THE SOCIAL ORGANIZATION OF SCOTTISH BLACKFACE SHEEP.

by

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This thesis has been composed by me and is a record of my own work.

ABSTRACT

This thesis describes the social organization of a home range group of Scottish Blackface sheep occupying an area known as the Howlet in the Pentland Hills, Midlothian, Scotland. Evidence to support the contention that these sheep constitute a home range group is presented.

The home range occupied by the group was found to be at a minimum in winter (the winter range) and at a maximum in summer (the summer range). Using cluster analysis on individuals´ location data it was shown that in autumn and winter there was little individual variation in home range behaviour in comparison to summer. Variability in home range size showed a similar trend. Ewes in summer could occupy home ranges differing by as much as 40 ha. It was further illustrated that in winter ewes showed increased gregariousness, forming large sub-groups and being readily influenced by the movements of other sheep, whilst in summer the converse was true. It was concluded that these seasonal variations in social organization occurred largely in response to ecological changes; in winter a reduction in the variability in the quality of the hill swards and the worsening weather; in summer the increase in the dispersion of resources through the growth of the widley distributed Agrostis-Festuca swards. The presence of a lamb in summer would seem to satisfy the ewe´s proximal motivation to group, thus allowing her greater flexibilty of movement between Agrostis-Festuca swards.

In contrast to the findings of previous workers, the ewe-daughter bond was found to be of little significance beyond 7 to 8 months. Around this age ewe-lambs formed peer groups that during their first winter moved independently of other group members. In their second summer ewe-lambs became integrated into the larger social group. Early experience was found to be important in determining summer home range patterns of individual ewe-lambs. The cohesion of the home range group seemed to result from the animals´ preference for an area and their motivation to form sub-groups; specific bonds between individuals were not of importance in this respect.

Social organization was shown to negate supposed advantages of feedblocks, fed as a supplement to the group during winter. Ewe-lambs did not follow older ewes to the feedblock; 2 and 3 year old ewes did not compete succesfully with older ewes when feeding at the block; further the feedblocks apparently decreased the size of ewes home ranges, which it seems must have led to the overuse of the lower parts, and conversely underuse of upper parts of the range.

The results are discussed in relation to literature on wild, feral and domestic sheep. It is concluded that whilst in general terms the social behaviour of domestic sheep remains close in form to that found in feral and wild populations, that there remain unresolved questions over the function of aspects of social behaviour in domestic ungulates. It is argued that that a better understanding of the effects of domestication on, for example, anti-predator behaviour in domestic sheep would help in the construction of a theoretical framework for the study of the ethology of farm animals.

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My thanks and gratitude go to all my family who have also suffered in the making of this, particularly my parents Henry and Jess Lawrence. Finally I would like to especially thank Candace who has supported, encouraged and organized me throughout. It was she who exonerated me not to write anything in the acknowledgements that would be an embarrassment 6 months later, and in particular not to thank the sheep or to quote from Bertrand Russel or the late Emperor Shai. As a prologue therefore the following will have to suffice;

"Like Alexander the Great they have spread all across the known world. Unlike him, they no sooner arrive than they get sheared, barked at, castrated, thrown into dips, and left all night up mountains. Is it any wonder they go everywhere in terrified gangs?" (Pile 1983, ´The Joy of Sheep´).

CONTENTS

CHAPTER 1 GENERAL INTRODUCTION

Sheep (Ovis) are believed to have evolved in southwest and central Asia and to have subsequently spread westwards towards the Mediterannean, and eastwards across Siberia and into North America (Devendra and Coop 1982). They have in evolutionary terms been a successful species being the most widely spread of the Bovidae (Ryder 1983). At least part of their success seems attributable to them pioneering new habitats in the wake of glacial retreats (Geist 1971).

There is a great deal of dispute surrounding speciation of the genus Ovis. Ryder (1983) inclines to the view that as most types of wild sheep will interbreed freely they should be regarded as a single species, whilst Geist (1971) maintains that inter-breeding in zoos is too artificial a situation to use as a basis for taxonomy. For present purposes it is enough to note that Geist (1971) considers wild sheep as forming 6 species, 2 of which, Ovis musimon (mouflon) and Ovis Canadensis (bighorn sheep) are mentioned in this thesis.

The present day domesticated sheep (Ovis aries) originated from wild species present in southwest Asia 8000-10000 years ago (Zeuner 1963). The spread of domestic sheep can be regarded as a series of migrations. The first of these was of hair sheep, the Soay sheep of St Kilda being descendants of these (Campbell 1974). Secondly came white wooled sheep introduced by the Romans into Western Europe. These were to become major contributors to British breeds (Devendra and Coop 1982).

Ryder (1983) has listed the major morphological changes in sheep following domestication. These are: a reduction in horn size and a lengthening of the tail; the development of the woolly under coat at the expense of the hairy outer coat and a decreased tendency to moult; a decrease in coat pigments and finally a decreased a brain size and reduced diameter of the eye socket.

