposed to winds from all directions.

Position B. 2.5 m. from the top of the deciduous tree, half way between the periphery of the crown and the trunk. These sensors were facing east i.e. exposed to wind from 0° to 180° approximately.

Position C. The same as (B) but the aspect was facing west i.e. exposed to winds from 180° to 360° approximately.

Position D. 4 m. from the top of the deciduous tree, half way between the periphery of the crown and the trunk. The aspect of this sensor was facing south i.e. exposed to winds from 40° to 310°.

A passive light intensifier telescope was used in order to obtain detailed information of the behaviour of birds in the roost. It intensified light 40,000 times and magnified optically by 2. By permanently positioning it on a stand, a clear 'picture' of birds and the study tree could be obtained. Superimposed over this 'picture' was the grid (already mentioned) which was painted with phosphorescent paint (diluted) so that a rather blurred but useful image appeared on the intensifier.

Although the view of the deciduous tree was oblique rather than horizontal, the 'picture' was constant each night and any inaccuracy in counts would have been systematic. I found no means of overcoming this problem.

The criteria used in distinguishing adult rooks from young rooks and from jackdaws were (a) rooks were distinguished from jackdaws by the greater body size of rooks and (b) young rooks from adult rooks by the lack of, or partial lack of, facial feathers. Using the light intensifier, body size was easily distinguished, but facial feathering was more difficult as it was only when the feathering was less than $\frac{1}{2}$ (see Dunnet _et_ _al_. 1969) did the bare-facedness show up in the viewer. Thus the criterion for calling a rook young or adult was decided on whether the face showed some white bareness or not. Some birds put their bills under the shoulder feathers obscuring their faces, nevertheless by making some small noise (e.g. flicking the window) most birds would become alert and show their faces.

The twenty-one nights on which counts of the numbers of birds and weather measurements were made were as follows:-

1971	September	25-28
1971	October	20-23
1971	November	16-19
1971	December	18-20
1972	January	29-31
1972	February	1-3

Mode of analysis of the relationship between the weather and the distribution of the birds.

In order to analyse any relationship between the weather and the distribution of birds stepwise multiple regression was used (for explanation of technique see Appendix 5).

The dependent variable used in the analyses was the number of birds in each tree (or tree position) expressed as a percentage of the sum of the birds in all four trees (or the four-tree positions).

The independent variables were as follows:-

(1) the rain duration for the preceding hour measured at Turnhouse Meteorological Station (in tenths of an hour).

(2) the cloud cover measured at Turnhouse Meteorological Station (in octas) each hour.

(3) the wind direction measured at Turnhouse Meteorological Station (in degrees of compass) each hour.

(4) the temperature measured at each tree (or tree position) each hour.

(5) the mean windspeed for the preceding hour measured at each tree (or tree position) each hour.

Linear, cubic, quadratic, logarithmic and exponential transformations of the dependent variable were tried. The logarithmic transformation gave the 'best fit'.

Henceforth the dependent variable was the logarithmic transformation of the percentage number of birds.

It could be argued that simply to chose a transformation because it fits the data best (i.e. the highest r^2 value; r^2 is the variance explained in the dependent variable by the independent variable), but which has no biological justification, is meaningless. However I disagree, because in this instance we are interested in producing a model approximating to the actual relationship between weather and bird behaviour. The transformation enabled a more sensitive comparative analysis to be done from month to month.

Moreover I used the simplest transformation which was capable of being used in any future analyses. I have adopted this procedure in the way of Pearce (1965), who stated that no transformation is perfect but is used because it is better than no transformation at all.

Nevertheless, the fact that a logarithmic transformation of the percentage number of birds was found to be appropriate may not be chance, particularly as the relationship between temperature and heat loss (even when it rained or there was a wind) was also logarithmic (see Chapter 5). The inference is that, as weather conditions became more severe in a particular tree, the numbers of birds leaving increased logarithmically.

In the regression analyses concerning the vertical distribution, the numbers of adult or young rooks or jackdaws occurring in the different sections of the tree were expressed as percentages of the total number of adult or young rooks or jackdaws occurring throughout the tree. The same transformation (i.e. logarithm) is used in these analyses.

The weather measurements were made hourly while the counts were made every three hours. However when analysis of the relationship between weather and numbers of birds were made only weather measurements made at the same time as the counts (i.e. every three hours) were used.

The technique of stepwise multiple regression is a controversial analytical tool. The approach must be used very cautiously for a number of reasons (Simon 1954; Brownlee 1960; Chisholm and Muller 1966; Mead 1971) in addition to those that will be mentioned in Appendix 5.

(1) The necessary assumptions of linear relationships and normal distributions of errors are questionable. Theoretically however, these difficulties may be overcome by appropriate higher order terms and transformations of the data.

(2) Multiple regression procedures are appropriate only in those situations in which each of a series of variables is believed to affect the dependent variable in an additive manner. This is considered true in these analyses.

(3) Weather parameters are highly interdependent. In such circumstances most possible combinations of values of independent variables may never occur in the raw data. In this investigation a very large number of observations were collected with widely varying and extreme conditions, and this I consider to constitute a valid sample (see Mead 1971).

In each analysis the data are divided according to the wind direction. The wind direction sectors chosen are (a) 50°-120° (i.e. blowing from east end of the wood); (b) 130°-310° (i.e. blowing from the west end of the wood); and (c) 320°-40° (i.e. blowing from the north side of the wood). This is done in order to simplify discussion of the results.

Results

The distribution of birds in the roost

The mean number of birds roosting in each of the four trees for the winter 1970/71 is shown in Table 1.

Although there were significantly more birds at trees 3 and 4 (leeward) than at tree1(windward) ($t = 5.1$ and 4.2 respectively, $P < 0.001$), there was no significant difference between the mean numbers of birds at trees 1 and 2 ($t = 1.2$, $P > 0.20$) or 3 and 4 ($t = 1.2$, $P > 0.20$).

If we turn to the vertical distribution in the roost; the mean numbers of adult rooks, young rooks and jackdaws observed are shown in Table 2.

TABLE 1

The horizontal distribution of birds between the four trees from November to February 1970/71.

	Tree 1	 2	 3	 4
Mean number of birds	22.1 ± 0.2	21.5 ± 0.1	24.2 ± 0.1	25.1 ± 0.2

Figures are mean ± standard errors of mean . Each figure is based on 208 separate counts.

/

TABLE 2

The vertical distribution of adult rooks, young rooks and jackdaws between the four tree positions. (1971/72)

Tree Position (See Figure 10)

	A	B	C	D
Mean number of adult rooks	18.1 ± 1.2	6.0 ± 0.8	5.3 ± 0.5	1.4 ± 0.5
Mean number of young rooks	0.3 ± 0.1	7.9 ± 0.5	6.7 ± 0.5	3.8 ± 0.4
Mean number of jackdaws	0.1 ± 0.1	4.3 ± 0.3	5.6 ± 0.4	3.0 ± 0.4

Figures are mean ± standard error of mean.
See App. 4, Table 5.

There was a significant difference between the mean number of adult rooks at position A and position B ($t = 78$, $P < 0.001$) i.e. there were generally more adult rooks at the top of the deciduous trees than in any other position. The difference between the numbers of adult rooks at position B and C was not significant ($t = 0.8$, $P > 0.20$).

There were significantly more young rooks roosting in position B than position A ($t = 2.6$, $P < 0.01$) and significantly fewer at position D than position C ($t = 4.0$, $P < 0.01$) although there was no significant difference in the mean number of young at positions B and C.

The distribution of jackdaws was more even than that of the young rooks, although there were significantly fewer at position A than position B ($t = 2.4$, $0.02 > P > 0.01$); not significantly more at position C than position D ($t = 1.3$, $0.20 > P > 0.10$) and no significant difference between positions B and C.

In summary, there were more birds to the east end of the wood (leeward) than to the more westerly end (windward). There were more adult rooks at the top of the deciduous tree than at any other part of the tree, while the young rooks and jackdaws were mainly gathered just below the tree top below the adults. The bottom half of the deciduous tree crown was normally vacant.

The weather and climate in the roost.

The mean temperature and the mean windspeed for the winter 1970/71 in each tree is displayed in Table 3. Tree 1 (windward) was significantly colder than tree 4 ($t = 12.9$, $P < 0.001$) which was to leeward. Tree 1 was also significantly colder than tree 2 ($t = 3.1$, $0.01 > P > 0.001$),

TABLE 3

The mean windspeed and mean temperature in each tree from November to February (1970/71).

	Tree			
	1	2	3	4
Mean windspeed (m/sec)	3.2 ± 0.1 (268)	3.2 ± 0.04 (772)	3.1 ± 0.1 (539)	2.6 ± 0.1 (278)
Mean temperature (°C)	2.3 ± 0.3 (93)	3.2 ± 0.1 (932)	3.6 ± 0.1 (925)	3.4 ± 0.1 (722)

Figures are mean ± standard error of mean (with the number of measurements each figure is based on).

and tree 3 was not significantly different in temperature from tree 4 ($t = 1.2$, $P > 0.20$).

There was a significant difference between the mean windspeed at tree 1 (windward) and tree 4 (leeward) ($t = 7.5$, $P < 0.001$), tree 1 being in a windier position than tree 4. However there was no significant difference between the mean windspeed at one tree and the next ($t = 1.4 - 1.6$, $0.20 > P > 0.10$).

Thus the end of the wood represented by tree 4 was warmer and less windy than the part represented by tree 1.

The mean temperature and mean windspeed in each tree position (vertical distribution) during the winter 1971/72 is shown in Table 4.

The mean temperature at tree position A was significantly higher than that at position B ($t = 5.3$, $P < 0.001$); the mean temperature at position B was not significantly different from that at position C. Position D was significantly colder than position C.

Thus it was colder from the top of the deciduous tree down.

The mean windspeed at the top of the deciduous tree was significantly different from that in position B ($t = 2.1$, $P < 0.05$) and position B was significantly less windy than position C (Position B is to leeward of the more frequent westerly winds). Nevertheless position D was significantly less windy than position C ($t = 2.3$, $P<0.05$).

Thus apart from getting warmer as one descended the crown of the deciduous tree it also became less windy.

The effect of changes in weather on the changes in the distribution of birds in the roost.

The numbers of birds roosting in the study trees varied and seemed to follow a trend (see Table 5) which was broadly similar in both periods

TABLE 4

The mean temperature and mean windspeed in each tree position from September to February (1971/72)

Tree Position (See Figure 10)

	A	B	C	D
Mean temperature (^{o}C)	5.5 ± 0.3	4.7 ± 0.3	4.8 ± 0.4	3.9 ± 0.3
Mean windspeed (m/sec)	5.0 ± 0.2	4.1 ± 0.2	4.3 ± 0.2	3.2 ± 0.2

Figures are mean ± standard error of mean.

The number of measurements each figure is based on is 378.

TABLE 5

The trend in the mean numbers of birds in all four trees (1970/71) or four tree positions (1971/72).

Month	Mean numbers of all birds 1970/71	1971/72
September	-	49.5 ± 3.2
October	-	88.5 ± 5.9
November	67 ± 10.1	76.9 ± 5.1
December	144 ± 23.2	73.0 ± 5.6
January	100 ± 12.1	56.5 ± 4.5
February	90 ± 7.2	31.2 ± 2.5

Figures are mean ± standard deviation

of the field study.

Because interest was centred on weather changes and the distribution of birds within the trees, or tree positions, I have presented the analyses in the form of a change in the percentage of the total number of birds in the four trees, or tree positions, moving to (+) or away from (-) each tree, or tree position, and the extent to which this is explained by weather (expressed as the variance explained).

The influence of weather changes when the wind is from 130°-310° on distribution of birds in trees 1 and tree 4 is shown in Table 5. This is the first of the stepwise multiple regression analyses referred to earlier in this Chapter and explained fully in Appendix 5. However in order to interpret the following Tables a short explanation is required. As a result of the significant correlation between many of the weather variables the order in which the variables were inserted into the regression analysis was influenced by their dependence upon variables already in the regression equation. The stage at which they were inserted was not related to their value as a predictor. Although this does not invalidate the approach, discussion of the influence of individual variables is made difficult. In order to simplify this problem the five weather variables measured were considered as a group, and the contribution of this group (called 'weather') towards explaining the variance in the dependent variable (the percentage numbers of birds) was studied.

In some instances a weather variable was not included in the final regression analysis because it did not contribute significantly to an increase in the variance explained in the dependent variable. However some equations may only contain, for instance, two weather variables, and yet this group of independent variables I still called 'weather'. To justify the use of this overall label ('weather') to describe a group of any or all of the weather variables measured, it is worth considering the effect of the deliberate removal of a variable already included in the analysis. In this event a reorganisation of the variables in the regression equation would generally occur with another variable or variables, being brought into the analysis sustaining the former r^2 value for the final equation.

Table 6 then means the following:- In November 5.9 per cent of birds in the four study trees left tree 1 and 10 per cent moved into tree 4. In both instances, weather was very strongly correlated with this movement. It is of course impossible to say that birds moved from tree 1 to tree 4 but this is inferred a) because the - and + values agree fairly well and b) because direct observation in the roost showed that this is what was happening. The general movement in the trees was from tree 1 to tree 4 in December, January and February.

When the wind blew from the other direction, namely 50°-120° (i.e. from tree 4 to tree 1), the general movement in the trees was from tree 4 to tree 1 (Table 7). Once again the values of the mean change in the proportions in both trees were in fair agreement and direct observation confirmed that this movement took place.

The changes in the vertical distribution of adult rooks induced by changes in weather when the wind is from 130°-310° is shown in Table 8. The principal movement of adult birds was from position B (and C) to the top of the tree (position A), except in October and December when the net movement, smaller than in the other months, was from the top of

TABLE 6

The mean change in the proportion of birds which left (-) or arrived (+) at tree 1 and tree 4 and the r^2 value for the influence of weather on these movements in the roost (wind direction 130°-310°)

1970-71	Change in the percentage of birds and (Variance explained)			
	Tree			
	1 (Windward)		4 (Leeward)	
	i	ii	i	ii
November	-5.9	0.775	+10.0	0.911
December	-4.4	0.247	+10.1	0.106
January	-6.9	0.048	+8.1	0.038
February	-6.8	0.074	+8.0	0.034

Notes:
(a) each pair of figures is (i) the mean change in the proportion of birds arriving (+) or leaving (-) the tree and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of birds at that tree.

(b) trees 2 and 3 are omitted for reasons of clarity. The data concerning these trees are presented in Appendix 4; these data have values intermediate between trees 1 and 4. (Appendix 4 Table 1)

(c) wind direction was from 130°-310°C (i.e. approximately from 1 to 4).

(d) the average number of birds in all trees (1, 2, 3, 4) was November 67, December 144, January 100 and February 90.

(e) the number of counts in each tree was November 25, December 119, January 40 and February 30.

(f) the mean numbers of birds in each tree is presented in Appendix 4 Table 3.

TABLE 7

The mean change in the proportion of birds which left (-) or arrived (+) at tree 1 and tree 4 and the r^2 value for the influence of weather on the movements in the roost (wind direction 50°-120°)

1970-71	Change in the percentage of birds and (Variance explained)			
	Tree			
	1 (leeward)		4 (windward)	
	i	ii	i	ii
November	+8.5	0.305	-6.7	0.118
January	+10.1	0.297	-8.8	0.211
February	+6.9	0.222	-2.1	0.027

Note: (a) each pair of figures is (i) the mean change in the proportion of birds arriving (+) or leaving (-) the tree and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of birds at that tree.

(b) December is omitted as there were no records for that month. Trees 2 and 3 are omitted for reasons of clarity. The data concerning these trees are presented in Appendix 4; these data have values intermediate between trees 1 and 4. (Appendix 4 Table 2).

(c) wind direction was 50°-120° Ii.e. approximately from 4 to 1.

(d) the average number of birds in all trees (1, 2, 3, 4) was November 67, December 144, January 100 and February 90.

(e) the number of counts in each tree was November 11, January 20 and February 9.

(f) the mean numbers of birds in each tree is presented in Appendix 4 Table 4.

TABLE 8

The mean change in the proportion of adult rooks which left (-) or arrived (+) at the four tree positions and the r^2 value for the influence of weather on the movements of adult rooks in the tree.

1971-72	Mean number of adult rooks in all positions	Change in the percentage of adult rooks & variance explain							
		Tree position (See Figure 10)							
		A		B		C		D	
		i	ii	i	ii	i	ii	i	ii
September	18.5 ± 3.6	+8.1	0.183	-3.9	0.287	-8.0	0.263	-0.1	0.059
October	43.5 ± 8.7	-0.8	0.313	-0.5	0.216	+3.2	0.216	+0.1	0.068
November	45.7 ± 9.1	+7.7	0.059	-6.5	0.134	-2.7	0.077	0.0	0.035
December	41.0 ± 10.0	-3.7	0.249	+2.8	0.191	+2.8	0.191	0.0	0.065
January	22.6 ± 5.6	+19.1	0.541	-11.1	0.561	-11.1	0.561	0.0	0.009
February	13.3 ± 3.3	+5.7	0.288	-5.7	0.625	-10.4	0.319	0.0	0.003

Notes: (a) each pair of figures (i) is the mean change in the proportion of birds arriving (+) or leaving (-) the tree position and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of adult rooks in the tree position.

(b) the mean number of adult rooks is ± the standard deviation.

(c) wind direction was from 130°-310°.

(d) the number of counts at each tree position was September 23, October 68, November 63, December 54, January 8 and February 16.

(e) The mean numbers of adult rooks in each tree position is presented in Appendix 4 Table 5.

the tree to position C. This reversal in the movement of adult rooks in these two months may be due to a marginally higher wind velocity at night than in the other months (Table 11) which would influence birds at the top of the tree more than those lower down. Nevertheless what is of more interest is the similiarity in the movement between adult and young rooks and jackdaws. The general monthly trend in the movement of young rooks (Table 9) is the same as that of the adult rooks i.e. when adults move down the tree so did the young rooks or vice versa. In January, however, young rooks moved from the top of the tree to position B (and from positions C and D to position B) when adult rooks principally moved to the top (cf. Table 8). The principal movement of jackdaws (Table 10) each month is very similar to that of young rooks each month. This behaviour of the birds is discussed more fully at the end of this Chapter.

All the movements of adult rooks, young rooks and jackdaws within the study tree have been directly observed; moreover the values of the mean change in proportions in each tree position do equate or balance fairly well.

No winds were recorded from 50^0-120^0 or from 320^0-40^0.

To summarise; the movement of birds within the roost wood were strongly influenced by the wind direction and the weather in general. The principal movement of adult rooks was generally between the top of the tree and the positions (B and C) slightly below the top; the young rooks and jackdaws generally moved between positions B, C and D. The influence of the weather on changes in the distribution of young and adult rooks and jackdaw was strong.

The actual numbers of birds in the four trees, and the four tree positions, showed a trend of increasing and then decreasing numbers of

TABLE 9

The mean change in the proportion of young rooks which left (-) or arrived (+) at the four tree positions and the r^2 value for the influence of weather on the movements of young rooks in the tree.

1971-72	Mean number of young rooks in all positions	Change in the percentage of young rooks and variance explained							
		Tree position							
		A		B		C		D	
		i	ii	i	ii	i	ii	i	ii
September	17.5 ± 3.5	0.0	0.025	+4.2	0.250	0.0	0.253	-3.8	0.30
October	29.0 ± 5.8	0.0	0.013	-3.1	0.297	+5.5	0.208	-5.5	0.25
November	16.2 ± 3.2	0.0	0.013	+2.0	0.129	+0.1	0.091	-8.6	0.15
December	19.0 ± 4.7	0.0	0.075	-5.3	0.274	+0.4	0.158	-2.8	0.25
January	19.6 ± 4.9	-0.6	0.602	+13.7	0.543	-13.1	0.561	-13.1	0.51
February	11.3 ± 2.8	0.0	0.043	+7.0	0.563	-1.6	0.574	-5.0	0.31

Notes: (a) each pair of figures (i) is the mean change in the proportion of birds arriving (+) or leaving (-) the tree position and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of young rooks in the tree position.

(b) the mean number of young rooks is ± the standard deviation.

(c) wind direction was from 130°-310°.

(d) the number of counts at each tree position was September 23, October 68, November 63, December 54, January 8 and February 16.

(e) the mean numbers of young rooks in each tree position is presented in Appendix 4 Table 6.

TABLE 10

The mean change in the proportion of jackdaws which left (-) or arrived (+) at the four tree positions and the r^2 value for the influence of weather on the movements of jackdaws in the tree

1971-72	Mean number of jackdaws in all positions	Change in the percentage of jackdaws and variance explained Tree positions A		B		C		D	
		i	ii	i	ii	i	ii	i	ii
September	13.5 ± 2.7	0.0	0.025	+2.0	0.291	-1.4	0.287	-4.7	0.329
October	16.0 ± 3.2	0.0	0.013	-1.6	0.324	+7.1	0.052	-6.8	0.194
November	15.0 ± 3.0	0.0	0.035	+1.5	0.021	+2.4	0.085	-5.8	0.085
December	13.0 ± 2.2	0.0	0.075	-9.7	0.177	-1.5	0.216	+6.3	0.11
January	14.3 ± 3.0	-1.1	0.541	+19.1	0.561	-11.0	0.561	-11.0	0.509
February	6.6 ± 1.4	0.0	0.043	+0.5	0.338	8.3	0.388	-6.9	0.488

Notes: (a) each pair of figures (i) is the mean change in the proportion of birds arriving (+) or leaving (-) the tree position and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of jackdaws in the tree position.

(b) the mean number of jackdaws is ± the standard deviation.

(c) wind direction was from 130°-310°.

(d) the number of counts at each tree position was September 23, October 68, November 63, December 54, January 8 and February 16.

(e) the mean numbers of jackdaws in each tree position is presented in Appendix 4 Table 7.

TABLE 11

General weather conditions for 1970/71 and 1971/72 recorded at Turnhouse Meteorological Station on those nights that bird distribution was studied in the roost.

		SEPT	OCT	NOV	DEC	JAN	FEB
Mean Minimum Nightly Temperature (°C)	1970/71			3.2	2.1	2.2	2.7
	1971/72	8.9	7.1	3.4	5.6	2.3	1.1
Mean Nightly Wind Velocity (m/sec.)	1970/71			5.0	4.7	4.1	4.7
	1971/72	3.9	5.4	5.0	7.0	5.1	4.2
Total Nightly Rainfall Amount (mm)	1970/71			66.4	25.4	33.9	47.4
	1971/72	30.2	33.3	46.9	26.6	63.5	49.1
Snow Lying (date)	1970/71						15
	1971/72			18,19		30,31	1,2

birds through the roosting period (Table 5). By observation it seemed that the four trees, or tree positions, were not different from the rest of the roost and so this trend is presumably similar to that in the total roosting population. Nevertheless, no independent evidence of the size of the roosting population each month was available for my study roost so that the representativeness of the four trees, or tree positions, remains an assumption although I suggest a reasonable one.

The effects of weather judged by the proportion of the birds occupying different parts of a roost wood, or roost tree, were on many occasions appreciable. This relationship between weather and the distribution of birds was seemingly unaffected by the actual numbers of birds in the wood (see Table 12). The trends of actual numbers and r^2 values show no similarity.

Aggressive encounters between birds in the roost

Aggressive encounters (defined here as any aggressive interaction between two birds on a perch, regardless of the outcome) were only observed when birds first alighted in the trees in the evening and after movements occurred in the roost. Apart from these occasions no aggressive encounters were observed at all.

On roost entry, birds alighted on the top most branches of the trees and some (mainly the young rooks and jackdaws) descended almost immediately to the lower branches; during this time aggressive encounters between birds were noticed. When a large scale movement of birds across a wood occurred, and readjustment of their spatial organisation took place, some aggressive encounters were seen. Aggressive encounters were also noticed when adult rooks descended the tree because of inclement

TABLE 12

The trend in the mean number of birds in all four trees (1970/71), or all four tree positions (1971/72), compared with the trend in the influence (r^2) of changes in weather on changes in bird distribution each month

Month	1970/71 Mean number of birds.	r^2	1971/72 Mean Number of birds	r^2
September			49	0.183
October			88	0.313
November	67	0.775	77	0.059
December	144	0.247	73	0.249
January	100	0.048	56	0.541
February	90	0.074	31	0.288

The mean number of birds in the four trees, or four tree positions, is to the nearest whole number. The r^2 values for (1970/71) are from Table 6 (tree 1) and those for 1971/72 from Table 8 (tree position A).

weather. Adult rooks interacted with young rooks and jackdaws 'pushing' the latter down the tree. Aggressive encounters caused through this behaviour most frequently happened when rain was falling; if rain persisted some birds moved from the favoured deciduous trees to the spruce trees.

Habitual roosting positions.

Whether or not individual birds roost in the same places each night is a matter for conjecture, when individual marking is impossible or inappropriate. However sequential photographs were taken, one on each night, using ultra-fast film (near infra-red) of a particular tree in the winter of 1970/71. The camera was permanently mounted and photographs were taken until a series of four or five were obtained in near-identical weather conditions. Simultaneous projection of the negatives showed that bird positions were consistent each night.

Are these the same birds each night or are the birds observed simply perching on the most suitable perches? Two birds were shot with a silenced .22 rifle while roosting in the tree. On the following three nights (of similar weather conditions) the place where the removed birds used to perch remained vacant. An attempt was made to mark one bird by fixing a tube above a known perch. The tube was tied to the hide where it was connected to a rubber bulb full of white paint. By squeezing the bulb, white paint dropped onto the perch. The marking was successful, but the weather changed and the bird was not seen the next night. A week later the bird was spotted in the same part of the tree but not the same perch.

Kalmbach (1932) and Jumber (1956) have both demonstrated that individual starlings tend to have their own perch in the roost.

Discussion

Has stratification of birds been seen in a roost before?

Separation of birds by species, sex or some other criterion has been noticed by some authors. Swinebroad (1964) described the segregation by species of nocturnal shorebirds when roosting. Brown (1946), observing a starling roost, noticed that other species of birds used the same wood but a different part for roosting. No signs of interspecific aggression was noticed. Boyd (1932) noticed song thrushes (*Turdus philomelas*) and blackbirds (*Turdus merula*) roosting on the edges of a covert where starlings habitually passed the night in the centre.

Orians (1961) and Meanley (1965) both studied red-winged blackbird (*Agelaius phoenicus*) roosts. In Orians (*loc. cit.*) study a striking feature of the social organisation during the autumn and winter was the segregation of the sexes which,though by no means complete was very pronounced. He mentioned that during the daytime, feeding flocks were wholly or largely composed of one sex. He also observed a tricoloured blackbird (*Agelaius tricolor*) roost where there was no segregation by sexes; he does not mention whether the segregation occurs in feeding flocks or not.

A more recent study of the social organisation in a mixed species roost (mainly containing red-winged blackbird) by Meanley (*loc. cit*) revealed a more complicated structure. In the mixed flocks, segments of the population were segregated in virtually all roosts. He found that birds, which fed in segregated flocks during the day, returned to the roost the same way and that flocks of birds of one species or one sex returned to their favourite sections of the roost each evening. As an example he cites a roost in a deciduous thicket where starlings roosted highest in the trees; then came grackles (*Quiscalus quiscula* and *Cassidix mexicanus*) and male red-winged blackbirds; below them were cowbirds (*Molothrus ater*) and female red-winged blackbirds; lowest were rusty blackbirds (*Euphagus carolinus*) and more female red-winged blackbirds.

Stratification occurred in the roosts. Grackles were observed roosting in the more open part of the roost while red-winged blackbirds roosted in a part of the marsh where there was a scattering of willows, or in the more shrubby or wooded part of the marsh. Around the periphery of many large roosts Meanley observed small groups of roosting birds of one species or sex e.g. female red-winged blackbirds or rusty blackbirds.

Meanley considered that dense cover was important in roost site selection for the red-winged blackbird, strong winds were inclined to disturb the birds. He noted that in deciduous thickets with extremely high bird densities, birds were of necessity forced to roost in all available spaces.