Behaviourally domestic sheep although being found to be broadly similar to wild sheep are apparently different in some important respects. Both form social groups, individuals of which use common home ranges (home range groups) (Hunter 1964; Geist 1971). However wild bighorn ewes may be members of more than one group, occupying a number of different seasonal ranges between which they migrate (Geist 1971). In addition although in domestic sheep the mother-daughter bond has been reported to be permanent (Hunter and Milner 1963), in wild sheep the mother and daughter cease to associate beyond the end of the lamb's first year of life (Geist 1971; Berger 1979a). The agonistic and sexual behaviour of domestic rams (Banks 1965) bears some resemblance to that of the bighorn (Geist 1971; Shackelton and Shanks 1984). However domestic rams do not perform clashes (Geist 1971) and they use a combination of the front kick and the twist displays (Geist 1971) in a pre-copulatory behaviour pattern known as the nudge (Banks 1965) not found in wild sheep. Soay rams perform the nudge both in sexual contexts and in agonistic encounters with other rams (Grubb 1974a). Lawrence (1980a) made a qualitative assessment of the similarity between a range of behaviour patterns of domestic and wild sheep and found them to be broadly similar in form. However the question remains as to whether the same function can be ascribed to the same behaviour in the domestic animal as in the wild (see below).

The Scottish Blackface is today the most numerous breed of domestic sheep in the British Isles (Ryder 1983). It had apparently established itself by the middle of the eighteenth century gradually replacing a primitive dun faced native breed (Parnell 1939). It is interesting to note that it is in only relatively recent times that meat, through the production of fat lambs, has been recognised as the main product of sheep, previously milk being of primary importance, wool and manure being by-products and meat being unimportant (Ryder 1983).

Sheep at present are husbanded under a great variety of intensive, semi-intensive and extensive management systems (Owen 1976). In Scotland extensive farming of sheep is the most prevalent system and some 95% of the sheep meat produced is from less favoured marginal areas (Wilson 1984). Traditional hill sheep systems tend to be largely non-intrusive in their management. The breeding ewes are maintained on the hill throughout the year, fencing is largely absent and the sheep form home range groups (Hunter 1964) (see above). A proportion of ewes from each group are culled each year and the replacements are chosen from the same home range group. These replacements are either left with their dams on the hill or they are overwintered on low ground (Cunningham 1982). Under these conditions the behaviour of the ewe can be expected to have a greater significance to production than in more intensive systems, where the behaviour of animals is under greater management control. Hunter (1960) recognized the significance of understanding the ecology of sheep grazing systems to the improvement of hill farming. This realization also led him to study the behaviour of hill sheep and its relationship with production (Hunter 1962; Hunter and Davies 1963; Hunter and Milner 1963; Hunter 1964). Despite the recognition that behaviour is likely to have importance to the improvement of hill sheep systems, the work of Hunter and his co-workers remains virtually our sole source of information on behavioural aspects of hill sheep. It should be noted that Hunter's work at the Hill Farming Research Organization in the 1960's provided the basic framework from which arose The Two-Pasture System, a modern improvement to traditional hill farming in which improved pasture is set aside for the critical times of lambing and mating (Russel 1983).

Recently there have been efforts made to apply ethological methods and concepts to the study of farm animals (Wood-Gush 1983). In large part this has arisen through an increased concern over the welfare of farm animals and it seems that animal welfare will be a significant issue in the further development of livestock systems (Wilson and Lawrence 1985). There have also been a number of recent studies, particularly in Australasia, concerned with the application of ethology to the improvement of extensive systems of production (Arnold and Dudzinski 1978). McBride (1984) however still sees the practical contribution of applied ethology to livestock production as relatively unimpressive, principally because there is no organized and accepted body of theory on which an applied science can be built. Certainly there are unresolved difficulties in applying theories applicable under natural selection to animals which have existed under artificial selection for many generations. Often the basic information required to estimate the effects of domestication on adaptative behaviour in domestic animals is not available. Do we, for example, as Wood-Gush (1983) suggests keep farm animals in groups larger than they are adapted for? In order to answer this and other related questions Wood-Gush calls for further study of farm animals in environments where they can space themselves and form groups under their own volition.

With these points in mind the rationale behind the present study was based on:

1) The significance of Blackface sheep farming to the Scottish agricultural economy.

2) The likely importance that a knowledge of the ethology of hill sheep would have in deliberations over improvements to hill sheep farming.

3) The need for basic data on the ethology of free-ranging hill sheep on which to base welfare recommendations both for hill sheep and for those more intensively husbanded.

4) The lack of a modern study of the ethology of hill sheep.

The general aim of the study was to examine in detail the social organization of a home range group of Scottish Blackface sheep, living under more or less traditional and unrestrained conditions. The study was designed to answer the following questions:

1) What is the nature of ranging behaviour and how does that of different members of a home range group relate?

2) What types of social bonds exist between individuals: in particular what is the nature of the ewe-daughter bond?

3) Are there recognizable seasonal changes in the social behaviour of hill ewes, and if so what is their significance?