In rook and jackdaw roosts vertical stratification of rooks by age occurred. During movements in the roost during the night, adult rooks were free to position themselves without hindrance from young rooks and jackdaws; and to a lesser degree young rooks with the jackdaws. It will be seen in Chapter 4 that this behaviour is dominance-related.

What is the relationship between weather, climate in a wood and the distribution of rooks and jackdaws in roosts?

Several authors (e.g. in geese, Mathiasson, 1963) have found that only certain areas of a roost wood are regularly used by rooks and jackdaws for roosting (mentioned in Chapter 1). Conroy (1966) mentioned that rooks showed no preference for tree type, although the birds which first entered the roost chose the branches of the higher trees as perches.

A preference for particular parts of the roost was noticed in my study. The east end of the small wood appeared to be preferred. It was generally the most sheltered part. It was conceivable that birds became habituated to roosting at this end because it was to leeward. However this end also had a dense and high undergrowth which was absent in the rest of the wood. Geiger (1950) studied the climatic differences between a 65 year-old pine stand with a loosely closed, uniform crown and the same stand thickly undergrown with spruce so that there were tree tops at all levels. In the stand with thick undergrowth Geiger found that wind velocity was retarded greatly in the crown space, by comparison with the other stand. Furthermore, at night the crown space was relatively warmer in the stand undergrowth than in the other stand. He also stated that the highest temperature at night was to be found just above the crown space in the stand without undergrowth.

The majority of birds in the study roost perched in the large wood either because it was the larger wood, or because of the effect of its larger areas of undergrowth. It was windier, and warmer, going from bottom to top of the crown space in the deciduous study tree; the windward side of the tree was also windier but not significantly warmer than the leeward side.

The temperature in the crown canopy at night can vary independently of the vertical temperature in other parts of the stand. Geiger (1950) reported that on the whole, temperature differences are slight, either the whole air mass was isothermal or, if the crown canopy was sufficiently dense, the cold air remained above it. However in light stands (such as in this study) the sinking cold air of the crown space resulted in a low temperature on the forest floor. Seltzer (1935) observed two points of low temperature - one in the crown, the other on the ground. Additionally, Baumgartner (1956) measured the temperature profile of a dense pine stand and showed that it was warmer at the top of the trees than at the bottom. Dickinson and Dobinson (1969) found in a greenfinch (Carduelis chloris) roost that the position in which the birds roosted (base of bushes) was warmer than in the open.

Adult rooks preferred the top of deciduous trees whereas young rooks and jackdaws were found lower down but as near to the top as possible. However when the weather was severe, particularly when it rained, adult rooks were seen moving down the tree 'pushing' young rooks and jackdaws down the tree.

Brewer (1963) found that the numbers of starlings perching on a chimney were inversely proportional to air temperatures. He discerned no correlation with wind or light. He thought that starlings perched on chimneys if heat loss was slower than anywhere else and moved away if high winds or rain made heat loss greater than in more sheltered sites. Loefer and Patten (1941) considered the starling and blackbird roost they studied had a higher winter temperature than the open.

Ground roosting was observed by Jackson and Fiedler (1969) in American crow (Corvus brachyrhynchos) when the temperature was abnormally low and winds strong, (also seen by Widmann, in Bent, 1964). They suggested that conservation of heat was responsible for the behaviour, the lack of taller vegetation may have stimulated movement to the ground for protection from strong winds and cold temperatures. Elaborating, Fiedler (from his thesis, 1969), suggested strong winds may have resulted in the lack of suitable perches since smaller branches are more flexible and require a greater effort (energy expenditure) to balance on.

In clement weather, adult rooks are positioned at the top of the tree with young rooks and jackdaws below. When the weather becomes more severe, apart from the movement of the birds, aggressive encounters are observed. Vertically, in a tree, such aggressive encounters appeared to occur between the interface of adult rooks, and young rooks and jackdaws (sometimes between young rooks and jackdaws). Throughout the wood, movement of birds is followed by an increase in aggressive encounters. This leads me to think that numbers of preferred perching sites are limited or that the birds will compete to obtain the best sites they can. If one considers one tree, the number of perches available are limited if a bird prefers to perch facing the wind (as the perch must be at right angles, or nearly, to the air stream).

Which movement occurs first - vertical or horizontal? From my observations I suspect that vertical movement occurs first, with a gradually increasing horizontal shift. Under extreme weather conditions, horizontal movement is on a large scale, whole parts of the wood being vacated.

It has been mentioned that rain influenced vertical movements of birds and if rain persisted some birds were seen moving into the spruce trees. Hoppe (1896) stated that in a 60 year-old spruce tree two thirds of the whole amount of rain (up to 5 mm.) was caught by the crown. Little rain water ran down the trunk (5 per cent even in a cloud burst). The proportion of rain which dropped through the crown was least close to the trunk and increased towards the periphery (cf. birds preferred to perch near the trunk in the spruce trees). In winter, birds can gain little protection from rain in a beech tree, although lower down the crown, rain will be interrupted by the branches and twigs deflecting the rain down the trunk. Even a leafed beech tree allows more than 50 per cent of the rain to fall through its crown space (Geiger, 1950).

Labitte (1937) in notes of the roosting behaviour of the carrion crow (Corvus c. corone) mentioned that the birds perched between the middle and top of the tree crown; when rain fell or it was windy, near the trunk. However when the weather was calm and fine the birds moved to the top of the tree.

In this study I was unable to measure the number of birds in the roost but it has been mentioned by some authors that the number of birds at a roost increases when the weather becomes colder (Symonds (1965) and Vernon (1963). Jackson and Fiedler (1969) found small roost populations in the American crow when weather conditions were stormy with poor visibility, although cold re-established a large roost. Autumn roost formation was not related to a decline in average daily temperatures in the American crow (Fiedler, 1969) although large numbers of the more northern individuals migrate south to a belt 37°-42° North latitude in late summer (Bent, 1964). Frazier and Nolan (1959) noticed that communal roosting of the Eastern bluebird (Siala sialis) was elicited by 'bad' weather.

If an increase in numbers of birds occurs at a rook and jackdaw roost when the weather becomes colder, then some birds will perch in increasingly thermally - stressing positions - in those places less preferred by the older more dominant birds (see Chapter 4).

What is the relationship between heat loss in a tree canopy and a bird's heat loss?

Birds have a temperature-regulating mechanism that keeps their body temperatures at suitable levels. A bird makes adjustment to thermally-stressing surroundings by first selecting a roosting place, and then by fluffing the feathers, perhaps placing the head under the scapular feathers and by altering its stance. In these conditions a demand will be placed on the bird because of heat losses. If demand is low, it may be balanced by the heat produced by the birds lowest metabolic rate, standard metabolism (which occurs under thermoneutral conditions: see Chapter 5 for glossary). In weather conditions creating a greater demand, their metabolic rate rises. If the heat loss is large, body temperature may be permitted to fall somewhat and loss of heat can be reduced (see Chapter 5).

The movement and distribution of rooks and jackdaws in a roost is shown to be under the influence in part of weather changes and climate differences within the roost wood. It can be presumed that weather mainly influences rooks (or jackdaws) by affecting the rates of heat loss whether by conduction, convection or radiation.

Conduction is reduced by a bird by the fluffing of feathers when roosting. However wind would tend to destroy the insulation, consequently rooks and jackdaws either try to avoid exposure to the wind or face into the wind and simultaneously reduce fluffing (presumably to stop eddying lifting the feathers and breaking down the insulation). Rain would also reduce the insulation should it wet the feathers.

Natural convection will occur while a bird is roosting. In windy conditions forced convection will occur, the higher the wind velocity the greater the heat loss.

At night, all of the radiant energy affecting the bird is in the long wave length (infra-red) part of the spectrum. Such waves are emitted by the outer surface of a bird's plumage; by the ground, snow, twigs, leaves; by clouds overhead; and by water vapour and carbon dioxide in the atmosphere, even with a perfectly clear sky.

If a roosting bird is exposed to level ground below and to thick low clouds above, and assuming the bird's outer plumage surface temperature is the same as that of the ground, then it is possible that the net heat loss by radiation may be nil. The absence of haze or clouds usually means lessened downward radiation; low temperature and low humidity still further reduce it. Thus on clear, cold winter nights, downward radiation being received by the bird's upper surfaces may be much less than the radiation emitted by those surfaces. A severe net loss of radiation energy will result. Baumgartner (1956) measured the hourly mean radiation balance above and within a dense pine forest. He found that at night the effective loss of radiation at the tree top level was lower than that above the tree tops, because the horizontal radiation from the surrounding parts of the plantation reduced the outward radiation. The net heat lost by radiation decreased further down the tree. Thus a bird finds it necessary to get under an opaque cover. If the cover is made up of numerous branches or twigs the temperature of the lower layers, e.g. of the tree crown, will closely approach the temperature of the air and ground (or intermediate between the two). Such a cover will send downward much more radiation than would come from a clear, cold sky.

One field study on roosting birds showed that plant cover reduced (a) windspeed and (b) light penetration (which is akin to the density of the canopy which would influence heat loss by radiation). This study was by Klimstra and Ziccardi (1963) who investigated night-roosting habitats of bobwhite quail (Colinus virginianus) This ground-rooster preferred herbaceous plants as cover with low, sparse, open canopies with mean light obstruction values of 14.3 per cent in early winter and 9.3 per cent in late winter. The windspeed was reduced by 65-100 per cent at ground level (2 year average 92 per cent). The light obstruction value decreased through the winter thereby probably increasing the loss of heat by radiation. However, as ambient temperatures in late winter are probably lower than those in early winter, and if the cover increased in density, then very low temperatures would be found in the herbaceous plant trunk space (where the birds are roosting). By selecting through the winter different roosts of decreasing canopy density, the birds were in areas of greater mixing of the air (in the trunk space) by the wind and thus the temperature would not have been as low as in a roost of lower light penetration values. Likewise Moen (1968), investigating radiant heat loss from white-tailed deer (Odocoileus virginianus), found a greater quantity of heat energy radiating from cedar cover than from upland hardwood cover on nights with clear skies. He also observed that white-tailed deer had a preference for cedar cover during the most severe periods in winter. When food is in short supply the weather is stressing.

In the case of roosting rooks and jackdaws settled in a tree, the individuals need not be in contact in order to reduce radiation losses. From the position of any one bird, if the view in all directions is largely covered by others birds, then the birds are effectively radiating to each other: a completely surrounded view would result in no radiation loss whatever. However the outermost birds would radiantly lose heat from their exposed-view surfaces.

In conclusion, I suggest that rooks and jackdaws react to weather in a way so as to minimise heat loss. However adult rooks appeared to be able to choose their roosting position in contrast to young rooks and jackdaws, (see also Chapter 4). In the event of heat loss becoming stressing in the top of a tree adult rooks moved downwards. As these older rooks moved down the tree they seemed to force the younger rooks and jackdaws to perch in colder parts of the canopy. However, the relative merits of which is the more stressing, perching at the top of a tree or perching at the bottom of the canopy are arguable. By reference to Chapter 8 it can be seen that a rook might possibly save 9 per cent more energy in a night by perching at the bottom of the canopy than at the top.

The influence, found in this study, of temperature, windspeed, rainfall, cloud cover and wind direction on the spatial organisation of rooks and jackdaws in the roost raises important considerations of the rate of heat loss experienced by a bird in a particular roosting position. Additionally, since there is a strong suggestion that a dominance hierarchy (i.e. adults dominant to young) occurs in the roost, this aspect of the social organisation and its influence on the spatial organisation of a roost will be investigated.

CHAPTER 4

The social organisation of rooks in the laboratory.

Introduction

In order to extend and confirm my observations and conclusions regarding behaviour in the roost, the social hierarchy in captive flocks of rooks was investigated.

Observations on the postures of rooks on perches were made using a mixed age-group flock containing individuals of known sex and age (i.e. first year, second year and older). A series of investigations were made (i) to measure the hierarchy structure when feeding and perching so as to characterise some criteria of social hierarchy and dominance; (ii) to see how a small roosting group organised themselves socially and spatially and (iii) to ascertain the hierarchy structure in two and three age-group flocks.

Herewith a glossary of terms used frequently in the following Chapter:

A successful encounter is defined here as any aggressive encounter which results in the retreat of one of the birds involved. The retreating individual is termed subordinate, have "lost", and the other individual, or "victor" is dominant.

An aggressive encounter is defined as an aggressive interaction over perches or food between two birds, the outcome of which may result in a clear win for one bird or it may be unresolved with no clear winner.

A threat is an indication, by movement, of an intention to cause an interaction or attack.

An attack is defined as a physical assault.

Dominance/Subordinance postures of rooks on perches.

a) Dominance behaviour patterns

'Lateral' posture (Figure 11): An aggressive encounter is initiated by a dominant bird towards a subordinate which is too close. This generally consists of a rapid, side-stepping movement by the dominant towards the subordinate. The dominant keeps its body stretched up, its head pointing straight-ahead and in a lateral (side-on) position to the subordinate. The subordinate meanwhile remains in the normal posture.

If the subordinate does not retreat, the dominant will lunge with its body outstretched towards the subordinate. The bill generally misses as it does not reach as far as the other bird, but in most cases this causes the subordinate to move away. If the subordinate remains, the dominant will move closer and peck at the head of the other bird (unless the subordinate goes into the "down-stretch" posture which is described in the following part on subordinate behaviour patterns).

Bowing and tail-fanning (Figure 12): Subsequent to a successful perch encounter a male dominant will return to his mate (if there is one) and perform the 'bowing and tail-fanning' described by Coombs (1960). During the posturing the female will bow lower than the male. Only dominant pairs seem to perform this action which is sometimes followed by a food begging action by the female.

Wing- and tail-flipping (Figure 13): This was mentioned by Coombs (1960) "the folded wings are quickly lifted from the back, they may be separated a little at the tips and at the same time the tail is opened slightly. The action is a quick flick and the body and head do not appear to be involved".

This movement is a precursor to a successful encounter. It is seen when a dominant bird is threatening a near-dominant bird and it is generally associated with an advance step-by-step along a perch towards the near-dominant. In every instance the bird involved in wing- and tail-flipping is successful in displacing the other bird.

The despot, in particular, freely uses this movement seen by Marler in chaffinches (1955) and most especially when closely surrounded by other birds (e.g. at a food bowl when the birds are hungry).

Bill-jabbing is used to keep other birds at a distance when perching and is a forewarning that further advance will precipitate an attack.

Bill-pointing is used by dominants to threaten another bird. It is seen especially in roosting at night if a subordinate perches too closely to a dominant the latter will simply face the subordinate, with its neck slightly outstretched. The subordinate will normally retreat immediately.

The bill points towards the opponent and, at its maximum intensity, the bill is raised. The tail is held horizontally and is often a little spread. The wing- and tail-flipping is rarely seen associated with this behaviour. This posture is mentioned by Lockie (1956) as the '½ or full forward' and by Coombs (1960) as the 'forward threat-posture'. Threat postures which resemble this posture have been seen in the robin (Lack, 1943) and great tit (Hinde, 1952).

b) Subordinance behaviour patterns

Food-begging (Figure 14): Fledgeling rooks when calling for food, flutter their wings; and famale rooks also beg for food using the same call and wing action. These reactions of the young to their parents and of the female to the male seem to be paralleled by the 'response' of subordinates to dominants as it was seen being used by subordinate rooks and jackdaws to"appease" attacking dominants.

Down-stretch (Figure 15) is seen when a subordinate bird is forced near to a dominant. This always occurs on perches, when for some reason many birds are perched close together. Pecking will occur and subordinates under attack will take up this posture to avoid continued pecking. It consists of leaning down so that the head is lower than the perch with feathers sleeked, body close to the perch and completely immobile. This submissive attitude immediately quells any attack. If the head is raised the attack will resume. It is strongly akin to the female low-intensity pre-copulatory display (Coombs, 1960) and also to the angle of the body in the maximum intensity fluffing response, i.e. down-stretch has qualities of submission and aggression. If the down-stretch occurs subsequent to a fluffing response, and the feathers are not sleeked, the dominant will continue pecking. The down-stretch posture is taken up just before flying from a perch.

It is very interesting to note that a diverted gaze (in 'Down-stretch' and the 'Lateral posture') has been remarked on by Moynihan (1955) and Chance (1962). Chance (loc. cit.) stated that closing of the eyes in a 'submissive' posture removes part of the stimulus provided by the attacker, from the subordinate's senses and so reduces the subordinates impulse to retaliate. However, Barnett and Evans (1965) suggested that it changes the visual stimulus provided by the defender and so reduces the likelihood of further assault, which seems more likely particularly as bill pointing (i.e. a direct gaze) is a threatening posture.

Feather erection or fluffing response (Figure 16): This feature occurred in many situations and in them all the birds were under some kind of threat. In every observed situation the two participants in the aggressive encounter were close to each other in the hierarchy. The more dominant approached the other slowly, usually with bill-pointing postures.

The sub-dominant invariably fluffed up its back feathers and the aggressive encounter was signified by several pecks from the sub-dominant. Not every sub-dominant was displaced, but this seemed to depend on spatial position, i.e. if lower or to the side of the dominant then the sub-dominant will retreat, if above it might win.

The high-intensity posture was with the head down, the body nearly horizontal. The low-intensity was nearer the normal body angle with feathers less fluffed.

An attack by a dominant ceased if the subordinate in a high-intensity posture sleeked its feathers i.e. 'down-stretch' posture. Brown (1964) found a correlation between the angle of erection at the crest and the degree of "agonistic arousal" in Stellar's jay (Cyanocitta stelleri).

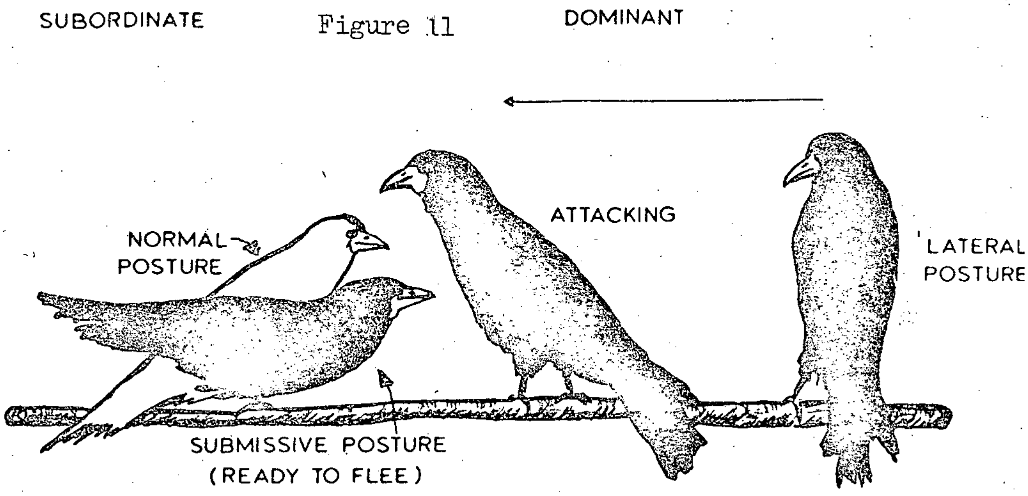
c) 'Subordinate-to-dominant' posture gradient (Figure 17)

In general, the angle of the body and head seems to have an important influence on the outcome of aggressive encounters on perches. The postures so far discussed all occurred in laboratory cages. Behaviour patterns involving erect postures are, on the whole, the preserve of dominant birds and those containing horizontal postures are those of subordinate birds.

In the laboratory situation, aggressive encounters over food are resolved almost exclusively by threats although in the case of subordinate first-year birds many feed amicably shoulder-to-shoulder. These threats are generally low-intensity 'lateral' postures with no lunging, or low-intensity pointing.

When competing for perches a range of postures, and of intensities of postures (e.g. fluffing response), was observed among birds. Floor

Figure 11



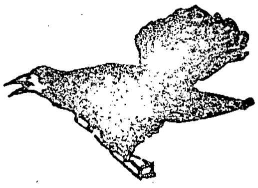

BOWING & TAIL FANNING

Figure 12

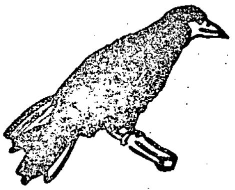

WING & TAIL FLIPPING

Figure 13

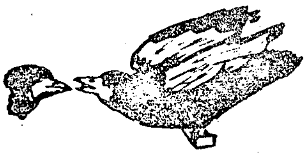

FOOD BEGGING

Figure 14

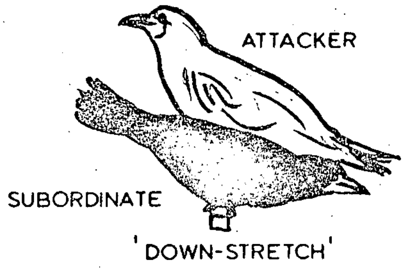


Figure 15

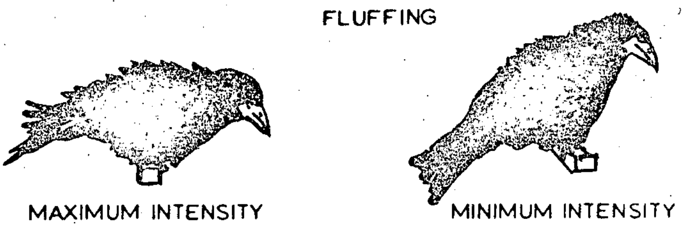


Figure 16

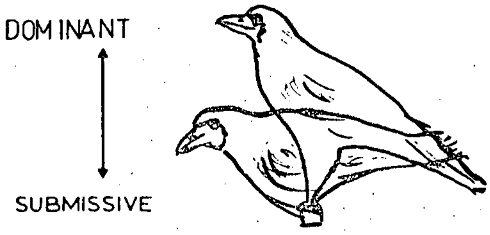


Figure 17

Figures 11-17. Postures seen in a captive flock of rooks

space in the aviaries is large and birds are easily able to avoid each other. However, there are a limited number of perches and rooks and jackdaws much prefer roosting on a perch than on the floor. Consequently, a greater persistence on the part of the subordinates to obtain a perch probably brought out this range of postures.

Lockie (1956) described seven aggressive postures of which five were involved in aggressive encounters over food. All postures he observed were conducted on the ground. In this context, the posture-gradient seemed to no longer hold as the two near-horizontal ground postures Lockie showed ('½ and full forward') were by aggressive birds. However, the most erect postures he described, 'take-off', 'bill-down' and 'bill-up' were also seen in aggressive birds.

It can only be assumed that movement towards a bird by another constitutes a threat in itself, and the body attitude indicates the state of 'confidence' each bird experiences. In static postures a gradient of dominance by erectness of body may still apply.

Behaviour of paired birds:

Paired birds always follow each other and perch shoulder-to-shoulder. There is a lack of threat postures towards each other and mutual preening is common. Frequently, when seen perching together, the female is crouched down on the perch while the male is slightly more erect. If another bird comes too close to the female, the male jumps over the female or bill-points over her back.

The social hierarchy structure of a single age-group flock when feeding or perching.

Successful encounters between individual birds provide the evidence of dominance or subordinance. This was possible because in every successful encounter observed only two birds were involved.

In, for example, Figure 18 and Figure 19, the letters are symbols for the colour rings (which did not appear to alter behaviour) and give the identity of individual birds. The top horizontal row of letters arranges the birds in order of their rank in the hierarchy with the dominant bird at the left. The left-hand vertical column gives the same list with the dominant bird at the top. The Arabic numerals record the number of encounters won or lost. Thus, for example, Figure 18 may be read from left to right as follows: RRB lost six times to RWS and nine times to RLR. Or the figure may be read down, RLWX did not win against RLRRW and won seven times against RLRW.

It is evident that in such a figure all the numbers would fall in cells below a diagonal drawn from upper left to the lower right-hand corner, if the rank order was completely linear. Hence the numbers entered above the diagonal record irregularities or exceptions to a linear hierarchy order.

The male usually performs the role of 'protector' to the female, intervening in many aggressive encounters which would otherwise have been directed at the female. A secondary consideration is that this ability (of the male to intervene) is effective only when the female is near to the male and vice versa. The female would generally threaten another bird only when her mate is near, and so the proximity of the male is important in determining a female's status at any time. The male and female are generally close, with the female following the male. However in constructing the social hierarchy figures each individual is treated separately and consequently the male and female are generally some distance apart in the hierarchy order.

The following additional information is shown in the figures concerning the social structure of flocks: the number of encounters won (bottom row but one) for each bird; the number of winning encounters expressed as percentage of the total number of encounters (won or lost) for each bird (bottom row); the number of encounters lost (last column but one) for each bird, and lastly, the total number of encounters lost or won for each bird (last column).

During the period 24/11/70 to 22/2/71 observations were kept specifically on successful encounters on perches and over food. The basic hierarchy structure was determined by observing the encounters (won or lost) over food with observations on encounters won or lost on perches.

Successful encounters on perches were measured for 30 minutes at dusk i.e. the time of going to roost, by allowing the birds access to a part of the aviary containing perches which were changed in position every day. Successful encounters over food were observed (through a one-way mirror) at dawn for 30 minutes on introduction of the food bowl, which was removed at dusk. The intercommunicating door between the two identical aviaries (7m x 2m x 2m each) was kept closed during the day to allow the perch positions to be changed. The aviary containing the food bowl had no perches and all the walls of the flights were solid. I made a total of 10 hours observation on both perching and feeding encounters.

The reason for changing the position of the perches each day was to prevent the hierarchy from settling down with a consequent reduction in encounters. There were enough perches for many times the number of birds in the aviary. The lay-out of the perches was changed from day to day in order to make the social hierarchy structure clearer.

The structure of the social hierarchy, determined by observing successful encounters over perches and food, is shown in Figures 18 and 19.

The dominant pair (RWS ♂, RIR ♀), the second most dominant male (RIRRW ♂) and RIRW ♀ were involved in the greatest numbers of encounters for food (which were won or lost) (Figure 18).

There were many fewer successful encounters on perches, in the same time interval, than over food. Moreover the social hierarchy structure changed somewhat; the subdominant pair moved up one position displacing RRWX ♀ down by two positions. Once again the three most dominant birds (RWS ♂, RIR ♀, RRB ♀) and RRWX ♀ were involved in the highest number of encounters, won or lost, (Figure 19).

To summarise: in a flock of $<$ 1 year old birds the peck-right hierarchy structure was fairly stable and the same straight-line hierarchy was involved in feeding and perching. (Very recently Murton et al. (1972) have shown that the social hierarchy in roosting and feeding flocks of feral pigeons (Columba livia var) is stable.) The observations were carried out during winter in an indoor aviary under a natural light regime with temperatures generally 5°C above ambient temperature.

By reference to observations of the roost (Chapter 3) similarities can be seen between the bird behaviour (e.g. aggressive encounters on perches) in the field and laboratory.

The relationship between perching position, or height, and social status in a single age-group flock

A further series of experiments was done to ascertain the relationship between social status and linear perching position.

A long perch was painted with alternate black and white numbered (counting from left to right, 1 to 16) sections 10 cm. in length, with a smaller perch beneath. There were no other perches present, but enough perching space was available on the top perch alone to accommodate all the

ENCOUNTERS OVER FOOD

Victor

		♂ RWS	♀ RIR	♀ RRB	♀ RRWX	♀ RLWX	♂ RIR RW	♀ RIRW	JIR	No. of encounters lost	Total encounters won or lost
Loser	RWS									0	78
	RIR	10								10	47
	RRB	6	9							15	34
	RRWX	2	5	5						12	22
	RLWX	6	8	3	2		1			20	32
	RIR RW	21	9	4	3	0				37	44
	RIRW	15	3	6	1	7	5			37	42
	JIR	18	3	1	4	5	1	5		37	37
Number of encounters won		78	37	19	10	12	7	5	0	N 168	
% wins (integers)		100	79	56	45	38	16	12	0		

Figure 18.

Matrix of encounters between individuals in a captive flock of one year-old birds which were trying to obtain food.