4) How is the social organization of the hill ewe affected by specific management practices and with what likely effects on production parameters?

General Methods are presented in Chapter 2, Results in Chapters 3 to 6 (each dealing with subdivisions of one of the questions outlined above) and a General Discussion in Chapter 7.

CHAPTER 2 GENERAL METHODS

2:1 THE STUDY SITE

2:1:1 Topography

The study site is illustrated in Figure 2.1. It is located in the Pentland Hills, Midlothian, on Kirkton Farm, Glencorse.

The area is a valley divided by Loganlee Reservoir. The south side of the valley is formed by Carnethy Hill and the north side by the Black and Gask Hills. The sides of Carnethy Hill are rather uniform and steep. Of the two burns found on this side one, Flesh Cleugh, has formed a fairly substantial gully which provides the sheep with some shelter from the prevalent SW winds, to which the steep sides of Carnethy are exposed.

The north side of the valley is much more variable in topography. East from the point where the Howlet burn enters the reservoir the slopes of Gask Hill run steeply and uniformly down to the water. West from the end of the Howlet burn there is a steep slope that rises some 30m before levelling off into a plateau. This gentle slope then later steepens and rises to another plateau which forms the top of the SW spur of the Black Hill.

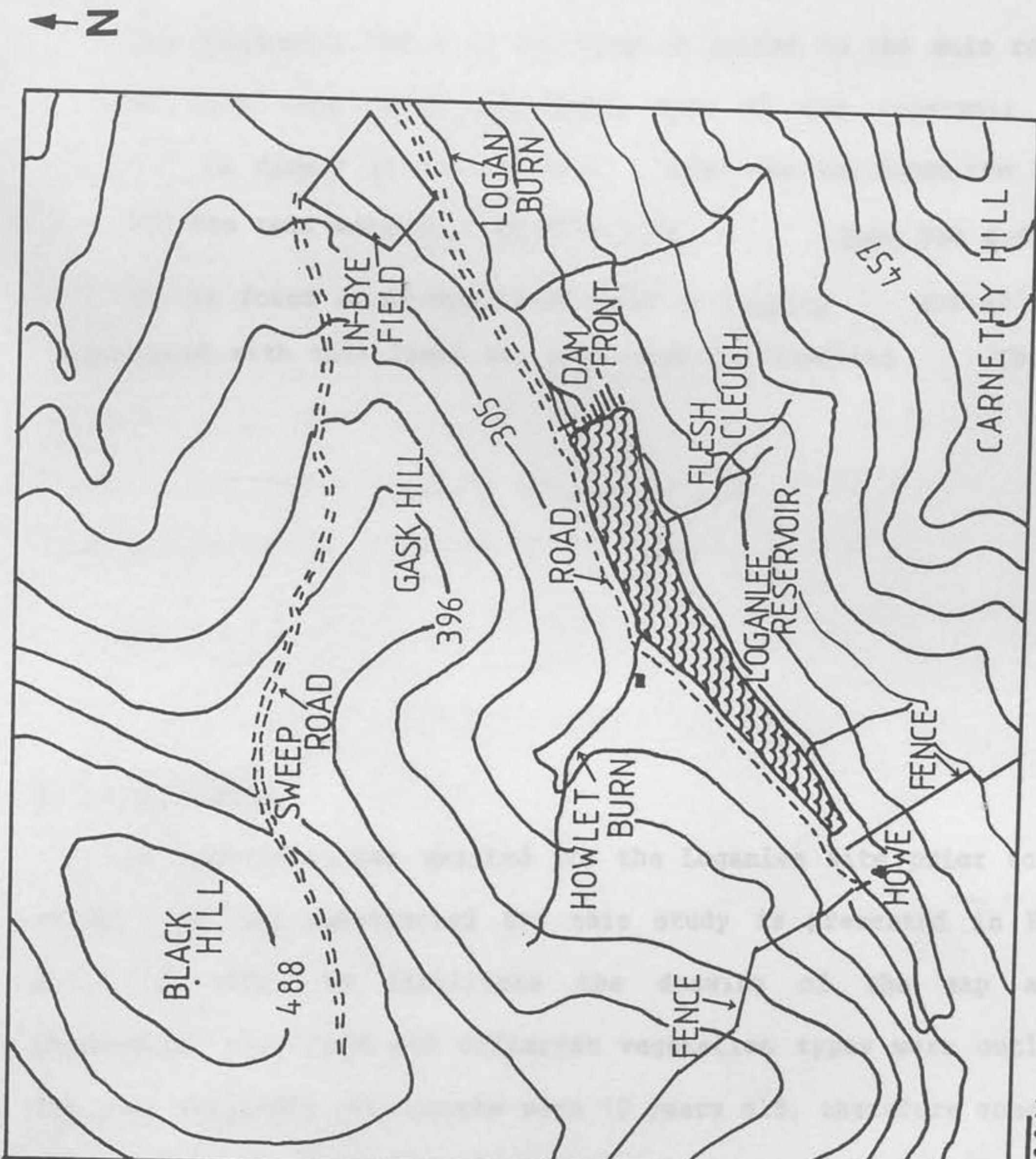
The Howlet burn separates this part of the area from a bowl formed by the main SE facing slope of the Black Hill and the SW facing slope of the Gask Hill. The floor of this bowl has two smaller burns that are tributaries to the Howlet burn.