Note: JIR is the single jackdaw and the tied males and females are mated pairs.

The numbers in the columns = encounters won.
The numbers in the rows = encounters lost.
Thus RRB won 5 + 3 + 4 + 6 + 1 and lost 6 + 9, it therefore won 19 of a total of 19 + 15 = 19/34 = 56%.

ENCOUNTERS ON PERCHES

		Victor									
		♂ RWS	♀ RLR	♀ RRB	♀ RLWX	♂ RLR RW	♀ RRWX	♀ RLRW	JLR	Number of encounters lost	Total number of encounters won or lost
	RWS									0	26
	RLR	8								8	19
	RRB	8	4							12	16
	RLWX	1	3	0						4	5
Loser	RLR RW	1	0	0	0					1	1
	RRWX	8	2	2	1	0				13	13
	RLRW	0	1	2	0	0	0		1	4	4
	JLR	0	1	0	0	0	0	0		1	2
Number of encounters won		26	11	4	1	0	0	0	1	N 43	
% wins (integers)		100	58	25	20	0	0	0	*		

Figure 19. Matrix of encounters between individuals on perches in a captive flock of one year-old birds.

Note: * It was decided not to include a percentage in this instance as it would be based on only two encounters.

birds, (six 1 year-old birds). Observations through a one-way window were taken from 13/1/71 to 22/2/71 at midnight. The position of each bird every night was noted. Table 13 shows the numbers of nights a bird was observed perching in a particular place on the longer perch.

Individual birds were found each night in approximately the same positions. Pairs roosted together with an unpaired individual between the pairs on most nights.

The jackdaw JLR (hierarchy position 8 i.e. the most subordinate bird) and RLRW ♀ (hierarchy position 7) always roosted on the smaller lower perch. On the long perch, the other six birds roosted in hierarchical order from 1 (RWS o) on the far left to 6 (RRWX ♀) on the right. The hierarchy positions were taken from Figure 19. Bird 1 perched on 32 out of 40 occasions on positions 1-4 while bird 6 always perched at positions 13-16.

A contingency coefficient (C) test was applied (Siegel, 1956) to measure extent of association between individual birds and perching position. The individual birds and perching position at night were significantly correlated at P 0.001 (X^2 = 256.07, C = 0.72).

A second experiment (using eight 1 year-old birds) was designed to test whether height of perching position and social status (from Figure 9) were related (Table 14). Three perches (20 cm. long), capable of only having two birds on each, were clamped $\frac{1}{2}$ metre apart on a vertical steel rod. This artificial "tree" swayed at the top. Observations were then taken of the number of times a particular bird was seen on one of the three perches, which were classified as high, middle and low. Each observation was taken at approximately midnight for fifty consecutive nights from 24/11/70 to 13/1/71.

There were two more birds than there were perches and, as a result

TABLE 13

A 3 x 8 contingency table showing the perching position on one long perch of 6 rooks of different hierarchical status on 40 nights.

Dominant ←→ Subordinate

PERCHING POSITION	SOCIAL STATUS (See Figure 19)	♂ RWS 1	♀ RLR 2	♀ RRB 3	♀ RLWX 4	♂ RLR RW 5	♀ RRWX 6	TOTALS
1-4	fEXP	11.2	11.2	11.2	11.2	11.2	11.2	67
	fOBS	32	35	0	0	0	0	67
	X^2	3.9	5.1	11.2	11.2	11.2	11.2	53.8
5-8	fEXP	6.3	6.3	6.3	6.3	6.3	6.3	38
	fOBS	8	5	13	7	5	0	38
	X^2	0.5	0.3	7.1	0.008	0.3	6.3	15.2
9-12	fEXP	9.3	9.3	9.3	9.3	9.3	9.3	56
	fOBS	0	0	27	21	8	0	56
	X^2	9.3	9.3	33.7	14.7	1.9	9.3	78.2
13-16	fEXP	13.2	13.2	13.2	13.2	13.2	13.2	79
	fOBS	0	0	0	12	27	40	79
	X^2	13.2	13.2	13.2	0.1	14.4	54.4	109.5
TOTAL observations of a bird at a particular perch.		40	40	40	40	40	40	

Note: the number in the top of each cell is the expected frequency, in the middle the observed frequency and in the bottom of each cell is the chi-square (X^2).

TABLE 14

A 3 x 8 contingency table showing the perching height on high, middle and low perches of 8 birds of different hierarchical status on 50 nights.

Dominant ←——————————————→ Subordinate

SOCIAL STATUS (See Figure 19)			♂ RWS 1	♀ RIR 2	♀ RRB 3	♀ RLWX 4	♂ RIR RW 5	♀ RRWX 6	♂ RIRW 7	JIR 8	TOTALS
PERCHING HEIGHT	High	fEXP	16.5	14	13.4	13.4	13.4	16.4	4.0	9.0	100
		fOBS	40	10	2	2	2	40	2	2	100
		X^2	33	1.14	9.5	9.5	9.5	33	1.0	6.6	103.2
	Middle	fEXP	16.6	14	13.4	13.4	13.4	16.6	4.0	8.6	100
		fOBS	8	30	14	10	10	8	2	4	100
		X^2	4.4	2.3	15.8	0.9	0.9	4.4	1.0	1.5	31.1
	Low	fEXP	16.6	14.0	13.4	13.4	13.4	16.6	4.0	8.6	100
		fOBS	2	2	10	28	28	2	8	20	100
		X^2	12.9	10.3	0.9	15.8	15.8	12.8	4.0	15.0	87.4
TOTAL observations of a bird at a particular perch			50	42*	40*	50	40*	40*	12*	26*	

Note: (a) the number in the top left hand corner of each cell is the expected frequency, in the bottom right-hand corner the chi-square (X^2) and in the middle of each cell is the observed frequency.

(b) *Because of the scarcity of perches and lack of dominance these birds, on some occasions, were found on the ground. thus bird 2 was found at high, middle and low perches on 10, 30 and 2 occasions respectively and on the ground 8 times.

some birds roosted on a perch on only eighty per cent of occasions or less. Because of problems of space only three perches could be placed on the artificial tree.

A contingency coefficient test was applied (Siegel, 1956) to measure the extent of association between social status and perch height. I found that social status and height of available perch were significantly correlated at $P < 0.001$ ($X^2 = 221.7$, $C = 0.65$) although there are anomalous individuals e.g. RRWX. In this experiment encounters were initially large for the "high" position when the "tree" was first introduced. However, on successive nights little or no aggression occurred between birds perched on different perches.

Because birds were involved in little aggression after the initial introduction of the "tree" suggests that each bird 'learnt' its roosting place. However, the "tree" was placed near to a door of the aviary in order to see clearly the birds in the dark through the one-way window. Unfortunately the birds appeared, for some unknown reason, to be slightly apprehensive when near this door. On some occasions, therefore, a bird would roost at the back of the aviary on the ground in preference to being on the "tree".

It is worth noting that presumed dominant birds in the study roost behaved in the same way i.e. they sought out the highest perches in a tree (Chapter 3).

Social structure of mixed age-group flocks

From the observations made on the hand-reared flock it was thought that a bigger and more complex situation should be developed to involve as many birds of known ages as possible.

Fourteen rooks (9 ⩾ 2 year-old; 5 < 1 year-old) were captured in a cage trap near the rookery within the study roost at Stevenson Wood, East Lothian on the 6/6/71 and 7/6/71. They were housed in the same aviaries as previously used for other social hierarchy experiments.

Hierarchy structure was ascertained by noting all successful encounters for five minute periods for a total of 5 hours 20 minutes between 27/6/71 and 29/6/71.

There were 24 wins of adult (i.e. ⩾ 2 year-old) over adult, 6 wins of juvenile (i.e.< 1 year-old) over adult, 33 wins of juvenile over juvenile and lastly 56 wins of adult over juvenile. There were 93 encounters involving juveniles and 86 involving adults (Figure 20).

Although the juvenile group was generally subordinate to the adults, two adults (a pair) were subordinate to several juveniles. All the males and females in pairs, which were all ⩾ 2 years old, were close to each other in the hierarchy order.

The results of some successful encounters were the reverse of what was expected. This occurred mainly when juveniles were involved.

Although no clear pattern evolved, the lower seven birds in the hierarchy were involved in more encounters than the top seven birds (142:96) and males were more involved than females (134:104). Additionally dominants beat dominants (i.e. the top seven birds in the hierarchy) 15 times and subordinates 62 times whereas subordinates beat subordinates (i.e. the lower seven birds) 38 times and dominants 4 times.

A second experiment involving a three age-group flock was set up by introducing on 30/6/71 six hand-reared 2 year-old birds into the two flights containing the same 14 wild ⩾ 2 year-olds and juveniles used in the previous experiment.

	Age		Victor															
			RWH ♂	RRRWW ♂	RlRB ♀	RRWWLW ♀	RRWW ♂	RlRR ♀	RRBRB ♂	RlRWRB ♂	RRBB ♂	RLWW ♀	RLW ♀	RLBBB ♂	RRRR ♀	R ♂	Number of encounters lost	Total number of encounters lost or won.
	3	RWH					1										1	16
	3	RRRWW					1										1	14
	3	RlRB	2														2	10
	3	RRWWLW	2	1			1			1							5	23
	3	RRWW	1	3						1							5	20
	3	RlRR			1					2							3	9
Loser	3	RRBRB		2													2	4
	1	RlRWRB	3	3	1	4	3	1			1	1	1				18	34
	1	RRBB	1	1		1	1			3		1	1				9	15
	1	RLWW	2	1	2	2	1			1				2			11	18
	3	RLW	1			2				2							5	8
	1	RLBBB			1	4	1	2	1	2	3		1		1		16	25
	1	RRRR		2	3	2	6	3	1	4	2	5		7			35	36
	3	R	3			3											6	6
Number of encounters won			15	13	8	18	15	6	2	16	6	7	3	9	1	0	N 119	
% wins (integers)			94	93	80	78	75	67	50	47	40	39	38	36	28	0		

Key - Age 3 = 2 years old
Age 1 = 1 year-old

Figure 20. Matrix of encounters between individuals in a two age-group captive flock which were either (a) trying to obtain food or (b) on perches.

Note: Tied males and females are mated pairs.

All successful encounters were recorded for five minute periods for a total of five hours and twenty minutes from 4/7/71 until 23/10/71. All conditions were identical to the previous investigation of a mixed age-group flock.

The hierarchical situation in a three age-group flock is displayed in Figure 21. There were 10 wins of $\geqslant 2$ year-olds over $\geqslant 2$ year-olds, 13 over 2 year-olds and 65 over < 1 year-olds. 2 year-olds won 9 encounters over $\geqslant 2$ year-olds, 16 over 2 year-olds and 31 over < 1 year-olds. Finally < 1 year-olds won 14 encounters over $\geqslant 2$ year-olds, 1 over 2 year-olds and 36 over < 1 year-olds. A total of 196 successful encounters were recorded.

As before $\geqslant 2$ year-olds were generally more dominant than the < 1 year-olds and the 2 year-old individuals were intermediate in the hierarchy. Mates were more separated within the hierarchy structure than in the two age-group flock.

The hierarchy structure within the $\geqslant 2$ year-old and < 1 year-old group in the three age-group flock was slightly changed from that in the two age-group flock. The hierarchy structure within the 2 year-old flock also changed very little from its initial order.

Successful encounters where the victor had been expected to lose were mainly between near-neighbours in the hierarchy or a subordinate male and a dominant female. Males were dominant to females in each age group; the top ten birds in the hierarchy were involved in fewer encounters (lost or won) than the lower ten birds (167:226) and males were more involved than females (241:151). The dominant birds (i.e. the top ten birds in the hierarchy) beat other dominants 26 times and subordinates 109 times whereas subordinates (i.e. the lower ten birds) beat dominants 6 times and other subordinates 55 times.

			Victor																				
	Age		RWH ♂	RRRWW ♂	RRBRB ♂	RLRW ♀	RRWW ♂	RLRB ♀	RWS ♂	RLR ♀	RRWWLW ♀	R ♂	RRB ♂	RLRR ♀	RRBB ♂	RLBBB ♂	RLRRW ♂	RLRWRB ♂	RLWW ♀	RRRR ♀	RLW ♀	RRWX ♀	Number of encounters	Total number of encou lost or won
	3	RWH																					0	7
	3	RRRWW																					0	16
	3	RRBRB																					0	1
	2	RLRW																					0	11
	3	RRWW							1						1								2	29
	3	RLRB					1		1														2	21
	2	RWS		3		1				1	1	1					1						8	34
	2	RLR	1						4			4											9	23
	3	RRWWLW	1						1							1							3	7
	3	R		1		1		2		1			1		2								8	18
Loser	2	RRB										1											1	3
	3	RLRR				1	1								2			1					5	9
	1	RRBB	1	1		2	1	3	2			1						1					12	21
	1	RLBBB	1	2	1	1	7		3	4		1		1	3		1	3			1		29	45
	2	RLRRW		2		1			2	1								1					7	10
	1	RLRWRB		7		3	7	9	2	6	2	1	1	3		1							42	58
	1	RLWW					5	2	3		1				1	5	1	8					26	34
	1	RRRR	3				2	2	2			1				8		1	5				24	26
	3	RLW				1	2	1	1			1				1		1	3	2			13	14
	2	RRWX							4	1													5	5
Number of encounters won			7	16	1	11	27	19	26	14	4	11	2	3	9	16	3	16	8	2	1	0	N 196	
% wins (integers)			100	100	100	100	93	91	77	61	57	56	50	45	43	36	30	28	24	7	7	0		

Key Age 1 =<1 year-old
2 = 2 years old
3 =≥2 years old

Figure 21. Matrix of encounters between individuals in a three age-group captive flock which were either (a) trying to obtain food or (b) on perches.

Facial feathers

During July 1971 it became obvious that some of the 16 month-old hand-reared rooks were barer around the forehead, lores and lower jaw than others of the same age. The most dominant bird was considerably bare in the aforementioned regions, as was the next most dominant individual. The other birds showed some signs of bareness but the most subordinate bird showed no bareness at all. On 6/7/71 the following facial feather record was noted: RLRW ♀, $\frac{1}{4}$ feathered; RWS ♂, $\frac{1}{2}$ feathered; RLR ♀, full to $\frac{3}{4}$ feathered; RRB ♂, full feathered; RLRRW ♂, $\frac{3}{4}$ feathered; RRWX ♀, full feathered; and this is the order of these birds' dominance (the first is the most dominant) as shown in Figure 21. The method of notating degree of facial feathering was developed by Dunnet et al. (1969).

Discussion

As in many species (Schjelderup-Ebbe, 1935; Collias, 1944; Allee, 1950) the outcome of aggressive encounters between rooks which know each other is more or less predictable.

Although the laboratory flock showed a peck-right hierarchy (Schjelderup-Ebbe, 1922), it cannot be assumed that this is the form of the social hierarchy in field conditions until observations have been made at more than one station. This straight-line pecking order in winter flocks of wild passerines has been seen by Sabine in Junco hyemalis (1949, 1959), Hardy (1961) in the Mexican jay (Aphelocoma ultramarina arizonae), Kikkawa (1961) in wild white-eye (Zosterops lateralis) and by Marler (1955) in captive chaffinch (Fringilla coelebs).

The social hierarchy established among rooks as a result of disputes over food was similar to that established by disputes over perches. Indeed Marler (1955) considered, in chaffinches, that they may be identical in structure. The postures used were similar. In the field and laboratory an encounter usually occurs because a bird, for some reason, comes too close to another. When a certain distance, or zone, around each bird (the 'individual' distance, Hediger 1950) is transgressed, signs of aggression always appear. Food and perches may be involved in encounters only because they bring rooks close together.

In this laboratory investigation, individual birds generally seemed to have habitual roosting positions. Kalmbach (1932) and Jumber (1956) have both observed individual starlings returning to exactly the same position each night in a winter roost. Moreover removal of certain individuals caused a gap to be left for several nights before it was reoccupied by other individuals.

The rooks also preferred the highest available perches. In consequence a hierarchical gradient from dominant to subordinate normally occurred going from top to bottom in any perch system e.g. a tree. Coombs (1961) mentioned that recently fledged captive rooks try to avoid roosting immediately underneath any companions, and while in that position they are noticeably restless. Hardy (1961) noticed that the choice of roosting place of the dominant Mexican jay (Aphelocoma ultramarina arizonae) in a captive group varied somewhat from week to week, depending on the weather conditions. Its choice affected the choice of roosting place of all its subordinates. In clear, warm weather, the jays roosted in the open, except for the lowest bird in the order, which went to roost last. Although ample space for roosting remained in the open, the lowest bird always roosted where it happended to be when darkness fell. This was usually in a thicket of branches at the back of the cage.

Hardy (1961) mentioned that dominant and subordinate behaviour was most clearly seen when captive Mexican jays were preparing to roost and Tordoff (1954) observed in captive red crossbills (Loxia curvirostra) that intense "competition" occurred for roosting sites. Conversely Lockie (1954) observed few aggressive encounters in a rook and jackdaw roost.

In my rook and jackdaw roost in the field most disputes over roosting places occurred soon after the birds arrived; between 15 to 30 minutes afterwards the number of disputes fell unless the weather changed (or there was some other disturbance) and the birds had to move within the roost to new perching places when there was a temporary revival of disputing. Therefore laboratory and field observations are in agreement.

It appeared that birds showing submissive behaviour were allowed to come closer to a dominant before an aggressive encounter was precipitated than those showing dominant behaviour. Male rooks dominated females (noted in jays by Hardy op. cit.) within each age group and in general lost or won more encounters than females. Dominant individuals in mixed age-group flocks were involved in fewer successful encounters than subordinate individuals and the social status of any bird appeared strongly related to age.

A female's success was related to the proximity of her mate and would only press home a successful encounter or attack if the mate is near or if the opponent showed signs of fleeing or 'fear' (noticed in hens by Schjelderup-Ebbe, 1935 and in chaffinches by Marler, 1955). Thus a female's nominal status is affected by her mate (seen in Canada geese by Raveling where a family's status is dependent on the gander, 1970). This behaviour by the male resulted in males being involved in more successful encounters than females.

Dominant rooks were engaged in encounters less frequently than subordinate rooks, but have more successful encounters with subordinate birds than dominant birds. Conversely, Hardy (1961) noted that captive dominant Mexican jays had successful encounters more frequently than subordinate birds. However, subordinate rooks generally appeared to avoid any aggressive encounters with dominant birds (seen by Marler in chaffinches 1955) unless a localised food source forced them into closer proximity. Kikkawa (1961) found in winter flocks of wild white-eyes (Zosterops lateralis) that, unlike the birds in this study, the dominant birds interacted more often with birds of higher rank. However, Tordoff (1954) noted that in red crossbills there were fewer interactions between birds adjacent in the peck-order, except that the despot male was active in dominating the second-ranking bird.

Domm and Davis (1948) found that intersexual chickens with the most masculine plumage were near the top of the peck-order and those with the most feminine were at the bottom. Guhl and Ortman (1953), again working with chickens, found that a large comb has an advantage in paired contests. They concluded that deportment was an important stimulus for aggression (Engelmann, 1951). The deportment of subordinate rooks when near a dominant rook is restrained and tense, while a dominant is free in movement and alert in behaviour (also seen by Hardy in Mexican jays, 1961). In Mexican jays adults have black bills and subadults particoloured bills (Hardy 1961). Facial configuration in rooks may also be involved in deciding the result of successful encounters or even if an aggressive encounter will occur. Smith (1957) reported that ten-day old White Leghorn chicks discriminated against chicks of similar age and breed but of different flocks. Lorenz (1935) says that individual recognition between jackdaws occur by facial expression and voice. It is possible that in rooks facial bareness may enable individuals to recognize the status of other birds before an aggressive encounter may occur, (cf. Domm and Davis, loc. cit.) as the more dominant captive 2 year-old rooks had barer faces than the subordinate 2 year-olds.

Collias (1943) analysed the factors which make for success in the initial aggressive encounter between adult hens. He found that absence of moult, comb size, social rank and weight, in that order, accounted for 56 per cent of the variance. Rank order, or status, based on individual recognition could exist (in chickens Wood-Gush, 1955; Guhl, 1942, 1953). However, it is unlikely that there can be much individual recognition in a large roost and so it is my opinion that stable rank orders, in large rook roost flocks, are based on the recognition of status by facial bareness, deportment, different postures and levels of intensity of threat.

During the experiments on mixed age flocks once the hierarchy was established it remained more or less stable throughout the winter. Guhl and Allee (1944) compared well integrated chicken flocks with an established peck-order, to flocks undergoing constant reorganisation. The individuals in the organised flock pecked each other less, ate more and maintained body weight better when feeding was restricted than those in the other flocks.

Rooks coming into the roost alight in tops of trees, some immediately drop to the lower branches and others remain at the top. From the information of Chapter 3 on the social organisation of the roost and from the information in this Chapter on laboratory tests, younger and less dominant birds retire to the lower branches and the older birds which are dominant remain near the top. Older birds are free to move to any part of the roost wood or tree dislodging any subordinate if necessary. However in stable climatic environments (cf. Jumber, <u>op. cit.</u>: Kalmbach, <u>op. cit.</u>) individuals may habitually roost in particular positions.

Aggressive encounters in the study roost were very few in comparison to the numbers of birds present, apart from a few at roost entry (in the evening) at the top of the tree no more were observed <u>unless</u> movement within the roost occurred. The laboratory study clearly shows that it is only by moving perches around that successful encounters could be observed. Indeed no successful encounters on perches were observed at all at 'roosting' time unless this is done.

If movement occurred in the study roost encounters immediately increased in number suggesting a tightly organised structure. In the laboratory any movement of an individual during the roosting period generally caused aggression in others, although movement is rarely observed.

It is contended that individual recognition is unnecessary to afford this precise social organisation. Instead a system of status 'signs' could be employed to obviate an increased, and consequently inefficient, number of aggressive encounters during roosting where a very large number of birds could be involved.

CHAPTER 5

The rate of loss of heat by rooks in laboratory experiments testing different weather conditions and social situations.

Introduction

Having demonstrated a segregation of rooks within a roost which appears to be determined by social status and modified by weather, the next step was to investigate what effect this segregation had on the heat losses from individual birds.

A series of experiments were done using an indirect calorimetric method of determining heat loss within a chamber where the temperature and light regimes could be varied, and rainfall and wind simulated.

Glossary of terms

Thermoneutral zone is the zone of ambient temperature within which the metabolic rate is minimal in the resting bird, and within which any changes in ambient temperature have a minimal effect on the metabolic rate.

Lower critical temperature is the lower ambient temperature at which an animal's metabolic rate will begin to rise above the lowest or standard level of heat production.

Non-protein respiratory quotient (R.Q.). The relative amounts of fat and carbohydrate oxidised determines the non-protein R.Q. The R.Q. is the ratio of mols or volumes of CO_2 produced to mols or volumes O_2 consumed.

Calorigenic effect is the variable fraction of the metabolisable energy appearing immediately as heat (also known as the specific dynamic action, or S.D.A.)

Metabolisable energy is the energy available to the bird from the energy absorbed by the gut, after some has been lost as nitrogenous waste. Depending on the species of the bird, the composition of the ration and the environmental conditions, this fraction amounts to 70-90 per cent of the food energy ingested (Kendeigh 1949).

Thermal equivalent of the oxygen consumed or the carbon dioxide expelled by an animal is determined by the respiratory quotient:

$$\text{kcal/litre } O_2 = 3.815 + 1.232 \text{ RQ}$$

(King & Farner 1961)

Post-absorptive condition is when no digestion, or absorption of food is occurring.

Standard metabolic rate is the heat production per unit time when the animal is in a post-absorptive state (i.e. not digesting or absorbing food), that it is in thermoneutral surroundings and that it is as completely as possible at muscular and psychical rest.

Measurement of heat loss by indirect calorimetry (Respiratory metabolism)

King and Farner (1961), among many others, established a relationship between heat production, the consumption of oxygen and the production of carbon dioxide which permits the calculation of heat production from the measured respiratory exchanges. Certain established metabolic constants are used in this calculation as follows:

	Kilocalories per gram	Kilocalories per litre of oxygen	Respiratory quotient (R.Q.)
Fat	9.5	4.686	0.71
Carbohydrate	4.2	5.047	1.00
Protein	4.2	4.75	0.73 (King 1957)

The non-protein respiratory quotient (RQ) is used to compute the total heat production, instead of calculating the protein contribution and then the non-protein RQ and adding them. Urinary nitrogen excretion, determined in order to assess the contribution of protein oxidation to the total heat production, is often ignored in investigations of birds firstly because of the technical difficulty of collecting urine and secondly because of the negligible error incurred in animals' not digesting or absorbing food (Brody 1945, p. 311).

The non-protein RQ used in these calculations is the ratio of volumes CO_2 to volumes O_2, and this value can be inserted in the following equation:

kilocalories/litre O_2 = 3.815 + 1.232 RQ (King & Farner 1961)

where kilocalories/litre O_2 is the thermal equivalent of the observed oxygen consumption. Alternatively a value for the thermal equivalent of the observed oxygen consumption may be obtained from tables prepared by Lusk (1928).

The RQ of a mixed diet will lie between 0.71 and 1.00 and the caloric equivalent of the measured oxygen consumption will be between 5.047 and 4.686 kcal. per litre. Unusual RQs have been recorded, some possibly as a result of the conversion of metabolic substances into other substances (e.g. gluconeogenesis). Benedict and Lee (1937) recorded an RQ of 1.49 in force-fed geese and Merkel (1958) 1.18 in certain passerines. However it has been found that the thermal equivalent of oxygen would be the same as when the RQ is 1.00, (Benedict and Lee 1937) for reasons that are unknown. With RQs below 0.70 it is difficult to judge what the thermal equivalent of O_2 for calorimetric determinations might be. This dilemma caused Henry et al. (1934) to criticise indirect calorimetry for birds. Nevertheless, Benedict (1938) and King (1957) have rejected the criticisms as exaggerated. Respiratory quotients as low as 0.64 were recorded in this study but, because of the method of calculating heat/loss (i.e. in every case, the mean night RQ was at least 0.70), the problem of judging the appropriate thermal equivalent of O_2 did not arise.

Description of the controlled environment system for the measurement of respiratory metabolism (Figure 22)

The system, which was of the open circuit type, basically consisted of (a) a two channel pump, one channel of which drew air from outside the laboratory first into a reservoir tank and then into the metabolic chamber and (b) the other channel of the pump drew air from the metabolic chamber through a reservoir tank and then expelled the respired air outside the laboratory.

An IRGA (infra-red gas analyser, sensitive to carbon dioxide) and a Thermox meter (oxygen analyser) were both sited so as to measure the amount of oxygen and carbon dioxide in both the incoming and the outgoing streams of air by small flows bled from the main stream (Figure 22). A large two-channel diaphragm pump (Austen: MU 19/65) was used to circulate the air, as it gave a very consistent rate of flushing of the system over very long periods. During experimental periods, the entire system was kept going day and night to maintain a steady state condition.

All tubing used was clear Tygon; the entire system was checked for leaks by directing a stream of CO_2 gas at all junctions in the system and observing any reading change on the IRGA, and Thermox meter.