The flat col between the Gask and Black Hills forms a natural NW/SE division. From this col a track known as the "sweep road" moves almost due west across the SE slopes of the Black Hill. This track peters out as it approaches the top of the SW spur of the Black Hill. This area to the north of the reservoir enclosed within the sides of the Black and Gask Hills, but excluding their tops, will be

FIGURE 2.1

MAP OF THE STUDY SITE

This map was drawn from the OS 1:25,000 series, Sheets NT 16 and 26. The scale is approximately 1:12,500.


N
LOGAN BURN
IN-BYE FIELD
DAM FRONT
457
CARNETHY HILL
NT200600
FLESH CLEUGH
305
GASK HILL
ROAD
LOGANLEE RESERVOIR
396
SWEEP ROAD
HOWLET BURN
FENCE
HOWE
BLACK HILL
488
FENCE
100 M

known as the Howlet.

The fence that separates Kirkton Farm from its western neighbour runs from the SW end of the reservoir up and over the SW spur of the Black Hill. Likewise on the south side of the reservoir a fence runs up the slopes of Carnethy Hill again separating the two farms.

The shepherd's house at the Howe is joined to the main road by a track that runs along the north side of the reservoir. The reservoir is dammed at its NE end. From the dam front the Logan Burn and the road move in a NE direction. Some 300 m in this direction is found an in-bye field used at tupping and at lambing. Associated with this field are pens used for handling the sheep.