The Thermox meter was used with a Servoscribe recorder (RE511.20) which gave a recording span of 0.8mV equivalent to 0 to 32 ccO_2 with an accuracy of $\pm 0.1ccO_2$. The rate of flow in the sample system was kept

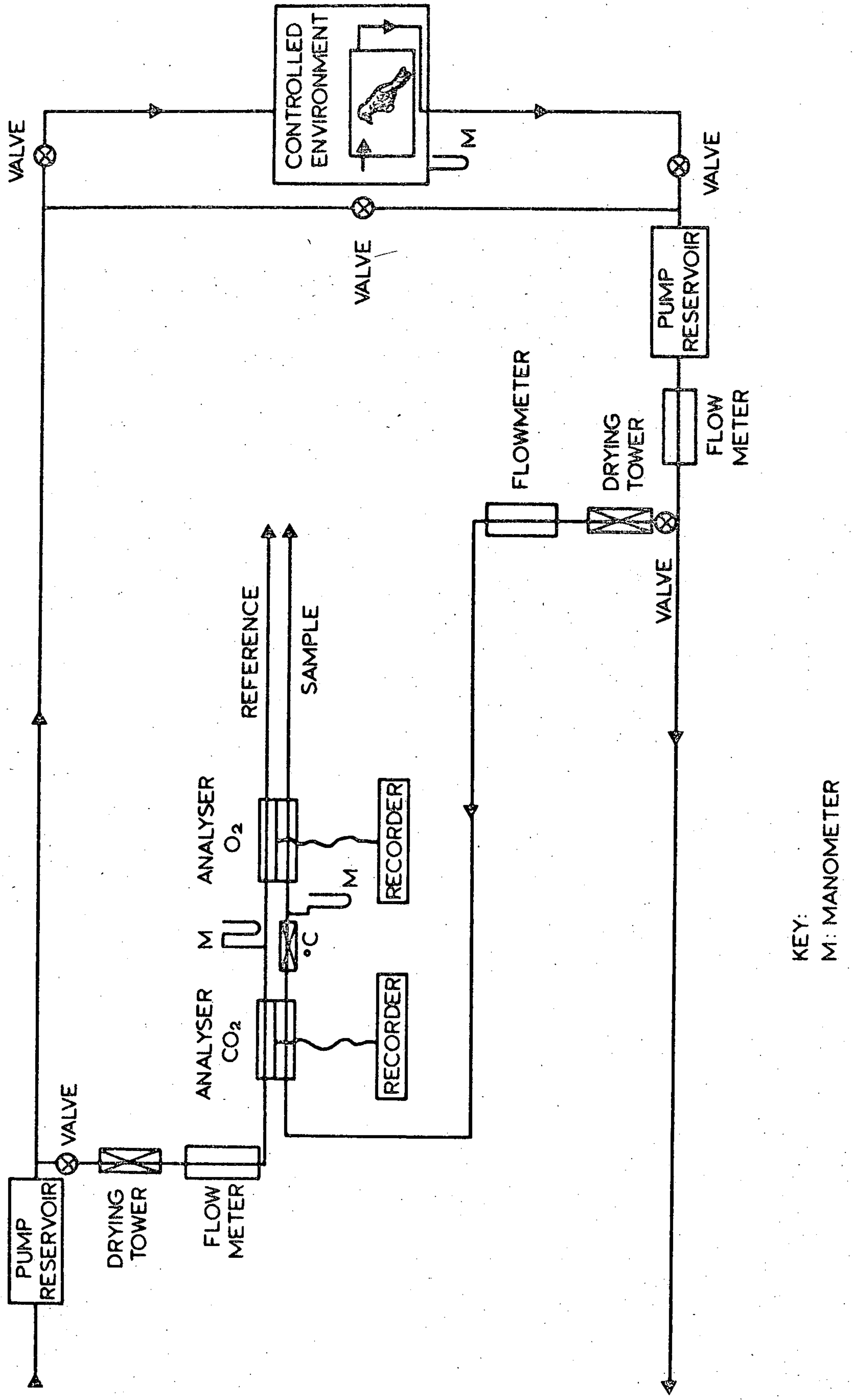


Figure 22. Diagram of the apparatus used to measure oxygen and carbon dioxide exchange of a rook kept in differing environmental conditions.

at 2cc/min, by means of a Flostat control valve and the rate of flow in the reference system was regulated to give a flow equal in pressure to the sample flow; both were monitored by two manometers. This was important as the Thermox meter was slightly affected by pressure differences in the two gas streams.

The IRGA was used in conjunction with a Honeywell Electronik 19 Pen recorder which gave a recording span of from 0 to 1250 ppm CO_2 i.e. each division was equivalent to 12.5 ppm CO_2 with an accuracy of $\pm$ 1.25 ppm CO_2.

The Metabolic chamber was a Controlled Environment plant growth cabinet EF7H made by C.E. of Canada. It was gas tight with a floor area of $0.65 m.^2$ Temperature, humidity and lighting programmes were all controlled by sensors.

Temperatures were controlled by a solid state resistance bridge amplifier and thermistor sensor. It had a control of $\pm$ 0.5°C. The humidity was controlled (to $\pm$ 2 per cent) by a solid state resistance bridge amplifier and humidity sensor. Lighting was automatically controlled by a time switch. The air inside the chamber was continually circulated by two fans. At high humidities a considerable amount of water collected on the floor of the chamber and this had to be run off through an air trap to a floor drain. At all times a positive pressure was maintained in the chamber (i.e. rate of inflow was greater than that of outflow) so that the CO_2 concentration of the air in the chamber was similar to that outside. This static pressure was of the order of 1/2 inch of water, measured and monitored by a manometer connected to the chamber. Temperatures were recorded during every experiment with a Casella thermohygrograph which had been calibrated ($\pm$5°C) against six reference mercury thermometers. The relative humidity accuracy (±3 per cent) was frequently checked with an Assman psychrometer.

Within the metabolic chamber was an opaque plastic tub 80 x 70 x 60 cm, its perspex lid being sealed with foam rubber. The lid was clamped to the tub rim by means of metal bars laid around the lid edge and then gripped by G-clamps. It was essential for the tub to be airtight. This was difficult to achieve as the seal on the lid had to be broken and made once a day. Eventually a kind of microcellular sponge rubber with unperforated sides and great resilience was found, which together with a silicone grease, made a good seal.

A hole was pierced at one end of the metabolic chamber and air was drawn out at the other through the pump to the IRGA. The tub was flushed with 5 litres/min of air. The tub was furnished with a perch of the same material as perches in the controlled environment aviary.

In many parts of the system silencers and filters and one-way valves were placed to quieten the air flow as it was found that the birds could detect and were upset by the sputtering noise of the air in the tubing. A fairly silent domestic fan was positioned in one corner of the plastic tub and encased in protective wire screens. It could be switched on from outside the metabolic chamber. It projected an air stream of 1.0 m/sec. at the perch.

A series of clear plastic tubes were attached to the undersurface of the perspex lid of the tub. A number of pin-prick holes were made in the tubes, which lay horizontally. These were connected to the humidifying system so that when this automatic system was on, water drops fell evenly all over the inside of the tub. Control of this rainfall apparatus was again outside the chamber. It was always arranged that rain fell for one quarter of the duration of the experiment by adjusting the humidity control.

For temperatures below 0°C the tub was placed in a cold unit when it was found necessary to adjust the rainfall apparatus because water froze in the tubes. By maintaining the connection with the C.E. cabinet and running it at 0°C the humidity control could be adjusted to allow rainfall for a quarter of the duration of the experimental runs. When the automatic sensor switched off the water supply, the water drained from the tubes in the tub before it was able to freeze.

The carbon dioxide and oxygen analysers: The carbon dioxide analyser used was a Grubbs Parsons Infra Red Gas Analyser (IRGA). Although this instrument is generally used in plant photosynthesis work it was successfully adapted here to work well with birds under differing climatic environments. The instrument has a sensitivity of 0.5 ppm CO_2.

The IRGA, according to the manufacturers, is insensitive to water in the vapour phase. The analyser is maintained at 8°C above room temperature and therefore the water is unlikely to condense. However, Parkinson (1970) has pointed out that the IRGA does react to the presence of water when considering very low concentrations of CO_2 although no effect was noticed in tests when high concentrations of CO_2 were sensed dried and then undried. Nevertheless, the sample air stream of the apparatus was passed through a tower of 500 gm of indicating silica gel.

The flow rate through the sample and reference systems was slow enough to allow no pressure gradient to form across the cell in the IRGA. All IRGA readings, however, had to be corrected to standard temperature and pressure.

In order to calibrate the IRGA a supply of pure CO_2 was bled into a dry air stream from which the CO_2 had been removed. The flow rate of both these streams were known and the CO_2 concentration of the resulting stream was therefore calculable. Adjustment of a liquid paraffin 'valve' regulated the flow. A manometer measured the pressure drop across the capillary tube. This pressure drop which had been calibrated against a soap bubble flow meter was proportional to the flow of air through the capillary tube.

The oxygen analyser used was a zirconium oxide ceramic cell manufactured by Thermo-Lab Instruments, Inc. U.S.A. Initially a Scholander Micro-Gasometric Technique (Scholander 1942) was considered but rejected as too inaccurate for this application.

The zirconium system was adopted to allow extremely accurate continuous measurements of relative oxygen concentrations. Bjorkman and Gauhl (1970) and Janac, Catsky and Jarvis (1971) mentioned the use of this instrument in higher plant photosynthesis. It is not affected by the presence of CO_2 or water vapour, by the vibrations from pumps, or by considerable changes in ambient temperature ($\pm 5^{\circ}C$). Another feature is that it needs no elaborate calibrations. Although its sensitivity does drop off with increasing O_2 concentration, making it unsuitable for photosynthetic measurements in an open system, it was perfectly suitable for the present purposes and in fact more accurate than any other system available commercially.

The response time of the zirconium oxide cell itself is according to the manufacturer, only 1 millisecond with an error of ±3 per cent (Bjorkman and Gauhl 1970). The analyser would presumably have a smaller inherent error. Atmospheric CO_2 concentration changes markedly, which is the main reason for having a system which compares the <u>relative</u>

air composition changes. The O_2 concentration is accepted as more stable. The National Bureau of Standards and the Environmental Science Services Administration indicated the O_2 abundance in clean air during 1967 to 1970 to be statistically the same as all reliable measurements reported since 1910. The average for all analyses is 20.946 mole per cent oxygen in dry air with a standard deviation of ± 0.0017.

Method

The birds used in this investigation were kept in indoor aviaries. Temperature was monitored with a max/min thermometer and compared with the same recordings made outside in another flight. The indoor flight was always 3°C warmer than the outdoor flight. Food (BOCM 509) and water were continually available. The photoperiod was that of natural daylengths as large windows covered one wall of the laboratory. The birds had two interconnecting 10 m. flights in which to move. There were nine birds; four $\geqslant$ 2 years old, three hand-reared 2 year-olds and two $<$ 1 year-olds. The $\geqslant$ 2 year-olds and $<$ 1 year-olds had been caught in June 1971 and kept under the aforementioned conditions until February 1972 when the experiments finished. The experiments on heat loss began in October 1971.

Each bird was weighed and placed in the apparatus an hour before the chamber lights were abruptly switched off (corresponding to civil sunset.) Temperature, wind speed and rainfall were held constant during the entire run. (Humidity was that of the outside environment unless rainfall was involved.) The chamber was kept in darkness until civil twilight (sunrise) when the lights automatically came on. The bird was immediately removed and weighed. However, if rainfall had been involved the bird was allowed to dry for one hour at room temperature in a darkened cage without food or water. The weight of each bird half way through each run was used in the calculations of heat lost. Four temperatures were tested +24.0, +11.5, +2.5 and -7.5°C. Each experiment ran for c. 15 hours, the mean interval between sunset and sunrise from October to January.

Individual rooks were tested at the four temperatures (+24.0, +11.5, +2.5, -7.5°C), a range of treatments linked factorially (i) without rain or wind (ii) with wind (iii) with rain (iv) with rain and wind. A total of 58 nightly runs were made; 19 runs were made without rain or wind (i.e. regime (i)) and 13 runs at the other three regimes (i.e. (ii) (iii) (iv)).

Pairs of rooks were also tested at -7.5°C and +11.5°C without rain or wind in order to test the hypothesis that the presence of another bird affected the rate of loss of heat. A total of 20 nightly runs were made; five runs at two different temperatures with two different pairs of rooks.

<u>The method of calculating heat loss</u>: During each run values of (a) the rate (litre/min.) of oxygen consumed and (b) carbon dioxide expelled were read hourly from the experimental trace. By calculating the ratio of the rate of carbon dioxide to the rate of oxygen for each hour the non-protein RQ was found. From this a mean nightly RQ value was calculated and by substituting this in the formula, kcal/litre $O_2 = 3.815 + 1.232$ RQ (from King and Farner 1961) the thermal equivalent of the observed oxygen consumption was found. The mean nightly rate of oxygen consumption was obtained from the hourly values of oxygen consumed (litre/min.). The thermal equivalent of the observed oxygen consumption (kcal/litre) was multiplied by the mean nightly rate of oxygen consumption to give a rate of heat loss in kcal/min. This heat loss figure was multiplied by 60

(to give kcal/hr) and then divided by the mean weight of the bird in kg. to the exponent 0.74. This was plotted in Figure 23.

It is well established that the metabolic intensity of vertebrates is inversely proportional to body mass i.e. large vertebrates produce less heat per unit mass than do small ones. This relationship is complicated by the fact that it is exponential rather than linear (see King and Farner, 1961, for a detailed review):

$$M = kW^2$$

where M is the metabolic rate in kilocalories per day and W is the body weight in kilograms. The value of the exponent n will be less than 1 as the metabolic intensity decreases with increasing body weight. King and Farner (<u>loc. cit.</u>) derived an equation for birds which gave a good linear correlation between the logarithm of metabolic rate and logarithm of body weight (above about 0.125 kg). The equation is:

$$\log M = \log 74.3 + 0.744 \log W \pm 0.074$$

from which can be extracted the exponent 0.74 (as $0.744 \log W = W^{0.74}$). Consequently in order to allow for differences in the body sizes of the rooks I have used the expression $kg.^{0.74}$ in calculating the rate of heat loss.

<u>Skin and cloacal temperatures</u>: To facilitate the measurement of skin and cloacal temperatures of two nearly-tame 2 year-old hand-reared rooks, a harness was constructed to hold the sensing thermocouples but not to disturb the bird unduly.

The harness, which was light and unobtrusive, was constructed of 7.9 mm. black PVC cable with 2mm. holes every 6mm. along its length. Lengths were run from the head to the tail dorsally and ventrally, and connected with fixing studs to two circles of strapping, one around the neck, and the other around the rump. The birds wore the harness without any sign of discomfort. The thermocouples were easily attached to the birds by threading the sensor through the holes in the harness. In the design of thermocouples for temperatures in the 20-50°C range, it was essential that the potential difference produced should be as large as possible and that the relationship between temperature and potential should be linear.

Several thermocouple alloys and constructions were investigated. The most suitable mode of construction was to remove the enamel from the first cm. of each wire of the different alloys, dip them in diethyl ether and solder together with a low corrosive flux (multicore 362 flux). The metal alloys ultimately employed were thermocouple advance (T.A.) and T.I. alloy (British Driver Harris Ltd.).

The recorder used was a Honeywell Universal Class 15 Electronik Chart recorder with 24 channel input and a range of -1.0 mV to +2.0 mV. This gave a temperature range with the T.A./T.I. thermocouple of 6-56°C (response linear). The accuracy of the recorder was ±0.020 mV. and the sensitivity 0.004 mV. Thus the accuracy of the temperature system was ±0.3°C and the sensitivity ±0.06°C (Specification: T.A. alloy - size 0.0040in, ohms/yd. 54.2, tare 0.195; T.I. alloy - size 0.0048in, ohms/yd. 54.0, tare 0.195). The reference temperature junction was held at 41°C.

A thermocouple was positioned 3 cm. into the cloacal and held in place by a heat-moulded plastic tube (0.1 cm. diameter). A second thermocouple was positioned on the surface of the skin at the dorsal apteria , and attached by a drop of collodion.

Birds were subjected, separately, to an environment which decreased linearly from 20°C to 0°C over a period of four hours. Each bird was tested in the dark, being kept at 20°C for two hours,from civil sunset, and before temperatures were decreased. They were not deprived of food or water prior to experimentation; they were both kept in an outside aviary being brought into the laboratory for instrumentation one hour before testing in experiments which were done in November.

Results

Metabolic data: The relationship between loss of heat and temperature (together with other variables) is shown in Figure 23. A standard analysis of variance could not be used in comparing the different heat loss systems, as the test for homogeneity was negative at the four selected experimental temperatures: 24.0°, 11.5°, 2.5° and -7.5°C (Box and Anderson, 1955). To compensate for the heterogenous population sampling a modified analysis of variance was employed (Welch, 1951).

The nature of these data, having tested square, logarithmic and exponential transformations, suggested a negative logarithmic function, and the regression analysis indicated that this transformation gave the highest r^2 values (Table 15).

Heat loss increased as temperature decreased, particularly in rainy and windy conditions. Moreover when rain and wind acted together hwat loss was more than in any other weather regime.

Specimen trace of oxygen consumption: A typical specimen trace of oxygen consumption at +24°C without wind and rain, and -7.5°C with wind and rain is shown in Figure 24. The same bird was used for both runs. The roosting metabolic rate at -7.5°C with wind (1m/sec) and rain (falling 25 per cent of the length of the run) was about 2½ times more than at +24°C.

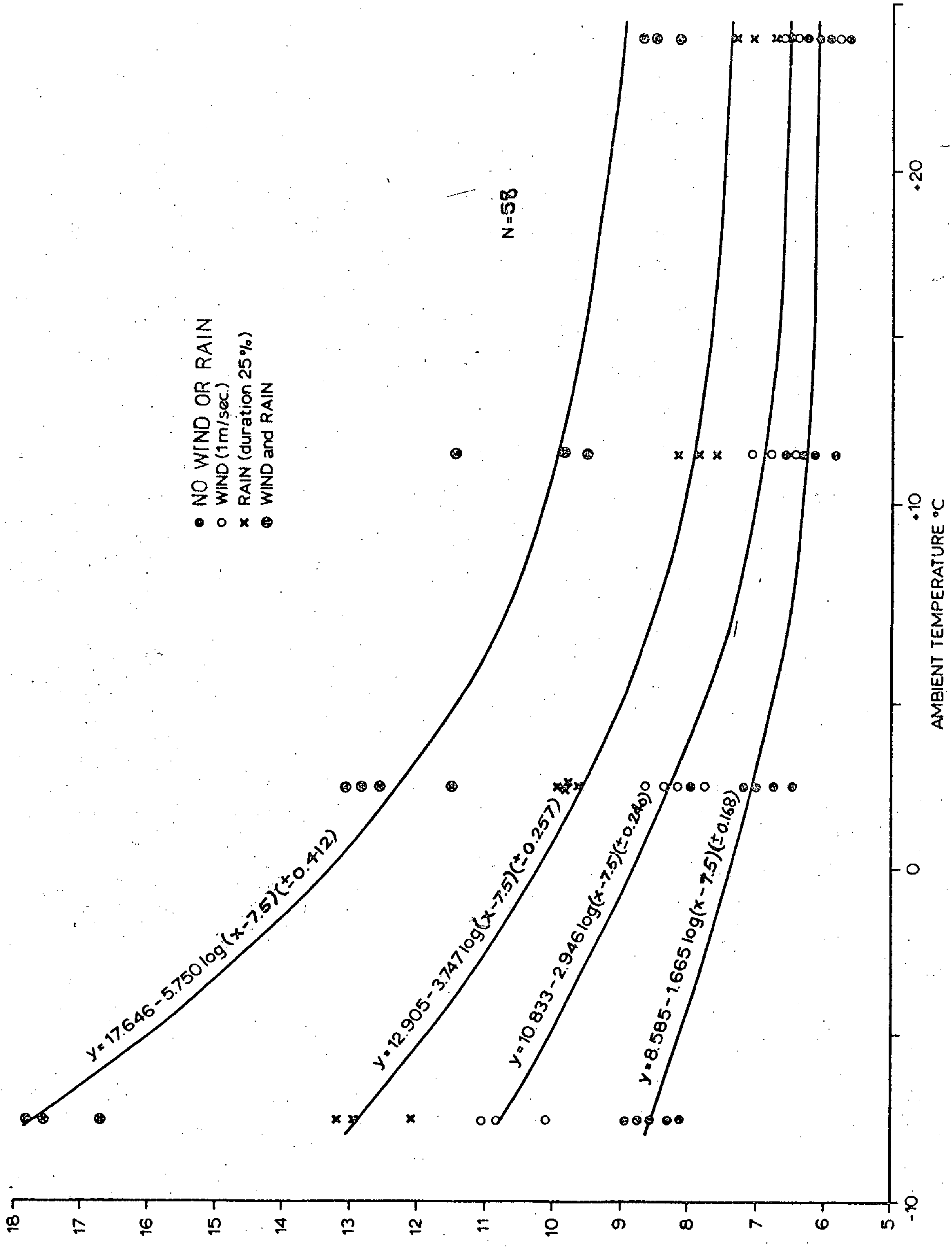


Figure 23. The rate of loss of heat (kcal/kg$^{0.74}$ hr) in relation to ambient temperature for rooks in differing conditions of rain and wind.

TABLE 15

The effects of differing environmental parameters on the mean heat loss of individual rooks

Regime	Mean heat loss (kcal/$kg^{0.74}$/hr. ± S.D.	Regression equation (± standard error of regression coefficient)	Variance explained (r^2)	F value and significance level
Without wind or rain	7.04 ±1.08	Y = 8.585-1.665 log (X-7.5)(±0.168)	0.853	98.8 $P < 0.001$
Wind	8.04 ±1.75	Y = 10.8333-2.946 log(X-7.5)(±0.240)	0.932	150.8 $P < 0.001$
Rain	9.40 ±2.30	Y = 12.905-3.747 log(X-7.5)(±0.251)	0.955	212.2 $P < 0.001$
Rain and wind	12.19 ±3.39	Y = 17.646-5.750 log(X-7.5)(±0.412)	0.947	195.1 $P < 0.001$

NOTE: S.D. = standard deviation; F measures the slope of the regression line and indicates at what level of confidence the slope is significantly greater than zero. (0.1 per cent = P = 0.001)

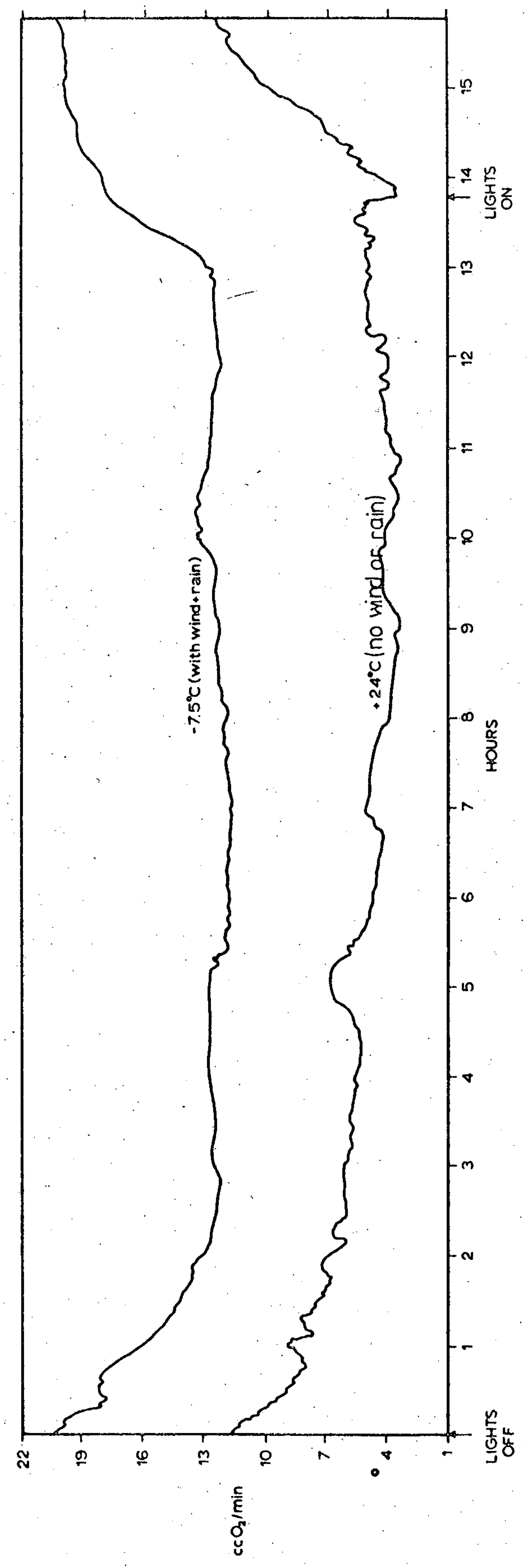


Figure 24. Contrasting oxygen consumption of the same rook when kept at -7.5°C with wind and rain and +24°C without wind and rain.

The stability of the trace is good. It shows that metabolic rate at +24°C without wind and rain reaches its basal roosting level about an hour after the onset of darkness and that it rises after the lights come on in the morning. In contrast, the -7.5°C run shows that the metabolic rate rises before the lights are switched on. (The times of lights-on and -off were the same as civil twilight i.e. the same regime used in the heat loss experiments).

The increase in oxygen consumption rate during light conditions, over that in dark conditions, was by a factor of between 2 and 3.

Social influences on heat loss: Pairs of $\geqslant$ 2 year-old rooks were tested at -7.5°C and +11.5°C under exactly the same conditions as individual birds during February 1972. They were not subject to wind or rain.

Two kinds of pairs were used; a true pair of a male and mate, and two individuals high in the dominance hierarchy but not mated. Each pair was tested on ten nights (i.e. 5 runs at each temperature). The results are presented in Table 16.

The total heat loss of the true pair, when each individual was tested alone, is more than the heat loss when measured in a pair i.e. 16.7: 14.8 (a drop of 11.4 per cent) at -7.5°C and 12.8:11.9 (7.0 per cent drop) at +11.5°C. With the false pair showing a slightly greater heat loss measured individually than together i.e. 17.2:16.0 (7.0 per cent drop) at -7.5°C and 12.2:12.1 (1.2 per drop) at +11.5°C. Although these differences are not statistically significant, a trend is apparent; heat losses are less for a mated pair than for a random pair or single bird.

Temperature data: The skin (dorsal apteria) and cloacal temperatures are shown in Figure 25. The data are plotted for each 6 minutes over the

TABLE 16

Heat loss in true and false pairs of rooks

Status	Identity	Heat loss of both birds. Measured for each individual alone and then summed -7.5°C	Heat loss of both birds measured together -7.5°C	Heat loss of both birds. Measured for each individual alone and then summer +11.5°C	Heat loss of both birds measured together +11.5°C
True Pair	RWH o	16.7 N = 1	14.8 $\pm$ 1.6 N = 5	12.8 N = 1	11.9 $\pm$ 0.8 N = 5
	RRWWLW ♀				
False Pair	Dominant RRRWW o	17.2 N = 1	16.0 $\pm$ 2.3 N = 5	12.2 N = 1	12.1 $\pm$ 0.8 N = 5
	Near-dominant RRWW o				

NOTE: Heat loss measured in kcal/kg $^{0.74}$/hr.; the standard deviation is included in the 4th and last columns and N is the number of runs or nights on which each value is based.