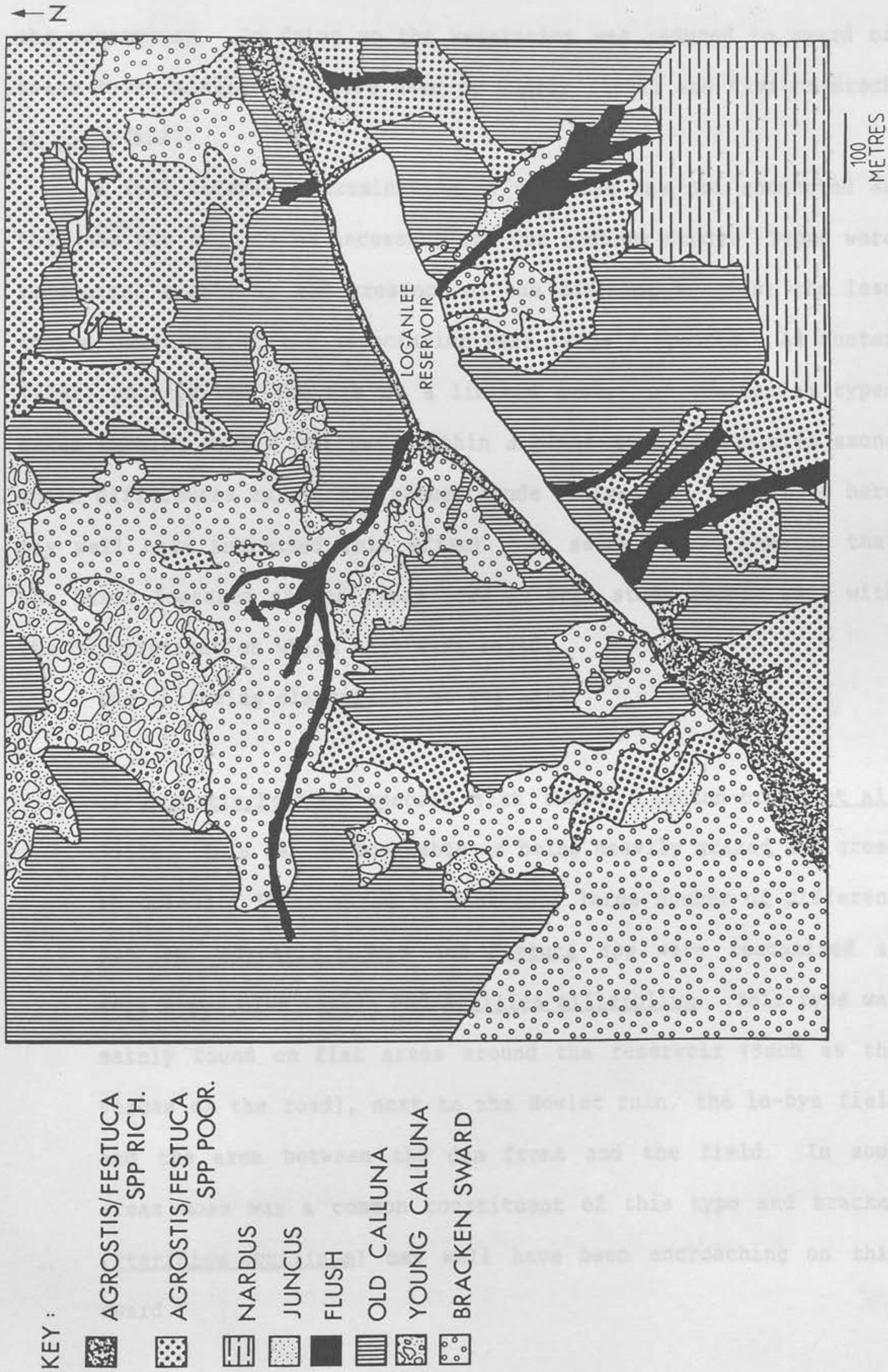
2:1:2 Vegetation

No vegetation map existed for the Loganlee site prior to this study. The map constructed for this study is presented in Figure 2.2. In order to facilitate the drawing of the map aerial photographs were used and different vegetation types were outlined. The only available photographs were 10 years old, therefore some time had to be spent in the field adjusting for changes that had occurred in the intervening period. The map should be treated with some caution therefore, as regards the exact positioning of the vegetation types.

FIGURE 2.2

VEGETATION MAP OF THE STUDY SITE.

This figure shows the distribution of the 8 common vegetation types found in the study site. This diagram was drawn originally from aerial photographs. It can only be said to give a basic description of the vegetational characteristics of the area. The key to the different types can be found overleaf.



N
100 METRES
LOGANLEE RESERVOIR
KEY:
AGROSTIS/FESTUCA SPP RICH.
AGROSTIS/FESTUCA SPP POOR.
NARDUS
JUNCUS
FLUSH
OLD CALLUNA
YOUNG CALLUNA
BRACKEN SWARD

Eight vegetation types based on those described by McVean and Ratcliffe (1962) and McVean and Lockie (1969) were used to categorise the vegetation. In doing so the vegetation was reduced to sward or graze types similar to those used by Hunter (1962) and Clutton-Brock et al. (1982).

A full botanical examination of the area was not conducted as this was not seen to be necessary for the present study. Types were recognised mainly by the presence of the dominant species; the less common constants of the association were largely ignored. As Hunter (1962) pointed out the use of a limited number of vegetation types makes mapping simple but puts within a plant type communities among which differences exist; the rather crude analysis of types used here may well have increased this effect. It seems likely however that the basic features of the types used in this study accord well with the descriptions on which they were based.

The following classification was used:

1) Agrostis/Festuca species rich sward (Clutton-brock et al. 1982). This was recognizable as being heavily grazed and green in colour. It appeared to contain a large number of different species. Agrostis tenuis and Festuca spp were recognized as were Ranunculus repens and Achillea millefolium. This type was mainly found on flat areas around the reservoir (such as the verges of the road), next to the Howlet ruin, the in-bye field and the area between the dam front and the field. In some areas moss was a common constituent of this type and bracken (Pteridium aquilinum) may well have been encroaching on this sward.

b) Agrostis/Festuca species poor sward (Clutton-Brock et al. 1982). This was recognized as being much less heavily grazed and much less green in colour. There appeared to be fewer species. Agrostis tenuis, Festuca spp, Deschampsia flexuosa, and Nardus stricta were found. Some Molinia caerulea was found in wetter areas. Vaccinium myrtilus was often found within this sward as were other heaths including Calluna vulgaris and Erica cinerea.

This type was very widespread, occurring in "stable" communities mixed with the heaths mentioned above and also occurring in local abundance wherever heather was burnt. On south facing slopes, such as the Howlet, heather quickly became dominant again after burning but on north facing slopes, such as Carnethy, burnt heather often seemed to have been almost totally replaced by this type. This sward also seemed to be present under the bracken canopy (see below) and dominated an area sprayed to eliminate bracken, Grid Area 18 (see 3:2:2).

c) Nardus heath-grassland (Hunter 1962). This was recognised as being dominated by mat grass (Nardus stricta), being of a white colour and being very undergrazed. Other grasses, such as Agrostis tenuis and Deschampsia flexuosa were present but in low quantities. This type was very common on the upper slopes of Carnethy but very little was found in the Howlet.

d) Juncus squarrosus grassland. This type was dominated by Juncus squarrosus and occurred in low lying wet areas. Ranunculus repens and Carex spp were found in this type as were some grasses such as Agrostis tenuis. This was not a common sward although Juncus did occur sporadically at low abundances through much of the lower lying areas.

e)Flush. This type does not indicate swards dominated by any one species but swards obviously associated with mineral flushes. These were recognised by their green colour and by a reasonably rich diversity of species including Agrostis tenuis, Festuca spp, Deschampsia flexuosa, Nardus stricta, Ranunculus repens, Bellis perennis, Juncus squarrosus and moss species. This type occurred in the vicinity of the large burns and also on the hillside, near moving tracts of water and where mineral flushes moved near the surface. It was decided to classify this type separately as there was more similarity between the species found along the length of the flush than between the surrounding communities. This was despite the obvious altitudinal differences found between the head and the bottom of the flush.