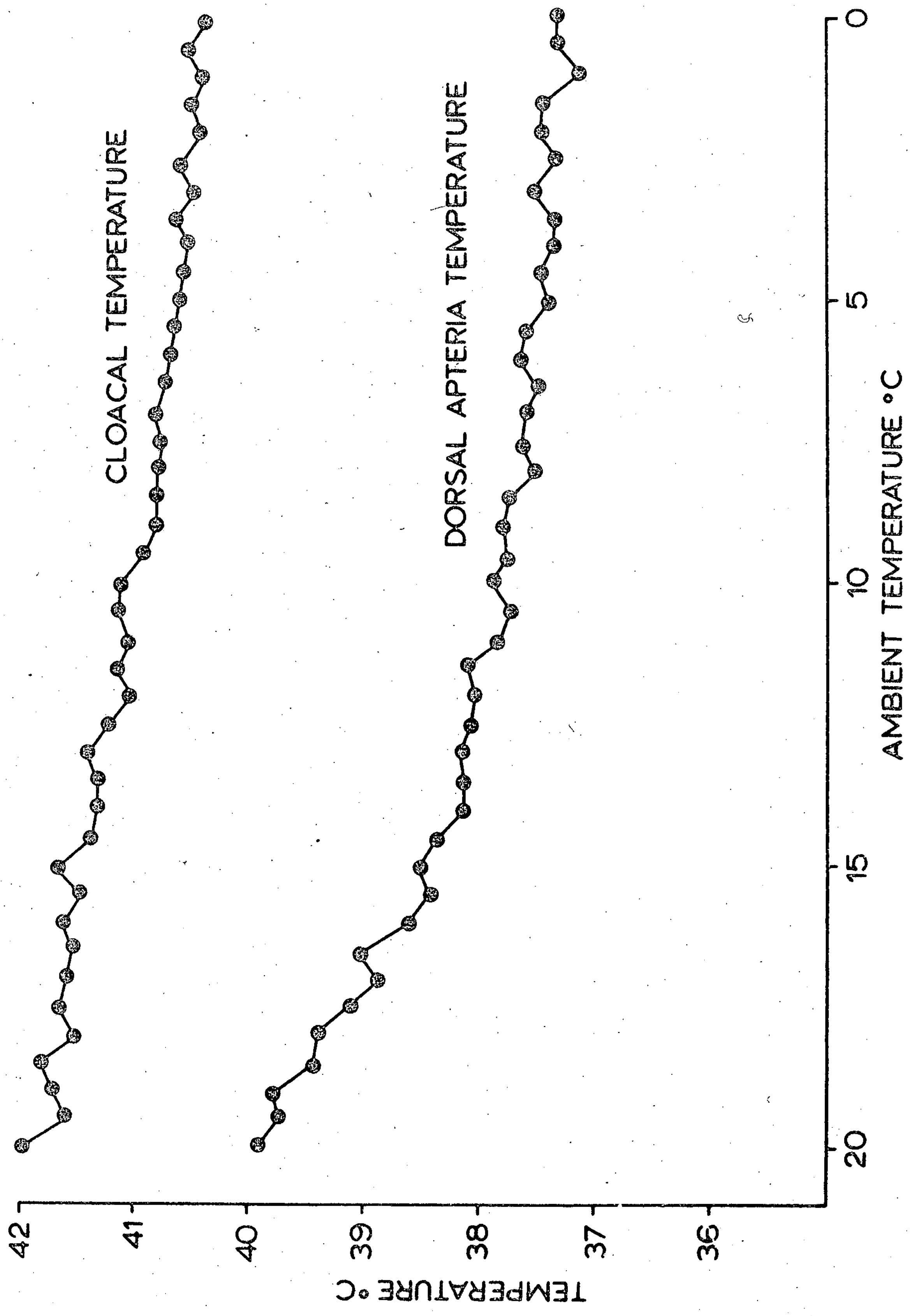


Figure 25. The temperature of the cloacal and dorsal apteria of rooks over a period of four hours when the temperature is reduced from +20°C to 0°C.

experimental period.

There is a greater change in skin temperature than cloacal temperature; the skin temperature changed from 40°C (at 20°C) to 37.4°C (at 0°C) whereas the cloacal temperature changed 1.5°C, from 42°C to 40.5°C.

Discussion

My own results from the rook (Corvus frugilegus) give a metabolic rate of 146.4 kcal/kg$^{0.74}$/24 hr. (see Figure 23) in the thermoneutral zone, during the night at rest, but not under post-absorptive conditions. This figure is similar to that given by Poczopko (1971) who recently recalculated the mean level of metabolic activity for passerine birds from existing data under standard conditions (i.e. physical and psychical rest, in post absorptive state and in thermoneutral surroundings) as 145.60 ± 3.99 kcal/kg $^{0.75}$/24 hr. Some of the data used by Poczopko (loc. cit.) concerned the few pieces of published work on Corvid metabolism.

Irving, Krog & Monson (1955) measured the metabolic rate of the Northwestern crow (Corvus caurinus). They found a standard metabolic rate of 189.64 kcal/kg $^{0.75}$/24 hr. in summer and 235.28 kcal/kg $^{0.75}$/24 hr. in winter. However they only used one captive bird, the tests were performed during the day and the bird was not in a post absorptive condition (although they did measure the R.Q.).

Scholander, Hock, Walters, Johnson & Irving (1950) measured the metabolic rate of two Canada jays (Perisoreus canadensis) during the daytime. They found it was 156.25 kcal/kg $^{0.75}$/24 hr. Veghte (1964) used a step-function experimental procedure to observe ambient temperature effects on metabolism, reducing the temperature from +25°C to -50°C over a period of four hours. He tested the Canada jays during the day and found a metabolic rate of 103.62 kcal/kg $^{0.75}$/24 hr.

Misch (1960) investigating the blue jay (Cyanocitta cristata) found the standard metabolic rate (at night) to be 115.79 kcal/kg $^{0.75}$/24 hr. and Lasiweski and Dawson (1967) examined the white-necked raven (Corvus cryptoleucus) and common raven (Corvus corax) which gave results of 110.49 kcal/kg$^{0.75}$/24 hr. and 105.67 kcal/kg$^{0.75}$/24 hr. respectively.

The fact that the rooks in my study were not initially in a post-absorptive state when their heat loss was being measured, and that no measurement was made of loss of heat by respiratory water, may have influenced the accuracy of the results.

The avian R.Q. and its significance in indirect calorimetry has been reviewed by King and Farner (1961) and more recently by Shannon et al. (1969), who showed that under normal conditions the R.Q. in a fasting bird (uncorrected for protein catabolism) is approximately 0.73. In order to simulate a rook in the wild which would feed before going to roost no birds were fasted before being tested. Many authors (for instance, Mellen & Hill, 1955; Romijn and Lokhorst, 1964; Poczopko, 1969) have reported respiratory quotients lower than 0.70 in fasting birds. Low RQs may be evidence that rooks were in a post-absorptive state by the end of each 15 hr. experimental period.

There is considerable literature concerning the calorigenic effect of food (for reference see Kleiber, 1961). Bladergroen (1955) gives an estimate that the difference between resting and fasting metabolism, when normal mixed diets are eaten, is 8 to 20 per cent. The decrease of metabolic level of the rooks lay in this range.

Loss of heat by respiratory water was not measured in this investigation. However, Salt and Zeuthen (1960) considered that evaporative heat loss was insignificant, because evaporative water loss in temperate climes at low temperatures is negligible.

The experiment concerning true and false pairs of rooks was designed to investigate the heat loss changes that might be induced in an individual by the presence of another rook.

Although the results were not statistically significant a trend in the saving of heat was apparent. The true pair saved more heat (probably through perching close together) than the false pair, particularly at the lower temperature (-7.5°C). However the false pair was expected to lose more heat (proportionally) than a single bird, under similar temperature conditions, because of the socially stressing situation. This did not happen perhaps because in a social species it is better to be with any other bird than alone.

Brenner (1965) considered the oxygen consumption rate of grouped and single starlings. He found the metabolic rate of single birds significantly higher than for birds roosting in pairs or groups of four. Moreover the single and paired birds kept for 6 hours at 2-4°C decreased their body temperature (cloacal) by 2.7° and 3.7°C and their surface temperature (skin) by 5.7° and 4.6°C. respectively. He concluded that as the survival time increased from one day for a bird roosting singly to 3 days for grouped birds at 2-4°C then this adaptive metabolic function had survival value. The temperature changes associated with a rook indicate the insulative changes which occur under thermally stressing situations.

Although the cloacal temperature changed from 42°C to about 40.5°C, the dorsal apteria temperature changed from just under 40°C to 37.4°C (i.e. a drop of 2.6°C) when the ambient temperature dropped from 20° to 0° in four hours. At the same time it was noticed that very extensive fluffing of feathers occurred so that on some occasions the bird resembled a ball, the head being sunk into the shoulders or the beak under the shoulder feathers.

Steen (1958) investigating the metabolism of 6 species of passerine birds found that when exposed to cold during the night, newly-caught birds were found to be unable to maintain their body temperature but they adjusted themselves to a lower one. However cold-acclimated birds showed a normal heat balance and Steen inferred that free-living birds do not normally expose themselves to cold during the night, but rather seek some sort of protective shelter, noctural hypothermia being a "second defence" against abnormally cold-weather. Steen also noticed fluffing into a ball at low temperatures at night. He deduced that this behaviour plus the lowering of body temperature saved 15 to 30 per cent of the metabolic cost over day metabolism.

Irving (1955) measured the depression of body temperature (cloacal) of a roosting magpie (Pica pica) during a 24 hr. period. The ambient temperature was -23.0°C at 9.30 am, -9.0° at 1 pm, -22.0° at 9 pm and -16.0°C at midnight; the magpie body temperature was 42.5° at 9.30 am decreasing to 40.0° at 12.0 pm i.e. a depression of body temperature of 2.4°C. Veghte (1964) studied gray jay body temperature when ambient temperatures were decreased from +20°C to -40°C in four hours. The cloacal temperature fell from 42°C to 40°C and the skin temperature from 40°C to 36°C. He showed that a rise in cloacal temperature occurs before sunrise in winter, in an outdoor aviary, but not in summer. Other species show a similar rise; (cf. rise in metabolic rate before lights on in a rook at -7.5°C with wind and rain in Figure 24). In a primate (Macaca nemstrina), Hoffman *et al* (1969) demonstrated that even very low light levels (6 ft-c. during the day, 0.6 ft-c. at night) are the overriding temperature synchronisers.

The radiant temperature of the sky, when clear, can be considerably colder than the air temperature. Within the experimental procedure used on my rooks no effect of radiant temperature could be simulated. Consequently some comment on the effect of radiant temperature on the heat loss of a bird is necessary.

Lustisk (1969) found radiant energy reduced oxygen consumption more in dark coloured birds than light coloured ones. He cited, as an example, the cowbird (Molothrus a. ater) which by basking can shift the lower end of the thermoneutral zone (i.e. lower critical temperature) down by as much as 10°C. Likewise, Heppner (1970) used white Zebra finches (Poephila castonotis) undyed and dyed black, to demonstrate differential absorption of radiant energy accounting for a 23 per cent metabolic economy of black-dyed over undyed birds. Similarly, Ohmart & Lasiewski (1971) studied sunning in roadrunners (Geococcyx californianus) and found a saving of 41.0 per cent of the standard metabolism. This was a result of skin pigmentation (black) which was exposed by plumage erection.

Stullken & Hiestand's (1953) results indicated that dark hair (i.e. dyed) is disadvantageous to mice at lower temperatures, for control over the loss of heat is less efficient than with white hair due to the greater heat loss. However, these authors ignored the fact that dying light hair does not produce true dark hair as large air spaces are present in light hair but not in dark hair. Their conclusion is therefore suspect. Hardy & Stoll (1954) found that the upper half of an animal's environment when the sky is clear is an important radiant energy sink, since the emissivity of an animal's surface is nearly 1.00. Hammel (1956) found all fur and plumage he studied to have an emissivity indistinguishable from 1.00. No Arctic fauna have apparently acquired a surface of low emissivity. The snowshoe hare (Lepus americanus) may avoid exposure to the sky by taking cover; the musk ox (Ovibos moschatus) and reindeer (Rangifer tarandus) herds forage beneath a cloud of exhaled moisture which acts as a radiation shield. Finally Svihla (1956) concluded that colouration has no effect on the conservation of heat radiation. He could find no difference between white and dark (dyed) coloured rats.

The vertical distribution of radiant temperature within a wood has been discussed in Chapter 3. The influence of roosting position on heat lost by radiation could be considerable.

Having now considered the social organisation, behaviour and weather in a roost, and also measured the rate of heat loss under similar weather conditions, it is important to investigate the effect weather and aggressive encounters over food have on energy replacement (i.e. food consumption). Moreover information on nightly energy reserves is also required. These aspects will be dealt with in the next two Chapters.

CHAPTER 6

A laboratory study of the relationship between food intake and weather.

Introduction

The components of weather, when they act to increase the demand of an animal for energy, can affect the amount of food eaten. In addition, the length of day may affect the amount eaten particularly if the animal is having to search for food for most of the day. The length of the night may also be important in that whatever food has been collected by day, together with the accumulated reserves (of fat and protein) must be sufficient to maintain the animal through the night until it feeds again.

The factors mentioned below are all capable of having an influence, but in the field some are more important than others and they may possibly interact.

This Chapter describes two experiments in which the following independent variables were tested against food intake:

1) the time food was available
2) day length
3) length of the night
4) the minimum and maximum temperature during the day and night
5) the mean wind velocity during day and night
6) the total rain duration during day and night

There is a total of 11 independent variables; see Appendix 8 for summary of weather data.

The dependent variable was the amount of food consumed each day expressed in joules of metabolisable energy per gram of bird present each day (The energy utilisable from wheat grains by poultry is 9405 joules/g; from Biester and Schwarte 1952).

Experiment 1

This investigation was done during October and November 1971 with 29 and 9 periods respectively of continuous 24 hr. monitoring of all the variables. A large outdoor aviary 15m x 3m x 3m was used. The sides of the aviary were boarded with a series of planks 30 cm. wide which were separated from each other by 5 cm. gaps. The roof was made of wire mesh except for a small part at one each which had a solid covering. At this end a one-way window was let into the wall to enable the birds, and an Avery weighing machine, to be readily viewed. The aviary was sited behind the Department of Forestry and Natural Resources, its orientation being west to east. The prevailing wind direction was south-west and blew against the side of the aviary away from the Department building. The sheltered end was at the west end of the aviary.

Twenty birds (mixed adults and juvenile rooks) were kept in the aviary and were given, at approximately 0900 hrs, a bucket (which was put on the Avery) containing about two kg. of wheat (far more than all the birds could possibly need). (Grit and water were freely available) At the same time by observing the reading on the Aviary weighing machine through the window weights of some birds could be obtained as they came to feed (an accuracy of ± 5g. was obtainable). This was done to see if individual birds were losing or gaining weight. At approximately 1700 hrs. the food bucket was removed and the weight of the remaining food recorded.

Only part of the aviary is exposed to rain and wind, the small covered part at one end effectively shields any bird perching there. However, during this experiment some birds were exposed to these weather variables, as perching space in the sheltered part was limited and there was a relatively large number of birds in the aviary.

During the progress of this investigation ten birds lost weight. They were removed from the aviary immediately any indication of a sustained loss in weight was observed. Table 17 indicates the hierarchy position (measured in the preceding Chapter 4), the order of removal, the date of removal, the identity, the age, the weight at the beginning of Experiment 1, the weight on removal and the percentage loss in weight. (The percentage loss in weight of the first bird probably results from losing most of its weight before the experiment began.)

Although food was always abundant during the hours of daylight, the food bucket was frequently unattended by birds, not even by subordinates whom, one would expect to take any opportunity to obtain food. There was a close relationship between loss in weight of individual birds and hierarchical position. The first bird to be removed from the aviary only lost 1.6% of its initial weight. As all twenty birds had been kept together before this experiment started the influence of the hierarchy operating under circumstances of localised food was already apparent. Age and weight also seem to be related to the order of removal of individuals from the aviary i.e. from young to adult and from low in weight to high.

At the end of Experiment 1, ten birds remained in the aviary. Table 18 describes their identity, age, hierarchy position, weight at the beginning of the experiment and their weight on conclusion of the experiment.

There was an insignificant change in weight in individuals between the beginning and the end of the experiment. Bird RRWX lost 3.2 per cent of its initial weight and RRWW 3.3 per cent; the remainder either lost or

TABLE 17

Hierarchy position and weights of birds removed during Experiment 1.

Hierarchy position	Order of removal	Date of removal	Identity	Age	Weight 29/9 (g)	Weight (g) on removal	% loss in weight
18	1	29/9	RRRR ♀	< 1	186	183	1.6
17	2	7/10	RLWW ♀	< 1	327	188	42.5
16	3	8/10	RLRWRB ♂	< 1	365	209	43.8
4	4	12/10	RLRW ♂	<2	370	253	31.6
15	5	13/10	RLRRW ♂	<2	383	220	42.5
11	5	13/10	RRB ♂	<2	400	263	34.2
12	6	24/10	RLRR ♀	$\geqslant 2$	393	217	44.8
10	7	8/11	R ♂	$\geqslant 2$	500	282	43.6
19	8	11/11	RLW ♀	$\geqslant 2$	450	244	45.8
3	8	11/11	RRBRB ♂	$\geqslant 2$	532	278	47.7

Note: the lower the hierarchy position number, the more dominant the individual e.g. 3 is dominant to 4.

TABLE 18

Hierarchy position and weights of birds remaining at the conclusion of Experiment 1.

Identity		Age	Hierarchy position	Weight 29/9(g.)	Weight 11/11(g.)	% change in weight
RWH	♂	⩾2	1	492	500	1.6
RRRWW	♂	⩾2	2	425	428	0.7
RRWW	♂	⩾2	5	486	470	3.3
RLRB	♀	⩾2	6	425	430	1.2
RWX	♂	< 2	7	470	471	0.2
RLR	♀	< 2	8	361	358	0.8
RRWWLW	♀	⩾2	9	365	370	1.4
RRBB	♂	< 1	13	364	362	0.5
RLBBB	♂	< 1	14	388	390	0.5
RRWX	♀	< 2	20	372	360	3.2

gained less than 2.0 per cent of the initial weight.

Although the situation which developed was not intentional, several birds succumbed even though they were removed immediately to a warm indoor aviary, free from interactions with other birds, and with ample food and water.

For some reason, which will be discussed later in this Chapter, these birds did not feed from the food bowls in the warm aviary, although the aviary was familiar to them. Subsequently their condition deteriorated and death followed. On post-mortem examination, death appears to have been through starvation.

The conclusion is that the birds must have developed some irreversible inhibition to feeding. The birds which died did so within 72 hours of their removal from the aviary.

The weather data were mainly extracted from the records of the Turnhouse Airport Meteorological Station (11.5 km. NW of the aviary site). These were:

1) the mean wind velocity during the night before (m/sec.) and during the day
2) the total rainfall duration during the night before (in 1/10 hr.) and during the day.

The temperature data were read twice daily from a max./min. thermometer in the aviary - when (a) the food was put in (night max./min.) and (b) taken out (day max./min.) each day.

The day length and length of night were taken from Brown's Nautical Almanac 1971, 1972. The times at which the weather variables were labelled as day or night and food put in, or taken out, of the aviary was determined as near as possible by the civil twilight (sunset and sunrise).

Because the only available continuous records of wind and rain were taken from instruments sited at Turnhouse Airport spot checks of the wind velocity inside the aviary were made. They compared well with the Turnhouse data in terms of variation (which is the important factor in the following analyses) but not quite so well in magnitude. The sides of the aviary although permeable to wind, cut the velocity by between 20-40 per cent depending on wind direction. Rain duration compared well, particularly as most rain was associated with a westerly wind which would pass from Turnhouse towards the aviary site (see Appendix 8 for weather data used in this Chapter).

Method

The data were analysed using stepwise multiple regressions (see Appendix 5 for a full explanation of the technique).

As a result of dividing the weather variables into those operating at night and those operating during the day, the highly significant correlations (Pearson product-moment correlations) existing between the weather variables was somewhat reduced. Consequently interpretation of the analyses was less difficult than in Chapter 3, where the variables were significantly correlated.

The most influential variable in determining food consumption is that nearest to the vertical axis of each Figure i.e. to the left of each histogram (e.g. Figure 26). A greater proportion of the variance is attributable to this factor than to any one other and it is also the first variable entered by the technique into the equation. Among the other variables no one can be termed more or less important as the order and contribution of each one is greatly affected by those already in the equation; they make a group contribution to the total variance explained in the dependent variable (i.e. food consumed) by all variables in the analysis. Some blocks of each histogram are unlabelled as the variable, or variables, represented by that block contribute less than 5 per cent of the total variance explained.

Results

The time food was available was the most important factor influencing the amounts of food eaten during October (Figure 26). In November the time food was available was less important when the weather variables became more influential.

Why were the amounts of food taken in, influenced more by weather in November than in October, with a corresponding diminuition in the influence of the time food was available? Eight birds were removed from the aviary during October leaving twelve birds throughout November.

An analysis of the difference in effect of night and day weather variables (excluding time food available) in determining food consumption showed that the minimum temperature during the day was influential in both months (Figure 27). However, weather had much more effect in November, than October, on the food eaten. In November the minimum temperature during the day replaced the former place of the time food was available. This occurred because the time food available explained slightly more of the variance than the minimum temperature during the day and it was only by deliberately excluding the former variable from the analysis that the weather variable appeared.

Conclusions

The amount of time food was available was effective in determining

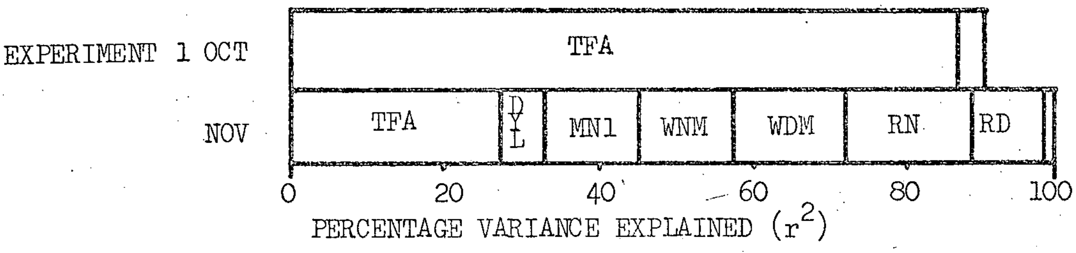


Figure 26. Relative importance in aviary experiments of factors influencing food consumed by 20 rooks in October and 13 rooks in November.

Note: the variable next to the vertical axis is the most influential (see text).

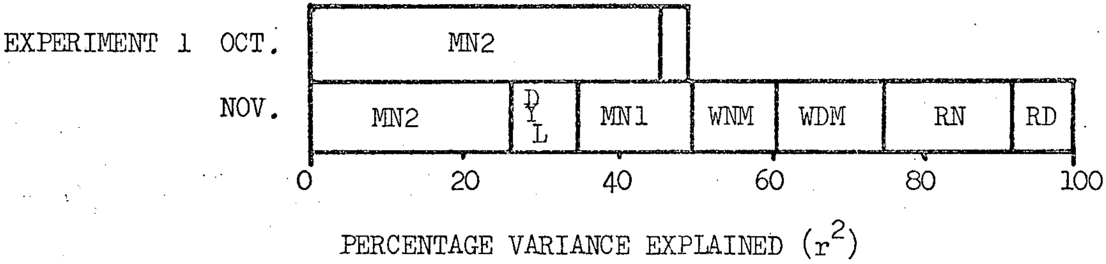


Figure 27. Re-analysis of the relative importance of differing factors influencing food consumed having first excluded the effect of the time food was available.

Note: the variable next to the vertical axis is the most influential (see text).

Key:

TFA	TIME FOOD AVAILABLE (hr.)
MN1	MINIMUM TEMPERATURE AT NIGHT (°C)
MN2	MINIMUM TEMPERATURE DURING THE DAY (°C)
WNM	MEAN WIND VELOCITY AT NIGHT (m/sec)
WDM	MEAN WIND VELOCITY DURING THE DAY (m/sec)
RD	TOTAL RAIN DURATION DURING THE DAY (in 1/10 hr.)
RN	TOTAL RAIN DURATION AT NIGHT (in 1/10 hr.)
DYL	DAYLENGTH (hr.)

food energy consumed. Nevertheless, even in such circumstances the minimum temperature during the day also affected the amount of food eaten.

Weather variables alone can explain a large proportion of the variance in the amount of food consumed (in joules of metabolisable energy) per bird gram.

During the experimental period the lighter more subordinate birds within each age group lost weight and showed inhibited feeding behaviour. The occurrence of this type of behaviour may have increased the importance of the time food was available in relation to food consumption. In November (by which time seven of the total number of twenty birds had been removed from the aviary) the influence of the weather variables was greater than in October.

Discussion of Experiment 1

In this experiment several subordinate individuals lost weight in the presence of excess food presumably by some form of interaction between dominants and subordinates at the localised food source; and died after removal from the aviary. However as the number of birds present in the flight was reduced, the rate at which birds had to be removed (because of a large weight-loss) decreased. Consequentially, I suggest that initially there were too many birds in the flight. By 'too many' I mean that each bird did not have sufficient time, because of interference by other birds, to feed adequately when only one food bucket was provided. By providing food only during the daylight hours the strong influence of the time the food bucket was in the flight on the amount of food consumed became apparent.

What seems important in this experiment is that with a large number of birds feeding at a localised source, the time available for feeding is far more important than weather variables in affecting food consumption. Additionally as the number of birds decreased (i.e. by November) the influence of weather on food consumption increased, and the influence of the time available for feeding decreased.

This suggests that interactions between birds at a feeding source is the form of competition in which some individuals get too little food for their needs. Petrusewicz (1966) found in a captive white mouse population (where mortality was high) that a reduction of food intake per head can be indicative of competition for food at localised sources. In this study on captive rooks and jackdaws the youngest and most subordinate individuals lost weight first. However, members of all three age groups succumbed, usually the least heavy individuals. This is particularly so in the first- and second-year birds, but the adults (i.e. ⩾ 2 years old) seemed to die regardless of their initial weight.

In the field situation Murton, Isaacson & Westwood (1966) and Murton (1968) measured the feeding rate of wood pigeons (Columba palumbus) and the amount of food available. Birds at the front of the moving flock fed less and they suggested that these were individuals of low status. Recently the same authors (1971) studied the feeding behaviour of wood pigeons from January to March. Underweight adults survived as well as normal adults; first year birds survived less well, especially those that were underweight. Although outside their study area survival was related to weight and was independent of age, they suggested that inexperienced, subordinate birds copy the movements of experienced birds at a food supply in order to maximise feeding efficiency, and the thwarting of the ability to achieve a satisfactory feeding behaviour is the reason for the stress situation.

In wild rooks Lockie (1956) argued that when food is short, a social hierarchy acting selectively operates to allow few animals to starve (those low in the hierarchy) while the remained subsist at an "adequate" level of nutrition. Senile and young deer are the first to die during starvation periods (North American elk (Cervus canadensis) Banfield 1949; Mule deer (Odocoileus h. hemionus) Leopold et al. 1951, Leopold & Darling 1953).

Apart from the contributions of Murton et al. (1971) and Lockie (1956), who had to make important assumptions, there are few indisputable records indicating that subdominant birds are prevented by dominants from feeding in the wild. Myers & Poole (1963) suggested in an unfenced population of rabbits that subdominants would emigrate into unfavourable habitats (where they would die) before catastrophic starvation set in. Less dominant individuals in the Australian magpie (Gymnorhina tibicen) (Carrick 1963) and red grouse (Lagopus lagopus) (Watson & Moss 1971) have access to food; in red grouse those which do not get territories are often excluded from the heather moor and are forced to live on grassy stream-sides unsuitable for grouse. Ashmole (1963) and Carrick et al. (1962) suggested that subdominant sea birds and elephant seals (Mirounga leonina L.) may be excluded from good feeding grounds within easy reach of their colonies, by the competition of more dominant individuals.

Although subdominants are possibly not excluded from food in the wild most of the time, they may be prevented from feeding at critical periods. Hardy (1961) studied another Corvid (Cyanocitta cristata) and found first-year birds emigrated in autumn and winter. Dunnet et al. (1969) also suggested that young (i.e. subdominant) rooks may emigrate at this time of year. It is uncertain whether the first year birds in these instances are expelled by adults or not; presumably there is survival value in so doing.

Most of the work reported in the literature seems either to examine the effect of competition or temperature or daylength or some single variable on food consumption. Nobody to my knowledge has studied the influence of interactions between birds and weather, simultaneously, consequently discussion is necessarily limited. It does appear that my findings concur with those of other workers on captive animal populations and that, in particular, my results do not conflict with those few field studies on the social hierarchy of birds and their food intake.

As a result of the presumed competition for food in this experiment some birds showed an inhibited feeding behaviour. The low-rank rooks showed this abnormal behaviour, subsequently leaving the vacant food source unattended even when no dominants were present. Calhoun (1963) noticed the same behaviour in brown rats (Rattus norvegicus) where low weight, induced by previous aggression by other rats during early life, can cause individuals less readily to "achieve priority in goals" during adult life. Strangely, subordinate rooks would immediately approach the food bucket, should another rook start to feed. Calhoun (1961, 1962) found that the inclination to feed at one food source, and neglecting others, induced an unstable social system in brown rats.

It may be that this 'fear' of the food bucket (unless other birds were there) was induced by a connection between proximity to the bucket an an inevitable interaction with a dominant bird and consequent rebuttal. It seems that a subordinate bird would rather not get near the bucket and thus forego feeding than be involved in an interaction which it would probably have to retreat from anyway.

Localisation of food sources infers that the search for food must intensify and that the time available for feeding becomes important in determining the amount of food consumed. Newton (1969) found that wild bullfinches (Pyrrhula pyrrhula nesa L.) at no time, could have survived a daylong fast and consequently the length of time available for food searching each day was critical. Evans (1969) also concluded in wild yellow buntings (Emberiza citrinella L.) that daylength, acting through temperature, influenced feeding and thus fat deposition. Only when inhibited feeding behaviour by subordinates was seen did the time available for feeding become important.

The time food was available was important during Experiment 1 and the minimum daily temperature was the next most important influence on food intake. In Chapter 2 it was seen that light intensity (in relation to the time) determined the length of the rooks' feeding day. Light intensity and cloud cover are closely related, as are minimum daily temperature and cloud cover, thus a link between minimum daily temperature and amount of time for feeding can be made through light intensity.

Experiment 2

This was a continuation of Experiment 1 with a pair of adult birds, instead of ten to twenty birds, and in which food was available night and day. This experiment was done during December, January and February, observations being made on 23, 27 and 8 unbroken 24 hrs. 'runs' respectively. The same variables as in Experiment 1 were measured or calculated with the exception of the time food was available which was no longer relevant.

In this experiment, during which the weight of the birds did not change by more than ± 2 per cent, the birds could get out of the wind and rain by sheltering in the covered part of the aviary. The food was put in the exposed part of the flight and so in order to feed, the birds exposed themselves to the weather; conversely should they wish to avoid the rain or wind they could not feed. During the night, both wind and rain would have a reduced influence because the pair would roost in the sheltered end.

The data were analysed by the methods used in Experiment 1.

Results

The influence of weather variables on food consumption in all three months was large (i.e. the total variance explained was above 0.700).

Daytime weather variables were more important in determining food consumption each month than night weather variables (Figure 28). This is understandable since the birds could shelter at night. In December and January the minimum temperature during the day was the most effective weather variable. The daylength, which is another measure of time available for feeding, was not significant, as expected, because of the much reduced number of birds. During February the amount of food consumed was appreciably influenced by rain duration during the day (Figure 28). This departure from the results of December and January (i.e. the importance of the minimum daily temperature) may be because of a change in the birds' behaviour with the onset of breeding.

Conclusions

The minimum temperature during the day is the most influential variable and night weather variables are secondary in their effectiveness to daytime weather variables in determining food energy consumed.

I cannot explain why rainfall duration during the day became the most influential variable, and minimum temperature during the day became of lesser importance, in February. However, the daily behaviour of the birds

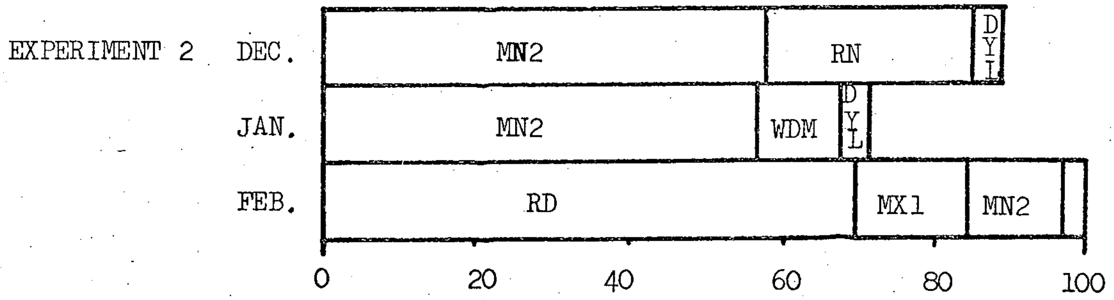


Figure 28. Relative importance in aviary experiments of factors influencing food consumed by a pair of adult rooks.

Note: the variable next to the vertical axis is the most influential (see text).

KEY:

MN2	MINIMUM TEMPERATURE DURING THE DAY (°C)
MX1	MAXIMUM TEMPERATURE AT NIGHT (°C)
WDM	MEAN WIND VELOCITY DURING THE DAY (m/sec)
RD	TOTAL RAIN DURATION DURING THE DAY (in 1/10 hr.)
RN	TOTAL RAIN DURATION AT NIGHT (in 1/10 hr.)
DYL	DAYLENGTH (hr.)

may have changed (e.g. the onset of more intense breeding behaviour) and increased their exposure to rain.

Discussion of Experiment 2

In captivity rooks and jackdaws were strongly affected in their food demand by the minimum daily temperature. An explanation for this may lie in the fact that the air layer close to the body is more mobile during the muscular exercise of the day and tends to decrease the ability to withstand cold. Kendeigh et al. (1969) appeared to contradict earlier work (Kendeigh 1934) by finding in captive house sparrows (Passer domesticus) and in captive white-throated sparrows (Zonotrichia albicollis) that weight-loss at night and temperature during the daytime varied the stimulus for feeding and thus the mean weight of the bird.

Giaja (1931) pointed out that the heat production connected with muscular work is always added to the resting metabolism regardless of ambient temperature. If this view is correct then energy reserves would be used faster during work, than during roosting, in the cold. Wallgren (1954) stated that thermoregulation soon breaks down and body temperature begins to drop during work in severe cold: an identical temperature may be endured for a considerable time by the organism at rest.

Wallgren (loc. cit.) concluded that the disappearance of the house sparrows during winter from some districts in Northern Finland were a result of the minimum day-time temperature. Moreover, the same author observed the importance of length of night and mean temperature at night in the yellow bunting (Emeriza citrinella) when considering its winter range. Nevertheless he considered that where food was available the range was extended. In the ortolan bunting (Emberiza hortulana) he found that rain, temperature and photo-period were the most important factors determining its winter range. It is worth noting that the yellow buntings roost in winter near the ground in dense shrubberies of small spruces sometimes covered by snow: this Wallgren (loc. cit.) considered would enable the bird to survive cold nights. Conversely, he noticed the ortolan (which is more sensitive to cold than the yellow bunting) roosting in open fields, which when covered by snow, would appear to be exposed to wind and cold. He offered no explanation for this apparent anomaly.

West (1968) found a relationship in captive willow ptarmigans (Lagopus lagopus) between day temperature and metabolised energy requirements in winter. He also found that day length was important, although in my study day length was only slightly effective in altering food consumption in a situation where it is unreasonable to think that there could be competition.

It seems that low day temperatures induce a greater demand for food. But low temperatures per se and the snow that often accompanies them also makes food less available (e.g. in rooks, Lockie 1956; Bull & Dawson 1969) and more localised (e.g. in starlings, Dunnet 1956; Hilden & Koskimies 1969), thus perhaps intensifying the difficulty of food collection for all or part of the population.

The influence of the social hierarchy in determining the social organisation of a communal roost has been demonstrated already (Chapter 3 and 4). The influence of temperature, rain, and wind on heat loss has been discussed and measured (Chapter 5).

Weather has a strong influence on the amount of food consumed. In particular, the minimum temperature during the day has the most effect. Furthermore when food demand increases (through the direct influence of the weather parameters measured in this Chapter) or when food availability decreases (possibly through the effect of severe weather or through some other agent) the influence of the social hierarchy seems to be increased, affecting subordinates disproportionately.

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CHAPTER 7

Body composition of rooks at the roost

Introduction

From the previous Chapters, information is available to make it possible to estimate amounts of heat lost by individual rooks in a communal roost.

Nevertheless, in terms of the survival of a bird in a communal roost, knowledge of heat loss is not enough; it needs to be supplemented with an understanding of the bird's energy reserves described in the following pages.

Methods

A total of thirty birds were shot (under licence from the Nature Conservancy) on four nights in December and February of 1970/71 and 1971/72, as they came to roost at Stevenson Wood, East Lothian; either a silenced .22 rifle or an automatic shotgun was used.

The birds were weighed and placed in polythene bags for later laboratory analyses when each bird was age as first-year or older by facial bareness, and sexed by dissection. Wing length (from carpal joint to the tip of the longest primary) was measured (± 0.1 cm). Carcasses were plucked and the plumage weighed; stored food was removed from the gullet and gizzard. After each plucked carcass had been minced five times, the resultant material was placed in an aluminium dish. Five samples were taken from different parts of the dish, using a 2 cm. diameter cork-borer. The samples were tested statistically (Box and Anderson 1955) and were homogeneous for their content of water, fat and lean dry weight. Finally the samples were analysed for water, fat and lean dry material by the method of Odum (1960), with petroleum ether as the fat solvent. This method of fat extraction is well established and widely used; it consists of refluxing the ether in a Soxhlet apparatus containing the dried sample of the bird carcass until all the soluble fat is removed. The weight of the sample residue is the lean dry weight.

Results

The total weight of each bird was divided into weights of (a) plumage, (b) undigested food stored in gullet and gizzard, (c) fat, (d) water and (e) lean dry material (mainly composed of muscle, protein and skeleton).

Some index of body size was required in order to make data from birds of different sizes comparable. The following were considered: wing length, bill length, and the tarso-metatarsal length. Wing length was rejected because young rooks had shorter wings than adults of the same sex (Table 19) as a result of the difference in wear of the primary feathers.

Bill length and tarso-metatarsal length were also rejected as size indicators. The bill in some of the sample carcasses was deformed and the tarso-metatarsal length could not be measured accurately.

Another possible measure of body size is lean dry weight. However, in order for it to be a suitable index for body size it must not vary appreciably during the winter. Young and adult rooks were separately sampled on a total of 4 occasions during the winters of 1970/71 and 1971/72 (Tables 20 and 21 respectively).

Within the groups of young and adult rooks no significant difference (i.e. $t < 2.5$, $P > 0.05$; see Appendix 4 for statistics) could be found between the lean dry weights on different dates, or between the total "live" weights. It was therefore assumed that there was a negligible

TABLE 19

Effects of age and sex on the mean wing lengths of rooks.

	Females		Males	
	Young	Adult	Young	Adult
Wing length (cm)	28.3 ± 1.4	29.7 ± 0.7	29.5 ± 1.9	30.7 ± 0.5

Figures are mean ± standard error of mean.

TABLE 20

The total "live" weights and lean dry weights of adult rooks.

Date	Number of birds	Lean dry weight (without plumage)	Total "live" weight
18 December 1970	1	126.0	520
1 February 1971	4	130.1 ± 1.6	543 ± 6.4
18 December 1971	4	129.0 ± 1.0	523 ± 8.3
1 February 1972	7	125.1 ± 0.5	519 ± 4.1

Weights (g.) are mean ± standard error of mean.

TABLE 21

The total "live" weights and lean dry weights of young rooks.

Date	Number of birds	Lean dry weight (without plumage)	Total "live" weight
18 December 1970	3	120.1 ± 1.8	492 ± 6.4
1 February 1971	2	124.3 ± 1.0	500 ± 8.0
18 December 1971	5	120.7 ± 1.1	485 ± 12.8
1 February 1972	4	120.1 ± 2.1	460 ± 19.1

Weights (g.) are mean ± standard error of mean.

change in lean dry weight of an individual throughout the winter. In contrast, Newton & Evans (1966) and Newton (1969) found the lean dry weight in bullfinches (Pyrrhula pyrrhula L.) reached a peak in midwinter although Evans (1969) studying yellow buntings (Emberiza citrinella L.) did not. Lockie (1954, in thesis) found that the rook increased in weight, reaching a peak in winter. Presumably the degree of change in lean dry weight varies from year to year although it remained the same in my samples and its use as a body size index was therefore considered justifiable. (Protein, a major constituent of lean dry weight, is continually used by a bird but as it is also being continually replaced (providing the bird is not starving - which they were not in this study see Table 22) it is thought that a constant level is normally maintained.)

The purpose of this study is to use the figures on fat and stored food to estimate survival times of roosting rooks (see Chapter 8). The amounts of fat and stored food in young and adult rooks which are shown in Table 22 indicate that adult birds had twice as much fat and more stored food than the young birds.

Although the mean total weights of adult and young birds showed only negligible differences in weight through the winter I found (like Evans 1969) considerable variation in several body components (which, henceforth, will be expressed as percentages by weight of the lean dry weight without plumage) of rooks.

The body composition of 30 rooks shot at the roost are shown in Table 23. The fat content of adult rooks is consistently higher (about twice as much) than in young rooks. Within each age group water and fat contents paralleled each other (i.e. significantly positively correlated); for young rook, df = 12, $r = 0.673$, $P < 0.01$ and for adult rooks, df = 14,

TABLE 22

The mean amounts of fat and stored food in young and adult rooks at the roost.

Date	No. of birds	Age	Weight of fat	Weight of stored food
18 December 1970	3	Y	32.3 ± 1.6	11.2 ± 2.7
	1	A	63.0	15.8
1 February 1971	2	Y	35.3 ± 1.1	12.2 ± 1.8
	4	A	81.4 ± 3.2	17.8 ± 1.4
18 December 1971	5	Y	29.3 ± 0.7	12.0 ± 1.4
	4	A	72.7 ± 1.8	18.1 ± 1.1
1 February 1972	4	Y	24.1 ± 3.8	9.8 ± 5.7
	7	A	58.0 ± 1.7	13.4 ± 1.0

Weights (g.) are mean ± standard error of mean.

A = Adult, Y = 1 year-old.

TABLE 23

Body composition of rooks in December & February 1970/71 and 1971/72

Date	No. of birds		Age Y = 1 year-old A = older	% of lean dry weight (without plumage)			
				Fat content	Stored food	Water content	Plumage
18 December 1970	4	3	Y	26.9 ± 0.9	9.3 ± 1.5	202.1 ± 2.8	3.4 ± 0.4
		1	A	50.1	12.5	190.4	3.0
1 February 1971	6	2	Y	28.4 ± 1.1	9.8 ± 1.8	212.4 ± 2.9	3.8 ± 0.5
		4	A	62.6 ± 2.0	13.7 ± 1.4	220.4 ± 3.0	4.2 ± 0.6
18 December 1971	9	5	Y	24.3 ± 0.7	10.0 ± 1.3	193.7 ± 1.9	3.6 ± 0.5
		4	A	56.4 ± 1.8	14.0 ± 1.1	202.9 ± 3.1	4.1 ± 0.5
1 February 1972	11	4	Y	20.1 ± 1.8	8.1 ± 2.7	180.0 ± 2.0	3.9 ± 0.3
		7	A	46.4 ± 3.4	10.7 ± 2.0	177.4 ± 1.4	4.2 ± 0.2

Figures are mean ± standard error of mean.

$r = 0.705$, $P < 0.01$. On 3 of the 4 sampling occasions the stored food in young rooks represents 9.0-10.0 per cent of the lean dry weight whereas in adult rooks this percentage is 12.5-14.0 per cent. In contrast, in the last sample taken in February 1972 the young rooks had 8.9 per cent of the lean dry weight in stored food and the adults 10.7 per cent, both percentages below the previous figures.

The main natural food of the rooks sampled in this study was found to be wheat grains (cf. Dunnet and Patterson, 1968). The average weight of stored food was slightly lower in February 1972 than in the other samples, although there was no significant difference from the other samples.

Variation in weights of plumage are not significant.

Discussion

Although the purpose of this Chapter was simply to measure the proportion of fat and stored food in rooks going to roost, several features arising from the existing literature are relevant. What do birds use as an energy substrate during different times of the day or night and what affects the levels of these energy reserves?

Investigations into fat content in birds has been conducted by many authors. Newton (1969) showed in wild bullfinches (Pyrrhula pyrrhula nesa L.) that extra fat was deposited on cold days in December and January and he suggested that this occurred through increased digestive efficiency and also an increase in food intake. He believed that food eaten during a winter day was primarily used to replace the fat store (an overnight energy reserve) and to sustain the bird during the day. In contrast, Ward (1969) could find no seasonal variation in the fat reserves of the yellow-vented bulbul (Pycnonotus goiavier), sufficient fat was accumulated each day to last through the night with a slight excess; but outside the breeding season many birds had insufficient fat for the night, suggesting a food shortage.

Pinowski and Myrcha (1970), in studying the tree sparrow (Passer m.montanus L.), could find no correlation between fat content and temperature on the day of capture or the preceding day, and a slight correlation could be demonstrated with temperatures, two, three and five days earlier. They found that changes in body weight in winter resulted mainly from changes in water content, and much less from lean weight or fat. They concluded, like Newton (loc. cit.), that fat reserves would not have supplied energy requirements for more than 24 hours without feeding.

In comparison with Pinowski and Myrcha (loc. cit.), Evans (1969) found, in the yellow bunting (Emberiza citrinella L.), that the mean fat reserve carried by the birds on a given date was correlated neither with temperatures during the preceding days, nor with the duration of obligatory roosting, but instead was strongly correlated with the long-term average temperature to be expected at that date. Moreover he calculated that the mean total energy reserves (fat plus food) carried by the birds as they entered the roost were higher than the energy requirements on each of the nine nights studied.

It has commonly been assumed that weight lost at the end of a period of stress consists wholly of fat. But, as Benedict and Lee (1937) indicated, the presence of large amounts of fat in the body does not mean that the animal cannot starve. Indeed the opposite is true.

Hanson (1962) noted when dissecting geese which had been wintering under conditions of food shortage, that even very thin geese usually possessed moderate stores of fat. When glycogen reserves are depleted (in geese they last about 24 hours, Benedict & Lee, loc. cit.) the fat stores are drawn upon. However, in order to utilise the fat, in the absence of glycogen, the protein reserves must also be available.

Hanson (loc. cit.) stated that geese in good condition must have near-maximum protein (i.e. muscle tissue) reserves in addition to considerable amounts of depot fat. He noted four "conditions" in Canada geese (Branta canadensis) induced by various stresses, one of these conditions being minimum protein reserves and moderate fat reserves. He found that this condition in wintering geese was associated with starvation during a period of excessive cold and snowfall.

Thus the extent of use of fat reserves may depend on the extent of the protein reserve, since both must be degraded simultaneously when glycogen is not available. In consequence, passerines with limited food intake and very low glycogen reserves will perforce use protein to metabolise fat during a winter roosting night. Thus, ultimately, it is not the amount of fat which limits a bird's energy reserves under thermally-stressing conditions, but the amount of protein.

Any calculation of percentage survival among populations of roosting birds calculated using figures for the metabolic rate, and fat and food reserves, must be based on an awareness that fat reserves alone do not determine whether a bird will survive. In all probability such calculations may over-estimate the number of individuals with sufficient reserves. Brenner and Malin (1965), Brenner (1965) and Evans (1969) have all used fat, food reserves and metabolic rates to determine survival rates and percentages. Morrison (1960) pointed out that reserve energy available to animals is dependent on the body weight (i.e. fat: protein) and Kuenzel and Helms (1967) found in white-throated sparrows (Z. albicollis) that the limit to fat deposition is fixed by the number of fat cells which can be filled. Moreover, Barnett (1970) found house sparrows (P. domesticus) were significantly fatter, and the fatty acids more unsaturated (i.e. more easy to break-down), in the winter than in the summer. Cold-stressed sparrows still have some fat reserves at death, but had lost significant amounts of protein.

CHAPTER 8

Synthesis

At the beginning of this study two questions were posed: Is heat loss affected by the behaviour of birds in the roost,and are losses of energy reserves occurring in the roost important in relation to survival? As might be expected these questions cannot be answered simply because different sections of the population behave differently being exposed to different conditions. The most obvious difference is between young and old. Young birds have smaller fat reserves than adults and slightly less food reserves on entering the roost and they have to take what are perhaps poorer roosting places.

Adult rooks roost in the topmost parts of trees whereas the young are lower down. If the adults descend (as they do in heavy rain) the young are forced still further down the tree. Under extremely stressing conditions the adults, followed possibly by the young rooks and the jackdaws, may move across the wood from tree to tree. These horizontal movements seem to be dictated and orientated primarily in relation to wind direction. Aggressive encounters increase in those places where birds accumulate and adult birds will be successful in displacing young birds.

Viewed horizontally the climate of the roost is by no means uniform there being a windy side and a less windy side; with the birds choosing the less windy side. The losses of energy by a typical rook while roosting on the windward and leeward sides of a roost are compared (Table 24) where the saving of energy on the leeward side is highlighted.

Now considering the roost in a vertical plane; tree tops (occupied

TABLE 24

The effects of roosting position on heat losses from a single rook in two parts of the roost wood during a period of 15 hours. I Windward v. leeward side of the roost

Position in roost	Mean windspeed (m/sec)	Mean temperature (°C)	Total heat loss during roosting ($kcal/kg^{0.74}/15$ hr.)
Tree 1 (windward side)	3.2 ± 0.1	2.3 ± 0.3	165
Tree 4 (leeward side)	2.6 ± 0.1	3.4 ± 0.1	147

Climate data are mean (± standard error of mean) and are calculated from the field data (see Table 3, Chapter 3)

Note: the total heat loss was calculated by using the equations derived in Chapter 5. For mean windspeeds in excess of 1m/sec. - the difference between the heat loss without wind (at that temperature) and with wind of 1m/sec. was multiplied by the difference between the mean windspeed and a speed of 1m/sec. A roosting period of 15 hours was used.

by adults) have a different microclimate from that occurring lower in the canopy and these differences are generalised in Table 25 in which it can be seen that rooks are likely to lose less energy if they roost lower down the tree canopy.

There are therefore possibly substantial advantages to the careful selection of a roosting position. But what is the significance of these savings of energy in relation to survival? To be able to answer this question, knowledge of what reserves of energy the rooks have and what each part of the population (i.e. young and older birds) in their respective roosting places lose in the course of a fifteen hour night is required.

Adult rooks were considered first, and their horizontal choice of position (Table 26). They conserve 10 kcals. by roosting on the leeward side of a roost and so the energy expended hardly exceeds that provided by food alone. Fat reserves are thus barely touched and would last at this rate for many weeks. However the protein requirements for the metabolism of fat have been ignored, for although protein is continually being used it is also being replaced from the food and consequentially maintained at an adequate level.

In the case of young rooks, the saving of energy by choosing a roosting place out of the wind might be important, not so much because of the size of the saving, but because of the smaller energy reserves available (Table 27). This can be demonstrated by considering the number of days that an adult and a young rook would survive under these conditions. If the food intake is assumed to remain constant during a period of unchanging weather, then a calculation can be made of the number of days a single bird would survive if it roosted in each of the two roost positions each night (i.e. windward and leeward sides of the roost) (Table 28). The

TABLE 25

The effects of roosting position on heat losses from a single rook in two parts of the roost wood during a period of 15 hours.II Top v. bottom of a tree canopy

Position in roost	Mean windspeed (m/sec)	Mean temperature ($^{\circ}$C)	Total heat loss during roosting (kcal/kg $^{0.74}$/15 hr.)
Tree position A (Top of tree)	5.1 ± 0.2	5.5 ± 0.4	170
Tree position D (lower half of tree canopy)	3.2 ± 0.2	3.9 ± 0.3	155

Climate data are mean (± standard error of mean) and are calculated from the field data (see Table 4, Chapter 3)

Note: the total heat loss was calculated by using the equations derived in Chapter 5. For mean windspeeds in excess of lm/sec. - the difference between the heat loss without wind (at that temperature) and with wind of lm/sec. was multiplied by the difference between the mean windspeed and a speed of lm/sec. A roosting period of 15 hours was used.

TABLE 26

The effects of roosting position on the balance of energy requirement and energy available. I Adult rooks-windward and leeward sides of the roost.

Position in roost	Maximum energy requirement (cal./bird g.)	Mean available energy (cal./bird g.)	
		Food	Fat
Tree 1 (windward side)	99	75 ± 2	1348 ± 118
Tree 4 (leeward side)	89		

Note: in this Table the mean fat energy available was calculated by multiplying the percentage fat content (Table 23) by 95 cal (1 g. fat yields 9500 cal of metabolisable energy: King and Farner 1961); conversion to cal/g. of lean weight by dividing by 3.0 (as 1 g. of lean dry weight is associated with approximately 0.25 g. plumage and 1.8 g. water to give about 3.0 g. lean weight); and lastly a correction for unmetabolisable fat by deducting 3 per cent (measured from a rook that starved to death accidentally).

Mean food energy available was calculated by multiplying the percentage food stored (Chapter 7) by 22.5 cal (1 g. wheat yields 22.5 cal metabolisable energy; Biester and Schwarte 1952) and then by dividing the result by 3 (see above).

The mean available energy (± standard error of mean) was calculated by taking the mean energy available in cal./g. lean weight for both winters and multiplying by $\frac{8}{10}$ to give cal./bird g. (The relationship between lean weight and total weight minus stored food, in rooks, is approximately 8:10).

The maximum energy requirement was calculated from the total heat loss figures in Table 24 by conversion from $kcal/kg^{0.74}/15$ hr. to cal./bird g. for 15 hr.

TABLE 27

The effects of roosting position on the balance of energy requirement and energy available. II Young rooks-windward and leeward sides of the roost.

Position in roost	Maximum energy requirement (cal./bird g.)	Mean available energy (cal./bird g.)	
		Food	Fat
Tree 1 (windward side)	99	55 ± 1	679 ± 18
Tree 4 (leeward side)	89		

Note:. in this Table the mean fat energy available was calculated by multiplying the percentage fat content (Table 23) by 95 cal (1 g. fat yields 9500 cal of metabolisable energy: King and Farner 1961); conversion to cal/g. of lean weight by dividing by 3.0 (as 1 g. of lean dry weight is associated with approximately 0.25 g. plumage and 1.8 g. water to give about 3.0 g. lean weight); and lastly a correction for unmetabolisable fat by deducting 3 per cent (measured from a rook that starved to death accidentally.

Mean food energy available was calculated by multiplying the percentage food stored (Chapter 7) by 22.5 cal (1 g. wheat yields 22.5 cal metabolisable energy; Biester and Schwarte 1952) and then by dividing the result by 3 (see above).

The mean available energy (± standard error of mean) was calculated by taking the mean energy available in cal./g. lean weight for both winters and multiplying by $\frac{8}{10}$ to give cal./bird g. (The relationship between lean weight and total weight minus stored food, in rooks, is approximately 8:10)).

The maximum energy requirement was calculated from the total heat loss figures in Table 24 by conversion from kcal/kg$^{0.74}$/15 hr. to cal./bird g. for 15 hr.

TABLE 28

The effects of roosting position on the theoretical survival times of young and adult rooks. I Windward v. leeward side of the roost.

Positions in roost	Approximate number of days of survival	
	Young	Adult
Tree 1 (windward side)	15	57
Tree 4 (leeward side)	20	96

Note: Approximate number of days of survival was calculated by dividing the maximum energy requirement per night into the total (fat plus food) mean energy available (assuming that no fat was accumulated).

protein requirements for the metabolism of fat are ignored as no evidence of starvation was found (see Chapter 7 for discussion). It is apparent that by roosting on the leeward side of the roost the young rook would increase its survival time by $\frac{1}{3}$ and the adult rook by $\frac{2}{3}$. Nevertheless the survival time of the adult rook on the windward side of the roost is nearly four times longer than that of the young rook. Therefore any saving of energy that the young rook can make would be more important for its survival than any saving the adult rook can make.

We now consider the same problem of survival time but concerned with the effects of roosting position on the energy balance of young and adult rooks at the top and in the lower half of a single tree canopy. Adult rooks would conserve 9 kcals. by roosting in the lower half of the tree canopy (Table 29) and the maximum energy requirement for this part of the tree for a 15 hrs. roosting night only just exceeds the energy available from food alone. The young rooks, even if they roosted in the more sheltered position (the lower half of the tree canopy), would use all their energy from food and approximately the same amount of energy again from their fat each night (Table 30). It is possible to demonstrate the importance of young rooks roosting lower down the tree (rather than adults) in relation to their smaller energy reserves. If we assume that food intake remains constant during a period of unchanging weather, the survival time can be calculated (Table 31). By roosting in the lower half of a tree canopy (instead of at the top) young rooks would extend their survival time by $\frac{1}{4}$ and adult rooks would increase their's by nearly $\frac{1}{2}$. Even at the top of the tree adult birds would survive three and a half times longer than the young birds (and four times longer at the bottom of the canopy).