f)Old Calluna heath. This sward consisted of in the main a monoculture of Calluna vulgaris maintained by the practice of muirburn (McVean and Lockie 1969). The heather in this type had probably not been burnt for at least 6 years and was in the building or mature phases described by Gimingham (1972). For the sake of simplicity, those communities where Calluna achieved almost total dominance and those where its cover was reduced down to 60% and replaced by Agrostis-Festuca species poor sward are combined together.

g)Young Calluna heath. This sward consisted of heather stands that had been burnt within the last 6 years and were recognizably young in form (corresponding to the pioneer phase (Gimingham, 1972)). If the heather had been recently burnt, the young heather had to cover at least 60% of the area (as estimated by eye) to be placed in this type. If the cover of young heather was less than 60% generally the area would be classified as Agrostis/Festuca species poor sward.

h)Pteridium aquilinum sward. Large tracts of the lower lying areas of the Howlet were infested by bracken (Pteridium aquilinum). Often the cover of bracken was dense, all but destroying other vegetation beneath it. As mentioned previously where vegetation did survive it was thought to consist basically of Agrostis/Festuca species poor sward, although (Hunter, 1962) thought that the creeping soft-grass Holcus mollis may have been encouraged to grow by the shading. It seems likely that the bracken infestation has been growing with each year.

2:2 THE STUDY ANIMALS

2:2:1 The Animals and the Area

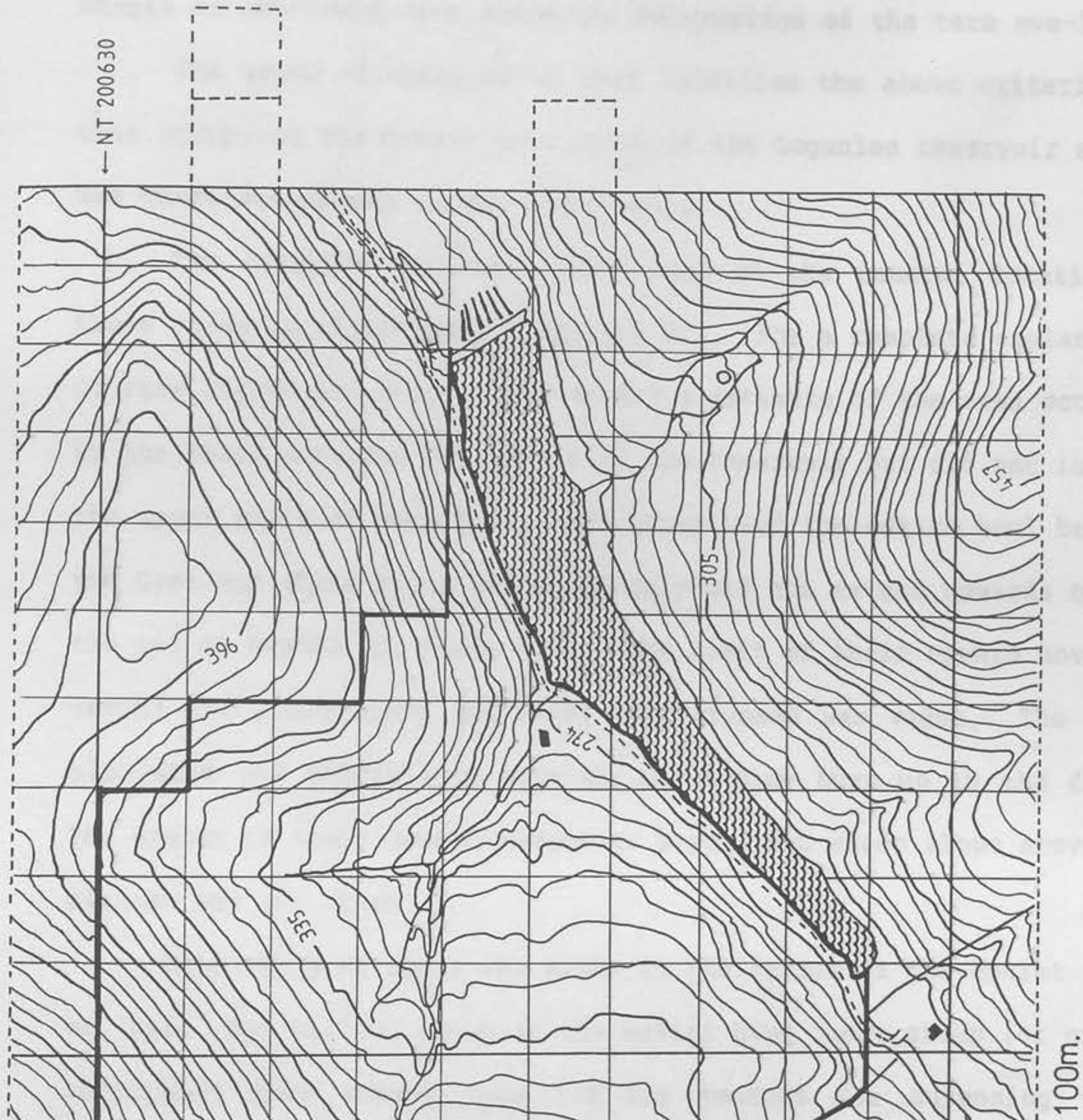
All sheep in the study were of pure Blackface stock.