To summarise this part of the Chapter; it appears that a rook will

TABLE 29

The effects of roosting position on the balance of energy requirement and energy available. III Adult rooks-top and bottom of the roost tree canopy.

Position in roost	Maximum energy requirement (cal./bird g.)	Mean available energy (cal./bird g.)	
		Food	Fat
Tree position A (top of tree)	102	72 ± 10	1264 ± 121
Tree position D (lower half of tree canopy)	93		

Note: in this Table the mean fat energy available was calculated by multiplying the percentage fat content (Table 23) by 95 cal (1 g. fat yields 9500 cal of metabolisable energy: King and Farner 1961); conversion to cal/g. of lean weight by dividing by 3.0 (as 1 g. of lean dry weight is associated with approximately 0.25 g. plumage and 1.8 g. water to give about 3.0 g. lean weight); and lastly a correction for unmetabolisable fat by deducting 3 per cent (measured from a rook that starved to death accidentally).

Mean food energy available was calculated by multiplying the percentage food stored (Chapter 7) by 22.5 cal (1 g. wheat yields 22.5 cal metabolisable energy; Biester and Schwarte 1952) and then by dividing the result by 3 (see above).

The mean available energy (± standard error of mean was calculated by taking the mean energy available in cal./g. lean weight for both winters and multiplying by $\frac{8}{10}$ to give cal./bird g. (The relationship between lean weight and total weight minus stored food, in rooks, is approximately 8:10).

The maximum energy requirement was calculated from the total heat loss figures in Table 25 by conversion from $\text{kcal/kg}^{0.74}$/15 hr. to cal/bird g. for 15 hr.

TABLE 30

The effects of roosting position on the balance of energy requirement and energy available. IV Young rooks-top and bottom of the roost tree canopy.

Position in roost	Maximum energy requirement (cal./bird g.)	Mean available energy (cal./bird g.) Food	Fat
Tree position A (Top of the tree)	102	55 ± 3	575 ± 37
Tree position D (Lower half of tree canopy)	93		

Note: in this Table the mean fat energy available was calculated by multiplying the percentage fat content (Table 23) by 95 cal (1 g. fat yields 9500 cal of metabolisable energy: King and Farner 1961); conversion to cal/g. of lean weight by dividing by 3.0 (as 1 g. of lean dry weight is associated with approximately 0.25 g. plumage and 1.8 g. water to give about 3.0 g. lean weight); and lastly a correction for unmetabolisable fat by deducting 3 per cent (measured from a rook that starved to death accidentally).

Mean food energy available was calculated by multiplying the percentage food stored (Chapter 7) by 22.5 cal (1 g. wheat yields 22.5 cal metabolisable energy; Biester and Schwarte 1952) and then by dividing the result by 3 (see above).

The mean available energy (± standard error of mean) was calculated by taking the mean energy available in cal./g. lean weight for both winters and multiplying by $\frac{8}{10}$ to give cal./bird g. (The relationship between lean weight and total weight minus stored food, in rooks, is approximately 8:10)).

The maximum energy requirement was calculated from the total heat loss figures in Table 25 by conversion from kcal/kg$^{0.74}$/15 hr. to cal./bird g. for 15 hrs.

TABLE 31

The effects of roosting position on the theoretical survival times of young and adult rooks. II Top v. bottom of the tree canopy.

Positions in roost	Approximate number of days of survival	
	Young	Adult
Tree position A (Top of tree)	12	42
Tree position D (Lower half of canopy)	15	60

Note: Approximate number of days of survival was calculated by dividing the maximum energy requirement per night into the total (fat plus food) mean energy available (assuming that no fat was accumulated).

save more energy by roosting on the leeward side of a roost and in the lower part of a tree canopy than in any other position. However adult rooks, having more energy reserves than young rooks, can survive for a much longer time than a young rook when roosting in any position.

The fat and stored food data for specific days were taken as indicating a general trend throughout the winter because of the consistency of the comparative levels of reserves in young and adult rooks. I was surprised at the consistently low levels of fat in young rooks in relation to the fat levels in adult birds.

The weather during the two roosting periods observed was warmer than the long term monthly mean (30 year); the mean monthly rainfall was slightly less than the 45 year mean, and the mean monthly wind velocity was a little higher than the 10 year mean (Table 32). However, a 'normal' winter roosting period would be marginally colder than the periods studied, in which case the energetic stress would be increased.

It is a subjective decision whether a saving of energy is important or not and it would be useful to have independent evidence as to whether or not adult and/or young rooks die during winter i.e. November to February, If they do, loss of energy might be involved. If they do not, then the savings by choosing a sheltered roost position may be trivial.

Holyoak (1971) presented information on the monthly mortality of rooks and jackdaws. During the first year of life, young rooks (i.e. 1 year-old) mainly died between hatching (April) and August, and during January, February and March. Moreover mortality in all successive age groups appears concentrated between March and June, the peak being April. In jackdaws, approximately the same pattern emerges with the main months for mortality in first year birds being May to September, <u>and</u> from January

TABLE 32

Turnhouse meteorological data showing mean monthly temperature, wind velocity and rainfall between October and March 1970/71 and 1971/72 and their departure from long term means.

	OCT	NOV	DEC	JAN	FEB	MARCH
Mean air temperature 1931/60 (^{o}C)	9.3	6.0	4.2	2.8	3.4	5.2
Mean air temperature 1970/71 (^{o}C) (and difference from mean 1931/60)	9.7 (+0.4)	6.1 (+0.1)	4.3 (+0.1)	4.4 (+1.6)	5.3 (+1.9)	5.3 (+0.1)
Mean air temperature 1971/72 (^{o}C) (and difference from mean 1931/60	10.7 (+1.4)	5.9 (-0.1)	7.5 (+3.3)	4.1 (+1.3)	3.9 (+0.5)	5.3 (+0.1)
Mean rainfall (mm.) 1916/50	71	60	51	62	42	40
Mean rainfall (mm.) 1970/71 (and expressed as percentage of mean 1916/50)	67.1 (95)	83.3 (139)	39.6 (78)	29.2 (47)	35.6 (85)	60.4 (151)
Mean rainfall (mm.) 1971/1972 (and expressed as percentage of mean 1916/50)	42.3 (60)	82.7 (88)	28.5 (86)	50.8 (82)	41.8 (100)	39.5 (99)
Mean wind velocity (m/sec.) 1963/72	4.75	4.9	4.8	4.5	4.7	5.6
Mean wind velocity 1970/71 (m/sec.) (and expressed as percentage of mean 1963/72)	5.5 (110)	5.0 (100)	4.7 (98)	4.1 (92)	4.7 (100)	4.4 (78)
Mean wind velocity 1971/72 (m/sec.) (and expressed as percentage of mean 1963/72)	5.4 (113)	5.7 (115)	6.9 (145)	5.1 (115)	4.2 (88)	4.6 (82)

to March. Adult mortality is normally distributed around May. Holyoak (1971) stated that the percentage annual mortality of first year rooks was 59 per cent, second year 51 per cent and for adults 25 per cent. For jackdaws he quoted 38 per cent for first year birds, 36 per cent for second year, and 43 per cent for older birds.

Busse (1963) found in Poland that the majority of adult rooks died in March and April, whereas the first year birds mainly died in December, May and June. Adult jackdaws mostly died in May and first-year individuals in December, April, May and June. He also quoted annual mortality figures for adult rooks as 38.4 per cent and first year birds 72.7 per cent. Young jackdaws had an annual mortality of 59.6 per cent, in the second year the rate drops slightly with a greater drop in the third year.

Dunnet and Patterson (1968) quoted Sage and Nau (1963), who gave the mortality of young rooks in the first year of life as 70 ± 10 per cent (derived from Coombes' (1960) figure of 60-80 per cent). Coombes (loc. cit.) gave adult mortality as 16 per cent per annum. Dunnet and Patterson (1968) give adult mortality as 7.5-11.5 per cent per annum.

Young rooks and jackdaws appear to have two periods of high mortality during their first year of life, at hatching and for a few months afterwards, and the later part of the winter (i.e. December to February or March). Older birds only experience high mortality during the breeding season and early summer. Although Dunnet et al. (1969) thought the drop in numbers of young rooks in autumn and winter and increase in spring could be due to the emigration of first-winter rooks in autumn and return in spring, he did point out that ring recoveries did not indicate a movement of this kind. If young rooks emigrate, where do they go? Holyoak (1971), reporting ringing returns in the U.K., stated that the proportion of rooks recovered at a distance from the home rookery appears to increase through the first winter of life and remains fairly high until the next winter, but lower in later winters. In jackdaws, he found young birds dispersed during the first autumn of life.

However, although old and young birds experience high mortality while breeding/hatching and afterwards, only young birds appear to succumb in the winter. Thus assuming that mortality in winter is caused by a loss of fat reserves, these studies of mortality support the view that any saving of energy by young rooks in a roost might well be important in their survival.

Is a rook's roosting position important in affecting its total energy balance or do other factors have a stronger influence? It has been shown that the minimum temperature during the day has a stronger influence than any other variable, either the day or night, on food demand. Moreover in times of food shortage, younger rooks will suffer more than the adults, and the underweight individuals more than any.

During the night, heat loss can be cut to a minimum by physiological mechanisms. Moreover, the lower critical temperature progressively decreases as the nutritional plane (energy level, or state) of a bird increases (King and Farner 1961) sparing energy which would be required, at a lower plane of nutrition, for thermoregulation. Thus adult rooks, apart from the advantage of having more energy reserves, are also able to withstand lower temperatures without raising their metabolic rate from base level. Consequently, the availability of food, and consumption of an adequate quantity and quality to maintain the correct energy level, appears the most important factor for survival during the winter. Moen (1968) indicated that deer will only seek heavy cover during extremely cold winter weather, when the diet was inadequate to maintain a positive energy balance.

Why adult rooks should choose the tops of trees, remains obscure. It is true that rooks, both in the field and in the laboratory, like to have a clear view around them. They are animals of open places and are not normally found feeding or resting on ground densely grown with shrubs, trees or crops. Thus when they use trees, for nesting or roosting, they prefer to take a position where they can see all around themselves for some distance rather than an obscured position where energy savings would be effected.

To summarise, rooks generally choose the more sheltered places to roost (with the exception of the adults apparent preference for the uppermost part of a tree) within the roost wood. They therefore (in general) use less energy than they would if they used the wood at random for roosting. However, the saving of energy is small. It is unlikely to be important for survival for adults in an average winter, but it may well be important for young birds which have much lower reserves to draw upon than adults. Some young rooks die in winter, but adults rarely, and this gives support to the view that the young need to save energy but due to their subordinate position may not always achieve the saving. Furthermore, in exceptionally cold periods, it is possible that birds able to choose their perching position may save considerably more energy than those which have no choice.

However, the saving of energy in a roost cannot be viewed in isolation. The more precarious position of the young results from their substantially lower fat reserves and this may be a function not only of roosting but also of daytime competition on the feeding grounds.

SUMMARY

1. A review of the autumn and winter roosting behaviour of rooks and jackdaws was presented. A critical summary of published hypotheses as explanations of communal roosting by Corvidae was given, and one hypothesis concerning the relationship between heat loss, social organisation and weather was chosen for detailed study.

Two questions were posed:-

(1) Does the behaviour of rooks and jackdaws in a communal roost reduce the rate of loss of heat energy?

(2) If energy is saved, is this saving likely to be critical for survival?

2. The synchronisation of the daily movements of birds to and from the roost was shown to be influenced by light intensity, although weather and other factors might have modifying influences. This behaviour affects the length of the feeding day, rooks feeding longer on bright days.

3. The results of an investigation into the interrelation between the spatial organisation in the roost and the weather showed that windspeed, rainfall duration, temperature, cloud cover and wind direction alter and change the distribution of birds both across the wood and vertically within a tree. The climatological characteristics of woods of different composition are discussed. In general birds preferred the warmer and less windy parts of the wood. Adult rooks perched at the tops of trees, while young rooks and jackdaws perched below. Aggressive encounters increased and decreased in relation to bird movement within the roost. The influence of shelter on heat loss is discussed.

4. The social hierarchy of groups of rooks of all ages was examined. The hierarchy was basically age-related, straight-line and peck right. Successful encounters over perches and food resulted in the same 'victor' or 'loser'. Both rooks and jackdaws preferred the highest available perches; the higher the perch, the higher the status of the incumbent.

Male rooks dominate females and older birds are dominant to first year-old birds. Status recognition (without aggressive encounters occurring) appeared to be based on posture, levels of intensity of threat, facial bareness and deportment.

5. The rate of loss of heat by rooks under different climatic and social situations was measured. An indirect calorimetric method was used, and skin and cloacal temperatures were also recorded. Heat loss increased with decreasing ambient temperature. With rain or wind the heat loss was increased still more, with rain and wind the heat loss was twice that with temperature alone at -7.5°C. A true pair of rooks (i.e. male and female) lost less heat than each bird did individually (under the same thermal conditions), and a 'false' pair (i.e. two males) lost only slightly less heat than individually. The results were not statistically significant although a trend was apparent.

6. The relationship, in captivity, between food intake and weather was analysed. When aggressive encounters between birds occurred the time food was available was important in determining the amount of food eaten, although the minimum temperature during the day was also of importance. Without aggressive encounters between birds occurring the minimum temperature during the day was the most important variable affecting food intake, night-time weather variables being secondary in importance and the length of the

day only slightly significant. Weather had a large influence on food consumption. Loss in weight of the lighter, more subordinate birds within each age group occurred through aggressive encounters between birds, at the food source, and also because feeding by the subordinates was inhibited.

7. The body composition of rooks was measured from specimens taken at the roost. Adult birds had almost twice as much fat as young birds and slightly more ingested food.

8. Heat loss in relation to energy reserves was considered for young and adult rooks in different parts of the roost. Survival times were calculated for both age groups indicating a much shorter time for young birds. Published information was introduced to show that it is mainly the young that die in winter. In conclusion, rooks chose the more sheltered places to roost in within the roosting wood. They therefore (in general) used less energy than they would if they used the wood at random for roosting. However, the saving of energy was small. It was unlikely to be important for survivalfor adults in an average winter, but it may well have been important for young birds which have much lower reserves to draw upon than adults. Some young rooks die in winter but adults rarely, and this gave support to the view that the young need to save energy but due to their subordinate position may not always achieve the saving. The more precarious position of the young resulted from their substantially lower fat reserves and this may have been a function not only of roosting but also of competition on the feeding grounds by day.

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APPENDIX 1

DETERMINATION OF SEX IN LIVE ROOKS AND JACKDAWS

Dunnet and Anderson (1961) have used discriminatory analysis in fulmars (*Fulmaris glacialis*); likewise Harris (1964) and Heppleston & Kerridge (1970) have used the technique on the great black-backed gull (*Larus marinus*) and in the oystercatcher (*Haematopus ostralegus*) respectively.

Within the British members of the Corvidae the plumage is alike in both sexes. In this short analysis I have used a discriminant function in determining the sex of 120 adult jackdaws and 63 adult rooks mainly from the East Lothian and Oxfordshire. The sex was determined by dissection.

Measurements were taken from birds of one year-old or more. The wing length (± 0.1 cm.) was taken from the carpal joint to the tip of the longest primary; the bill length (± 0.01 cm.) from the distal end of the upper mandible to the posterior edge of the nostril; and the bill depth (± 0.01 cm) from the dorsal edge of the upper mandible to the ventral edge of the lower mandible at the position of the nostrils. Birds with malformed bills were rejected. The rooks only had their weight and wing length taken. Hotelling's T^2 test was used for the analysis.

Hotelling's T^2 test.

This is a multivariate technique (Hotelling 1931) for studying the extent to which different populations overlap one another or diverge from one another. Given a number of related measurements made on each of two groups, one can apply a single test of the null hypothesis showing whether the two populations have the same means with respect to all the measurements. The actual version used here (Moroney 1968) was written as a computer programme (Table 1).

TABLE 1

The discriminant function analysis computer programme

```
    REAL N
C
C  DECLARATION OF ARRAY SIZE
    DIMENSION NN(2)
    DIMENSION N(2). SUMX(2). SUMY(2). SUMZ(2). SUMX2(2). SUMY2(2)
    DIMENSION SUMZ2(2). SUMXY(2). SUMXZ(2). SUMYZ(2)
    DIMENSION AVEX(2). AVEY(2). AVEZ(2)
    DIMENSION D(2)
         DIMENSION X(2.200). Y(2.200). Z(2.200)
C
C  INITIALISATION OF VALUES TO ZERO
    DATA SUMX.SUMY.SUMZ.SUMX2.SUMY2.SUMZ2.SUMXY.SUMXZ.SUMYZ/18*0./
    DATA SXX.SYY.SZZ.SXY.SXZ.SYZ/6*0./
C
C  START OF THE LOOP WHICH READS IN THE DATA FOR EACH GROUP
    DO 10 J=1.2
C  NUMBER OF CARDS IN THE GROUP IS READ IN
    READ(5.101) N(J)
    NN(J)=IFIX(N(J))
    NNN=NN(J)
    DO 10 I=1.NNN
    READ (5.102) X(J.I). Y(J.I). Z(J.I)
10  CONTINUE
C
C  AN = TOTAL NUMBER OF CARDS
    AN=N(1)+N(2)
C
C  START OF THE LOOP WHICH ANALYSES EACH GROUP IN TURN
    DO 11 J=1.2
    NNN=NN(J)
    DO 1 I=1.NNN
C
C  SUMMATION OF THE DATA IN EACH CATEGORY
    SUMX(J)=SUMX(J)+X(J.I)
    SUMY(J)=SUMY(J)+Y(J.I)
    SUMZ(J)=SUMZ(J)+Z(J.I)
C
C  SUMMATION OF THE SQUARES OF THE DATA IN EACH CATEGORY
    SUMX2(J)=SUMX2(J)+X(J.I)**2
    SUMY2(J)=SUMY2(J)+Y(J.I)**2
    SUMZ2(J)=SYNZ2(J)+Z(J.I)**2
C
C  SUMMATION OF THE PRODUCTS OF THE DATA IN EACH CATEGORY
    SUMXY(J)=SUMXY(J)+X(J.I)*Y(J.I)
    SUMXZ(J)=SUMXZ(J)+X(J.I)*Z(J.I)
    SUMYZ(J)=SUMYZ(J)+Y(J.I)*Z(J.I)
1   CONTINUE
11  CONTINUE
    DO 2 J=1.2
C
```

```
C   CALCULATION OF THE    SUMS OF SQUARE
       SXX=SXX+(SUMX2(J)-(SUMX(J)**2)/N(J))
       SYY=SYY+(SUMY2(J)-(SUMY(J)**2)/N(J))
       SZZ=SZZ+(SUMZ2(J)-(SUMZ(J)**2)/N(J))
C
C   CALCULATION OF THE    SUMS OF PRODUCT
       SXY=SXY+(SUMXY(J)-(SUMX(J)*SUMY(J)/N(J))
       SXZ=SXZ+(SUMXZ(J)-(SUMX(J)*SUMZ(J))/N(J))
       SYZ=SYZ+(SUMYZ(J)-(SUMY(J)*SUMZ(J))/N(J))
C
C   CALCULATION OF AVERAGES IN EACH CATEGORY IN EACH GROUP
       AVEX(J)=SUMX(J)/N(J)
       AVEY(J)=SUMY(J)/N(J)
       AVEZ(J)=SUMZ(J)/N(J)
C
C   PRINT OUT OF GROUP NUMBER
       WRITE (6. 204) J
C   PRINT OUT OF THE THREE AVERAGES IN THIS GROUP
       WRITE (6.201) AVEX(J).AVEY(J).AVEZ(J)
2      CONTINUE
C
C   CALCULATION OF THE DIFFERENCES OF THE AVERAGES WITHIN EACH CATEGORY
       DX=AVEX(1)-AVEX(2)
       DY-AVEY(1)-AVEY(2)
       DZ=AVEZ(1)-AVEZ(2)
C
C   PRINT OUT OF DIFFERENCES
       WRITE (6.202) DX.DY.DZ
       T1=(AN-2.)*DX
       T2=(AN-2.)*DY
       T3=(AN-2.)*DZ
C   CALLING THE SUBROUTINE TO SOLVE THE SIMULTANEOUS EQUATION
       CALL SIMUL(SXX.SXY.SXZ.T1.SXY.SYY.SYZ.T2.SXZ.SYZ.SZZ.T3.A.B.C.)
C
C   CALCULATION OF HOTELLING'S T2
       TT=N(1)*N(2)*(A*DX*B*DY+C*DZ)/AN
C
C   CALCULATION OF F
       F=TT*(AN-4.)/(3.*(AN-2.))
C
C   CALCULATION OF THE DISCRIMINANT FUNCTION FOR THE TWO GROUPS
       DO 3 I=1.2
3      D(I)=AVEX(I)*A+AVEY(I)*B+AVEZ(I)*C
C
C   PRINT OUT OF PARAMETERS
       WRITE (6.203) TT.F.A. B. C. D(1). D(2)
       SDX=SQRT(SXX/AN)
       SDY=SQRT(SYY/AN)
       SDZ=SQRT(SZZ/AN)
       DSX=DX/SDX
       DSY=DY/SDY
       DSZ=DZ/SDZ
       DSMIN=SQRT(DSX+DSY+DSZ)**2)
```

```
        DSD=SQRT(A*DX+B*DY+C*DZ)
        DD=ABS(D(1)-D(2))
        SDD=DD/DSD
        WRITE (6.206)DSX.DSY.DSZ.DSMIN.DSD.DD.SDD
        DO 7 J=1.2
        SUM =0.0
        SUM2 = 0.0
        NNN=NN(J)
        WRITE (6.207) J
        DO 8 I=1.NNN
        DD=A*X(J.I)+B*Y(J.I)+C*Z(J.I)
        SUM = SUM+DD
        SUM2 = SUM2 +DD**2
        WRITE (6.208) X(J.I).Y(J.I).DD
  8     CONTINUE
        SD = SQRT(SUM2/NNN-(SUM/NNN)**2)
        WRITE (6.209) SD
  7     CONTINUE
  C
  C   LOOP FOR READING IN AND FINDING DISCRIMINANT FUNCTION FOR
  C   INDIVIDUAL UNKNOWNS
        I=0
 26     I=I+1
        READ (5.103) XX.YY.ZZ
        DD=XX*A+YY*B+ZZ*C
        WRITE (6.205) I.DD
        GOTO 26
  C
  C   FORMAT STATEMENTS
101     FORMAT (F5.0)
102     FORMAT (F4.1.2F4.2)
103     FORMAT (F4.1.2F4.2)
201     FORMAT ('0'. 'AVERAGE X ='.F10.4.//'0'.'AVERAGE Y = '.F10.4.
      1/'0'.'AVERAGE Z = '.F10.4)
202     FORMAT (81'.'DIFFERENCE IN THE AVERAGES OF X ='.F10.4.
      1/'0'.'DIFFERENCES IN THE AVERAGES OF Y ='.F.10.4.
      2/'0'.'DIFFERENCES IN THE AVERAGES OF Z ='.F.10.4.
203     FORMAT ('1','H='.F10.4./'0'.'F='.F10.4./'0'.'A='.F10.4.
      1/'0'.'B='.F10.4./'0'.'C='F10.4////'0'.'DISCRIMINANT FUNCTION
      2 1 = '.F10.4. ///'0'.'DISCRIMINANT FUNCTION 2 ='.F10.4)
204     FORMAT ('1'.'GROUP '.15)
205     FORMAT ('1'.'BIRD '.15.'  HAS A DISCRIMINANT FUNCTION DF'F9.4)
206     FORMAT ('1'.3F10.3./'0'.F10.3./'0'.F10.3./'0'.2F10.3)
207     FORMAT ('1'.10X.'GROUP '.15.//'0'.7X.'X'.9X.'Y'.9X.'Z'.20X.
      1 'DISCRIMINANT './' '.53X.'FUNCTION')
208     FORMAT ('0'.3F10.3.20X.F10.3)
209     FORMAT ('1'.F10.3)
        STOP
        END

        SUBROUTINE SIMUL (A1.B1.C1.M.A2.B2.C2.N.A3.B3.C3.P.A.B.C)
        REAL N.M.N1.N4
```

```
B1=(B1*A2*(-1.))/A1+B2
C1=(C1*A2*(-1.))/A1+C2
M=(M*A2)/A1
N1=N-M
B4=(B3*A2*(-1.))/A3+B2
C4=(C3*A2*(-1.))/A3+C2
P1=(P*A2)/A3
N4=N-P1
C1=(C1*B4*(-1.))/B1
N1=N1*B4/B1
N1=N4-N1
C1=C1+C4
C=N1/C1
B=(N4-(C4*C))/B4
A=(P-(B*B3+C*C3))/A3
RETURN
END
```

The T^2 test was first applied to the jackdaw data to ascertain whether any significant differences existed in the three measurements between the two populations (males and females). The T^2 value was 286.03, which when tested using Snedecor's F (93.73) was found to be significant ($P < 0.001$). Thus the males and females are characterised by significantly different body measurements.

The basic discriminant function (D) equation is in the form $D = a\bar{x} + b\bar{y} + c\bar{z}$ where $\bar{x}$, $\bar{y}$ and $\bar{z}$ are the mean wing length, mean bill length and mean bill depth respectively. a, b and c are weighing factors which were calculated in finding T^2.

Thus, for the female jackdaw population, the

$$\text{mean } D = 2.63\ (22.80) + 38.29\ (2.27) + 10.49\ (1.32) = 160.8$$

and for the male population the

$$\text{mean } D = 2.63\ (23.64) + 38.29\ (2.45) + 10.49\ (1.38) = 170.4$$

However, in order to know how accurate a prediction of sex is, in relation to a particular individual, a means of estimating the percentage chance of misclassification, particularly with D values between 160.8 and 170.4, was developed.

Should the discriminant function value (D) of a bird fall between the mean D values of the two populations, a determination of the standard deviation for each distribution curve at that D value was calculated as follows:- by substituting in the formulae $V_1 = \frac{D - D_1}{S}$ for curve 1 (i.e. for female jackdaws) and for curve 2 (i.e. male jackdaws) $V_2 = \frac{D_2 - D}{s}$, where V_1 and V_2 are the standard deviations for each curve at the discriminant value D. D_1 and D_2 are the respective mean D values for curves 1 and 2, and S is the standard deviation of both curves (i.e. in the jackdaw analysis $S = 3.1$).

Then by consulting cumulative normal distribution function tables (Hald 1967) and taking the value read for V_1, as a percentage of the value read for V_2, the percentage probability of misclassification can be deduced (Table 2).

It was possible to ascertain, by the above method, the number of individuals in the experimental samples which would be incorrectly sexed. In the group of jackdaws sexed as male, 6.1 per cent were female and in the female group, 5.5 per cent were male.

The same analysis was performed on the rook data. The mean D value for the male population was 4.45 and for the female population 2.38. The T^2 test gave a value of 32.59 with an F value of 10.51 ($P < 0.001$). The equation for the male population is:

$$\text{Mean D} = 0.027\ (498.5) + 0.288\ (30.7) \quad 17.7 = 4.45$$

and for the female population

$$\text{Mean D} = 0.027\ (432.1) + 0.288\ (29.7) \quad 17.7 = 2.38.$$

TABLE 2

The percentage probability of a jackdaw, with a particular D value, belonging to the female group.