The study group was not chosen at random but in consultation with the farmer. Four important criteria had to be met; a) the group must not contain too many individuals; b) it should be reasonably

FIGURE 2.3

GRID MAP OF THE STUDY SITE.

This figure illustrates the grid map used to determine the location of the study animals, drawn from the OS 1:10,560 series, Sheet NT 16 SE. The thick line indicates the extent of the farmer´s original estimate of the area occupied by the Howlet group. The dotted lines at the top and bottom of the map indicate that those grid squares are not equivalent to one hectare (see 2:4:1, pg 31). Of the grid squares added to the eastern border, again not equivalent to one hectare, the top pair represent the easterly continuation of the road and in-bye field respectively, whilst the lower one represents a patch of Agrostis-Festuca species poor sward grazed by Howlet animals off the edge of Sheet NT 16 SE (see 2:4:1, pg 31).


NT 200630
396
305
274
335
457
488
GRIDS 100m x 100m
N

accessible; c) the shepherding regime should not be strict thus allowing the animals to express their behaviour freely; d) the farmer should use daughters born of the group to replace older culled ewes and weaning should be natural. These daughters will be known in the thesis as ewe-lambs (see below for description of the term ewe-lamb).

The group of sheep which best fulfilled the above criteria was that occupying the Howlet area north of the Loganlee reservoir and it was therefore chosen as the study group.

The farmer's original description of the general location of these sheep is illustrated in Figure 2.3. For a complete explanation of this figure see 2:4:1. The farmer's estimate of the area occupied by the sheep extended the length of the reservoir but did not include the upper parts of Gask Hill. The group used the entire bowl between the Gask and Black Hills but apparently did not extend upwards beyond the col or beyond the sweep road. The limit of their upward movement beyond the point where the sweep road stopped was vague. The group also used the entire area west of the Howlet burn up to the fence. The extent of their upward movements beyond the steep slope above the plateau was not clear.

This group of sheep was known to the farmer as the Howlet 'cut' or 'heft' but will be known as the Howlet home range group (or group) throughout this thesis (see 3:4 for reasons for supposing these animals constitute a home range group).

2:2:2 <u>Identification of Individuals</u>

It was essential to recognize all individuals in the group individually.

The initial method employed was developed from a technique used to identify Clun Forest ewes by Ewbank (1967). This consisted of a saddle of polypropylene material about 9" wide; stiffened by wood inserts at either end; painted red with 5" white letters and tied underneath by terylene tapes. In addition it was thought necessary to sew the material into the ewe´s fleece to prevent the material from slipping round the animal.

These saddles, although very time consuming to make, proved extremely useful in the initial stages of the study. The animals could be identified quickly from a distance, an important point as most of the animals took between 3 and 6 months to habituate fully to the observer. Also, because of the conspicuous nature of the colours used it was possible to spot marked ewes in unexpected places or amongst other groups of sheep. This facilitated accurate measurement of the home range of the group.

Despite their utility however these saddles proved occasionally injurious to the sheep. On occasions ewes trapped one of their hind feet underneath the rear terylene strap when lying down. Most of these animals were caught and had their foot released but on three occasions the strap was not trapped by the foot and it worked its way up the back of the leg, where it caused mild to serious abrasions to the thigh.

The saddles had to be removed for shearing in June 1981 and after then it was decided to mark the sheep with different colours of insulating tape wrapped around the horn. Six colours were used (red,

TABLE 2.1

DEMOGRAPHY OF HOWLET GROUP IN SUMMER 1981

Columns represent the different age classes (ie 1 YR means 1 year old; 1980 means born in 1980). The numbers in the columns are the identification numbers of the sheep in that age class.

1 YR 1980	2 YR 1979	3 YR 1978	4 YR 1977	5 YR 1976	6 YR 1975	7 YR 1974	8 YR 1973	? YR
49	1	10	6	2	8	38	117	21
50	5	11	9	3	14			32
51	7	12	15	4	31			44
52	13	16	18	25	39			114
53	17	22	28	29	42			
54	20	27	46	34				
55	26	35	118	36				
56	30	37	120	40				
100	33	48		41				
101	116	119		45				
113		121						

TABLE 2.2

DEMOGRAPHY OF HOWLET GROUP FROM AUTUMN 1981

(see Figure 2.1 for explanation)

1 YR 1981	2 YR 1980	3 YR 1979	4 YR 1978	5 YR 1977	6 YR 1976	7 YR 1975	? YR
68	49	1	10	6	2	8	21
69	50	5	11	9	3	39	32
70	51	7	12	15	4	42	44
71	53	13	16	18	34		114
72	54	17	22	28	36		
73	55	20	27	46	41		
74	56	26	35	118	45		
75	100	30	37	120			
76	101	116	48				
77	113		121				
78							
79							
80							
81							
82							
83							

blue, yellow, white, green and black) and combinations could contain 1 to 4 different colours. The code was duplicated on both horns.