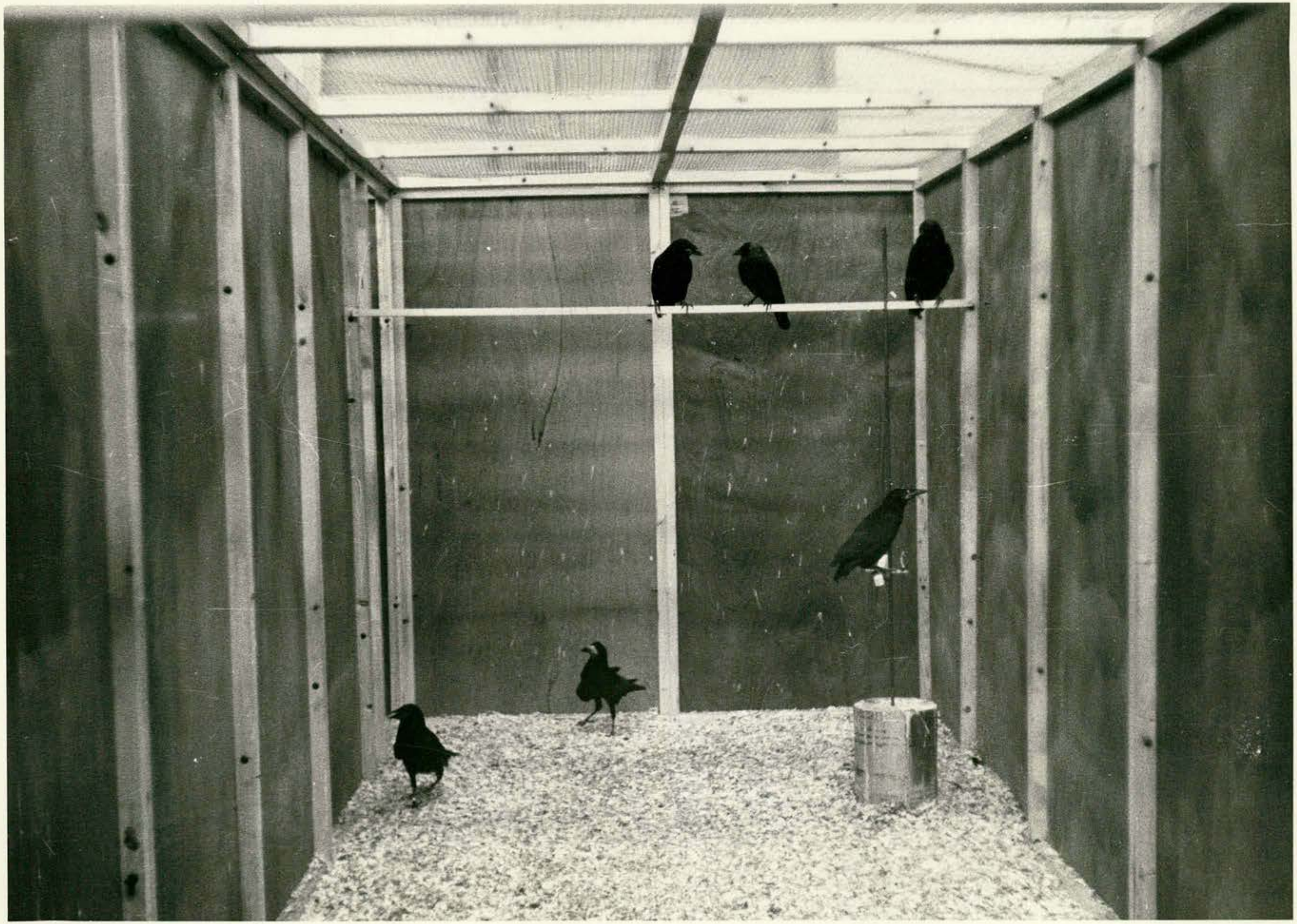
	Discriminant function (D) values								
	161	162	163	164	165	166	167	168	169
V_1	0.065	0.387	0.710	1.032	1.312	1.677	2.000	2.323	2.968
V_2	3.032	2.710	2.387	2.065	1.742	1.419	1.097	0.774	0.129
V_1'	47.2	34.8	23.9	15.2	9.51	4.65	2.28	1.02	0.149
V_2'	0.122	0.336	0.842	1.92	4.09	7.78	13.6	22.1	44.8
$V_1' + V_2'$	47.3	35.1	24.7	17.1	13.6	12.4	15.9	23.1	45.0
% probability of jackdaw belonging to group 1 (♀s)	99.8	99.1	96.8	88.9	69.9	37.4	14.3	4.4	0.3

NOTE: V_1, V_2 are the standard deviations of group 1 and 2.
V_1', V_2' are the percentage transformations of V_1 and V_2.

APPENDIX 2

PHOTOGRAPHS

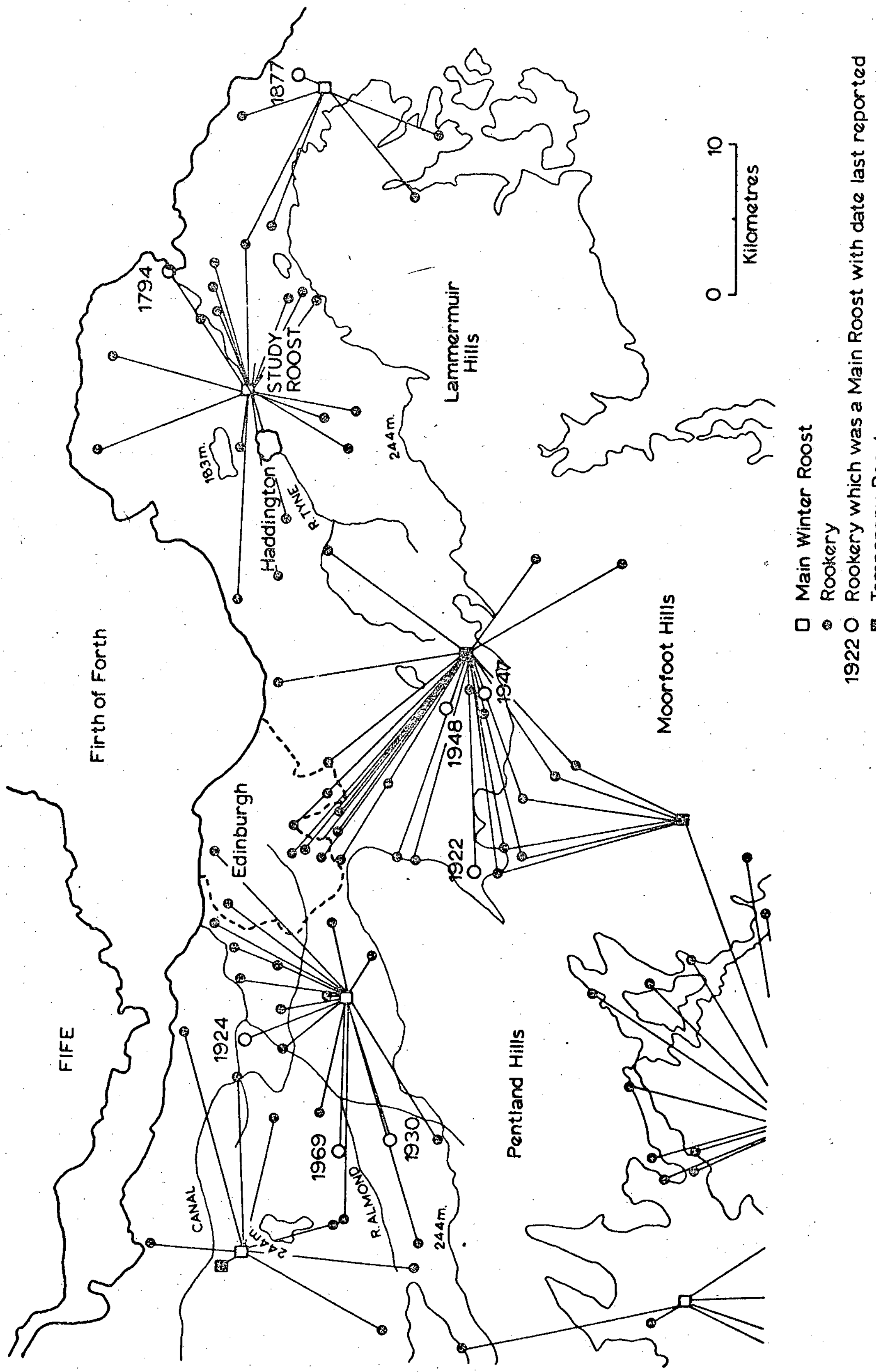
1. Final assembly of rooks and jackdaws before going to roost.
2. Final assembly of rooks and jackdaws in surrounding trees. All the birds point into the wind.
3. Mass roost entry.
4. Observation tower used during winter 1970/71.
5. Mobile laboratory and the deciduous study tree (winter 1971/72).
6. General view of trees from the mobile laboratory.
7. Photograph to show birds distributed both in the crown top and lower down.
8. View of one of the flights used to observe laboratory behaviour.
9. A dominant 1 year-old rook showing typical dominant posture.



APPENDIX 3

A SURVEY OF ROOKERIES AND ROOK ROOSTS 1969/72

The accompanying map shows the distribution of rookeries and rook roosts in the Lothians and Peebleshire. Each point was verified by me.



A survey of rookeries and rook roosts 1969/72

APPENDIX 4

ROOST FIELD DATA

TABLE 1

The mean change in the proportion of birds which left (-) or arrived (+) at tree 2 and tree 3, and the r^2 value of the influence of weather on these movements in the roost (wind direction 130°-310°)

1970-71	Changes in the percentage of birds and variance explained Tree 2 (windward)		3 (leeward)	
	i	ii	i	ii
November	-6.9	0.193	+6.8	0.262
December	-4.6	0.235	+4.2	0.334
January	-5.8	0.117	+4.7	0.029
February	-5.0	0.101	+3.4	0.018

Note: (a) each pair of figures is (i) the mean change in the proportion of birds arriving (+) or leaving (-) the tree and the r^2 value for the influence of changes in the weather on changes in the proportion of birds at that tree.

(b) wind direction was from 130°-310° (i.e. approximately from 2 to 3).

(c) the average number of birds in all trees (1, 2, 3, 4) was November 67, December 144, January 100 and February 90.

(d) data on trees 1 and 4 are in Table 6 Chapter 3.

(e) the number of counts in each tree was November 25, December 119, January 40 and February 30.

TABLE 2

The mean change in the proportion of birds which left (-) or arrived (+) at tree 2 and tree 3 and the r^2 value for the influence of weather on the movements in the roost (wind direction 50°-120°)

	Change in the percentage of birds and variance explained			
	Tree			
1970-71	2 (leeward)		3 (windward)	
	i	ii	i	ii
November	+6.7	0.246	-4.9	0.414
January	+9.1	0.153	-8.4	0.289
February	+4.5	0.047	-0.8	0.365

Note: (a) each pair of figures is (i) the mean change in the proportion of birds arriving (+) or leaving (-) the tree and (ii) the r^2 value for the influence of changes in the weather on changes in the proportion of birds at that tree. December is omitted as there were no records.

(b) wind direction was from 50°-120° (i.e. approximately from 3 to 2).

(c) the average number of birds in all trees (1, 2, 3, 4) was November 67, January 100 and February 90.

(d) data on trees 1 and 4 are in Table 7 Chapter 3.

(e) the number of counts in each tree was November 11, January 20 and February 9.

TABLE 3

Mean number of birds in each tree when the wind is from 130°-310° (1970-71)

Month	Number of counts in each tree	Mean number of birds Tree 1	2	3	4
November	25	14.2	14.5	18.3	20.0
December	119	31.5	33.0	38.0	41.5
January	40	20.7	21.3	29.1	28.9
February	30	20.0	19.5	23.5	26.5

Note: these data are presented in order to assess the information in Table 6, Chapter 3.

TABLE 4

Mean number of birds in each tree when the wind is from 50°-120° (1970/71)

Month	Number of counts in each tree	Mean number of birds Tree 1	2	3	4
November	11	18.6	17.9	15.2	15.5
January	20	24.8	26.9	24.3	23.6
February	9	25.3	17.7	21.2	19.5

Note: these data are presented in order to assess the information in Table 7, Chapter 3.

TABLE 5

Mean number of adult rooks in each tree position when the wind is from 130°-310° (1971/72)

Month	Number of counts in each tree position	Mean number of adult rooks Tree position A	B	C	D
September	23	10.9	3.6	3.1	0.8
October	24	25.6	8.5	7.4	1.9
November	24	26.9	8.9	7.8	2.0
December	18	24.1	8.0	6.9	1.8
January	17	13.3	4.4	3.8	1.0
February	17	7.8	2.6	2.9	0.6
Mean number of adult rooks		18.1	6.0	5.3	1.4

Note: these data are presented in order to assess the information in Table 8, Chapter 3.

TABLE 6

Mean number of young rooks in each tree position when the wind is from 130°-310° (1971/72)

Month	Number of counts in each tree position	Mean number of young rooks Tree position A	B	C	D
September	23	0.3	7.3	6.3	3.6
October	24	0.5	12.2	10.4	5.9
November	24	0.3	6.8	5.8	3.3
December	18	0.3	8.0	6.8	3.9
January	17	0.3	8.2	7.0	4.0
February	17	0.2	4.7	4.0	2.3
Mean number of young rooks		0.3	7.9	6.7	3.8

Note: these data are presented in order to assess the information in Table 9, Chapter 3.

TABLE 7

Mean number of jackdaws in each tree position when the wind is from 130°-310° (1971/72)

Month	Number of counts in each tree position	Mean number of jackdaws Tree position A	B	C	D
September	23	0.1	4.5	5.8	3.1
October	24	0.1	5.3	6.8	3.7
November	24	0.1	5.0	6.4	3.5
December	18	0.1	4.3	5.6	3.0
January	17	0.1	4.7	6.1	3.3
February	17	0.1	2.2	2.8	1.5
Mean number of jackdaws		0.1	4.3	5.6	3.0

Note: these data are presented in order to assess the information in Table 10, Chapter 3.

APPENDIX 5

STATISTICS

Stepwise Multiple Regression: Multiple regression allows the linear relationship between a set of independent variables and a number of dependent variables to be determined while taking into account the interrelationship among the independent variables.

The basic concept of multiple regression is to produce a linear combination of independent variables which will correlate as highly as possible with the dependent variable. This linear combination can then be used to predict values of the dependent variables.

Stepwise multiple regression provides a means of choosing independent variables which will provide the best prediction possible with the fewest independent variables. The method recursively constructs prediction equations, one independent variable at a time (in order of their value as a predictor - the 'best' first).

In the analyses testing roost behaviour/food consumption versus weather the independent variables (the weather variables) were highly correlated, consequently some variables were brought into the regression equation when their contribution to the variance explained (r^2) in the dependent variable by the independent variables was lower than subsequent variables. However Mead (1971) stated that this does not invalidate the approach. For the purposes of interpretation of the results of multiple regression analyses the contribution of the group of independent variables is of importance, and not the contribution or the order of single variables. Nevertheless, where the variable first selected by the technique as the 'best' predictor, is also the variable with the largest r^2 value, then this variable is considered to be the most influential single variable.

Furthermore, all matrices input into the multiple regression routines were generated by a Pearson product-moment correlation coefficient analysis. The reasons for choosing a conventional (parametric) method of analysis, rather than a non-parametric method, which should only be used if either the data do not lend themselves to a parametric model (e.g. if they are ranks) or there is difficulty in finding a suitably valid parametric model, were considered. However, apart from the aforementioned reasons, with actual measurements available there seemed no reason for not using a parametric analysis approximating to a real-life model. A parametric analysis is more efficient than a non-parametric one and in a preliminary comparative analysis of Pearson and Spearman (non-parametric) matrices in the multiple regression, neither r^2 values (variance explained) were significantly altered or the order of the variables entered in the equation.

With regard to the criterion of normal distribution of the variables in order to be able to use a parametric system, no particular distribution need be assumed in multiple regression analyses for the independent variables.

All equations used for calculating and testing significance etc. are in the Statistical Package for the Social Sciences (SPSS) manual (Nie, Bent and Hull 1970) which is a computer programme system.

Student's t test

For large samples ($N > 100$) the following equation was used to calculate t:-

$$t = \frac{\text{Difference of means}}{\sqrt{\frac{\text{Variance}^1}{\text{Sample size}^1} + \frac{\text{Variance}^2}{\text{Sample Size}^2}}}$$

and the number of degrees of freedom$^{(df)}$ = the sample size (N) - 2 (Moroney 1968, p. 232).

The significance of any correlation coefficient (r) used in this study was determined by comparing the quantity :

$$r \left(\frac{N - 2}{1 - r^2}\right)^{\frac{1}{2}}$$

With the Student's t distribution with N - 2 degrees of freedom (Nie, Bent and Hull 1970, p. 146 + 154).

The test of significance selected is two-tailed.

Variance

Variance is equal to the square of the standard deviation (Moroney 1968, p. 61f). Its formula is

$$\text{Variance} = S^2 = \frac{\Sigma (X - \bar{X})^2}{N}$$

where $\bar{X}$ is the arithmetic mean of the various values of X, and N is the sample size.

The Variance Ratio test or Snedecor's F test

This tests the significance of the difference between sample variances (Moroney 1968, p. 233f). It has been used in this study in regression analyses.

$$F = \frac{\text{greater estimate of the variance of the population}}{\text{lesser estimate of the variance of the population}}$$

Contingency coefficient (C)

This coefficient measures the extent of association or relation between two sets of attributes (Siegel 1956, p. 196).

$$C = \sqrt{\frac{\text{Chi - square}}{\text{N + Chi-square}}}$$

where chi-square is computed by the method presented below. The significance of C was checked by the chi-square test.

Chi-square test

This tests the independence (or lack of statistical association) between two variables but it does not measure the degree of association (Nie, Bent and Hull 1970, p. 275).

$$\text{Chi-square } (X^2) = \sum \frac{f_o^i - f_e^i}{f_e^i}$$

where f_o^i is the observed frequency in each cell, f_e^i is the expected frequency in each cell; with degrees of freedom, df = (Number of columns - 1)(Number of rows - 1).

APPENDIX 6

THE AUTOMATIC WINDSPEED AND TEMPERATURE SENSING SYSTEM.

The requirements for a windspeed and temperature system in this study were: a portable system using battery power; an integrated system; sensitive over a range of wind speeds from 0.1 m/sec to 15 m/sec and from -10°C to +20°C; capable of integrating the wind speed over a chosen time interval; and cheap. No existing system met these demands.

The wind instrument used was the counter pattern Sheppard cup anemometer (Sheppard 1940) supplied by Casella & Company Limited. The bearings and gearings of this instrument were designed to have a low torque, about 12 dyne/cm, and so provide the desired sensitivity at low wind speeds. The starting speed for cup rotation was 0.1 m/sec while the upper limit of operation was "in excess of 25 m/sec", well above the required upper limit.

An adapted version of this anemometer was used (the design was evolved and executed by Ferranti Ltd.). The instrument consisted mainly of a low torque 357° toroidally wound potentiometer on the 10000 units/rev spindle.

By using a near fully wound potentiometer the inconvenience of assessing and of allowing for the value of the gap between the ends of the winding and the consequence loss on information was reduced (Marshall 1966). The Ferranti modifications had two serious faults. Firstly, the wiper assembly began to slip on its spindle giving low readings and secondly, the potentiometer was held in place using double-sided adhesive tape. Both these faults were corrected by using epoxy resin adhesive.

The recorder used in this wind speed/temperature system was a Grant Temperature Recorder (Grant Instruments, Cambridge). The data medium was a strip chart and the power source was a pack of Eve Ready Nickel Cadmium cells giving 6 volts, enough power for 72 hours. Grant thermistor probes were used as temperature sensors. The temperature probes were lagged in dull black PVC adhesive tape to smooth out sudden temperature fluctuations, and to simulate the bird's plumage which is a near-perfect black body. Each probe was shielded from the effect of radiation loss to the sky by a small circular piece of cardboard, covered in black PVC fixed over the top (of the probe).

The recorder was operated using the -10°C to +40°C scale and when connecting the lead from an anemometer, a 1K resistance was incorporated so that 10,000 revolutions of the anemometer head were equivalent to a 0 to 40 (°C) deflection on the scale.

The advantages of this system over that of a magnetic tape data logger (used by Marshall) was that any faults could be immediately detected, instead of being discovered when the magnetic tape was 'read' by the manufacturer; secondly, there was less equipment and thirdly, it was cheaper.

The recorder automatically sensed the temperature and wind 'speed' values once an hour and by reference to a "change in recorder reading"/"wind speed" conversion (from the wind-tunnel calibration), a total wind speed was calculated.

Marshall (1966) who tested the adapted system, never used it in a long term applied experimental field situation. However, he did erect one short term study positioning two anemometers at 15 and 200 cms above the soil surface at Lochhouses Farm, East Lothian (10 km NE of the study area) and comparing this with data, at 10 m. above ground, from Turnhouse

Airport Met. Station, West Lothian (40 km. W of the study area). He found that, regardless of the intermittent (every 5 minutes) recording at Lochhouses, the windspeed records reflected those of Turnhouse in both directions and speed. The data showed similar directional changes, and changes in the same sense, though not in magnitude, of wind speed as the hourly records from Turnhouse.

The anemometers were calibrated individually both before and after each experiment. The calibrations were performed in a controlled environment wind-tunnel (in the Department of Forestry and Natural Resources) against two other air flow rate indicators, a Pitot Static Tube and an RM-137 Direct Reading Electronic Anemometer both manufactured by Airflow Developments Ltd., Bucks.

APPENDIX 7

THE SUITABILITY OF TURNHOUSE WEATHER DATA APPLIED TO STEVENSON WOOD.

The hourly wind velocity and temperature measured at Turnhouse and the mean hourly windspeed and hourly temperature in the roost were highly significantly correlated (Spearman rank correlation coefficient (r_s) for wind velocity = 0.8569, $P < 0.001$; temperature $r_s = 0.5522$, $P < 0.001$). However no hourly measurements of rain duration and wind direction could be taken at the roost. As these variables were considered important, some idea of how relevant the Turnhouse observations were in relation to Stevenson Wood was necessary.

Haddington Meteorological Station data for wind direction were compared with Turnhouse observations for 0900 hrs. each morning on November 13-26; December 8-26; January 3-8, 19-27; February 15-25. A Spearman rank correlation technique was used giving a highly significant correlation $r_s = 0.8758$, $P < 0.001$. Marshall (1966) also found that the wind direction at a site 10 km. N.E. of the study roost reflected the tendency of the averaged, continuously recorded direction at Turnhouse.

A significant Spearman rank correlation coefficient ($r_s = 0.4017$, $P < 0.05$) was found between Turnhouse rain data and that of Haddington, suggesting that the Turnhouse data could be used as a rainfall indicator for Haddington. I presumed that the duration of rainfall would be more important in relation to a bird's insulation than the amount of rain falling (see Chapter 5). Data on Turnhouse cloud cover were accepted as appropriate for Haddington, where no observations of cloud cover were obtainable.

APPENDIX 8

SUMMARY OF THE WEATHER DATA USED IN INVESTIGATING THE INFLUENCE OF WEATHER ON FOOD CONSUMPTION OF CAPTIVE ROOKS (CHAPTER 6).

	OCT		NOV		DEC		JAN		FEB	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
MX1	14.2	3.5	12.3	3.2	10.0	3.2	4.9	9.3	6.1	3.2
MN1	9.5	4.7	5.9	3.3	6.9	2.8	2.3	3.1	1.7	2.5
MX2	14.4	4.4	11.1	2.8	9.8	2.4	5.6	2.0	5.9	2.7
MN2	10.3	4.4	7.1	3.8	7.6	2.5	3.3	2.4	3.4	2.3
WNM	6.1	9.2	6.7	3.3	13.4	15.3	5.5	1.8	3.1	0.6
WDM	5.2	3.1	7.1	2.9	11.6	12.8	5.1	2.5	4.0	2.8
RN	4.3	9.4	2.0	6.0	6.2	16.0	16.2	21.8	25.7	32.0
RD	9.4	16.9	1.4	4.3	3.2	9.4	6.6	12.7	7.6	13.2

Key: MX1, maximum temperature during the night; MN1, minimum temperature during the night; (°C)
MX2, maximum tempeeature during the day; MN2, minimum temperature during the day; (°C)
WNM, mean wind velocity during the night; WDM, mean wind velocity during the day; (m/sec)
RN, total rain duration during the night; RD, total rain duration during the day. (in $\frac{1}{10}$ hr.)

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ABSTRACT OF THESIS

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Title of Thesis The social organisation of roosting in rooks and jackdaws.

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1. A review of the autumn and winter roosting behaviour of rooks and jackdaws was presented. A critical summary of published hypotheses as explanations of communal roosting by Corvidae was given, and one hypothesis concerning the relationship between heat loss, social organisation and weather was chosen for detailed study.

Two questions were posed:-

(1) Does the behaviour of rooks and jackdaws in a communal roost reduce the rate of loss of heat energy?

(2) If energy is saved, is this saving likely to be critical for survival?

2. The synchronisation of the daily movements of birds to and from the roost was shown to be influenced by light intensity, although weather and other factors might have modifying influences. This behaviour affects the length of the feeding day, rooks feeding longer on bright days.

3. The results of an investigation into the interrelation between the spatial organisation in the roost and the weather showed that windspeed, rainfall duration, temperature, cloud cover and wind direction alter and change the distribution of birds both across the wood and vertically within a tree. The climatological characteristics of woods of different composition are discussed. In general birds preferred the warmer and less windy parts of the wood. Adult rooks perched at the tops of trees, while young rooks and jackdaws perched below. Aggressive encounters increased and decreased in relation to bird movement within the roost. The influence of shelter on heat loss is discussed.

4. The social hierarchy of groups of rooks of all ages was examined. The hierarchy was basically age-related, straight-line and peck right. Successful encounters over perches and food resulted in the same 'victor' or 'loser'. Both rooks and jackdaws preferred the highest available perches; the higher the perch, the higher the status of the incumbent.

Male rooks dominate females and older birds are dominant to first year-old birds. Status recognition (without aggressive encounters occurring) appeared to be based on posture, levels of intensity of threat, facial bareness and deportment.

5. The rate of loss of heat by rooks under different climatic and social situations was measured. An indirect calorimetric method was used, and skin and cloacal temperatures were also recorded. Heat loss increased with decreasing ambient temperature. With rain or wind the heat loss was increased still more, with rain and wind the heat loss was twice that with temperature alone at -7.5°C. A true pair of rooks (i.e. male and female) lost less heat than each bird did individually (under the same thermal conditions), and a 'false' pair (i.e. two males) lost only slightly less heat than individually. The results were not statistically significant although a trend was apparent.

6. The relationship, in captivity, between food intake and weather was analysed. When aggressive encounters between birds occurred the time food was available was important in determining the amount of food eaten, although the minimum temperature during the day was also of importance. Without aggressive encounters between birds occurring the minimum temperature during the day was the most important variable affecting food intake, night-time weather variables being secondary in importance and the length of the day only slightly significant. Weather had a large influence on food consumption. Loss in weight of the lighter, more subordinate birds within each age group occurred through aggressive encounters between birds, at the food source, and also because feeding by the subordinates was inhibited.

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7. The body composition of rooks was measured from specimens taken at the roost. Adult birds had almost twice as much fat as young birds and slightly more ingested food.

8. Heat loss in relation to energy reserves was considered for young and adult rooks in different parts of the roost. Survival times were calculated for both age groups indicating a much shorter time for young birds. Published information was introduced to show that it is mainly the young that die in winter. In conclusion, rooks chose the more sheltered places to roost in within the roosting wood. They therefore (in general) used less energy than they would if they used the wood at random for roosting. However, the saving of energy was small. It was unlikely to be important for survival for adults in an average winter, but it may well have been important for young birds which have much lower reserves to draw upon than adults. Some young rooks die in winter but adults rarely, and this gave support to the view that the young need to save energy but due to their subordinate position may not always achieve the saving. The more precarious position of the young resulted from their substantially lower fat reserves and this may have been a function not only of roosting but also of competition on the feeding grounds by day.