The sheep were always marked in the pens ajoining the in-bye field, mentioned in Section 2:1:1, having been first gathered by the farmer and his dogs. They were released in small groups on completion of marking. No attempt was made to drive the animals back to the Howlet area.

2:2:3 Composition of the Howlet Home Range Group

In April 1981 at the start of observations the group consisted of 62 animals. Fifty-five of these had been marked on 24/02/81; seven unmarked ewes were subsequently added to the group (see 3:4). The demography of the group during this period is given in Table 2.1. There were 36 multiparous, or mature ewes (ranging from 3 to 8 years of age), 10 primiparous ewes, or gimmers, (2 years of age) and 12 ewe-lambs (1 year of age). Female lambs are termed ewe-lambs until they are mated at approximately 18 months of age when they become gimmers. A gimmer becomes a mature ewe at approximately 30 months or second mating. In this thesis mature ewes will be referred to as ewes unless a specific age-class is being discussed (e.g. 3 year old ewes). The age of the animals was known as the horns were branded with the last digit of the year that they were born (e.g. ′0′ for 1980). There were 4 ewes whose age was not discernable. During the summer of 1981 one ewe died (Number 117) and one ewe-lamb permanently left the group (Number 52).

TABLE 2.3

KNOWN FAMILY RELATIONSHIPS IN THE HOWLET GROUP (BEFORE AUGUST 1982)

The relationships identified by the farmer are marked by an asterisk; all others were identified by the observer. The year of birth of the daughters is given in brackets. The daughters identified in 1982 are not included as they were not used in the analysis of individual relationships.

Mother	Daughter	Sister
3	68(1981)	
4	69(1981)	29(1976)*
11	70(1981)	
12	71(1981)	
17	72(1981)	
18	56(1980)*	
22	73(1981)	
27	83(1981)	
28	74(1981)	
30	75(1981)	
31	49(1980)*	
32	76(1981)	
34	77(1981)	
35	78(1981)	
36	79(1981)	
38	26(1979)*	
40	80(1981)	
45	81(1981)	
116	84(1981)	
118	82(1981)	

In August 1981 the replacement ewe-lambs were retained (see 2:3) and in September 8 ewes were culled either due to old age or mastitis. Table 2.2 illustrates the demography of the group from October 1981 to August 1982. There was a total of 68 sheep including 37 ewes, 10 gimmers and 17 ewe-lambs. One ewe died in March 1982 (Number 13). Two ewe-lambs died in parturition in May 1982 (Numbers 78 and 83). No ewe-lambs left the group for any period longer than a month. Again the ages of 4 ewes were unknown.

In August 1982 the replacement ewe-lambs were again chosen and in September 13 old ewes were culled. The composition from this time until the end of the study was 34 ewes, 15 gimmers and 13 ewe-lambs. The ages of 3 ewes remained unknown. One ewe at least is known to have died in January 1983.

The known family relationships are shown in Table 2.3. Three of these were identified by the farmer , the rest by myself. In the latter cases I photographed all female lambs who had been chosen as replacement ewe-lambs, in the last 2 weeks in August; well in advance of natural weaning (see 4:3). When the group were next gathered in September these ewe-lambs were given the same colour code as their mothers, with a white tape at the front of the horn to distinguish them as lambs.

2:3 MANAGEMENT OF THE GROUP

It is important to describe the management of the animals as it affects the feeding behaviour , the movements and the composition of

TABLE 2.4

CALENDAR OF MANAGEMENT EVENTS WHICH AFFECT THE HOWLET GROUP

September:	One-fifth of the adult ewes are culled due to their age or because they are ill. They are replaced by ewe-lambs from the same group.
October:	Winter dip.
November:	Ewes are brought into in-bye field for tupping. They are kept there for 17 days and then released back onto the hill with the rams until January.
December:	Ewes are fed a feedblock ('rumevite') from the time they return to the hill with the rams until April.
April:	Anti-helminthic treatment.
April/May:	Lambing. Ewes are inspected twice a day. Lambs are caught, tagged and injected.
June:	Male lambs are castrated and the ewe-lambs are sheared.
July:	The adult ewes are sheared.
August:	First the best of the wethers (male castrates) are weaned and two weeks later all lambs, apart from the replacement ewe-lambs, are also removed from the hill.

the group.

Table 2.4 illustrates the calendar of management events. About one-fifth of the adult ewes in the flock are removed in September. Ewes are generally culled after 5 years on the hill but some animals are kept well past this age (e.g. Number 117 in 1981 was 8 years old).

These culled ewes are replaced by ewe-lambs from the same group. In 1982 the farmer was interested in building up the breeding stock on the Howlet. He therefore kept back an unusually large number of ewe-lambs. In this way the composition of the flock becomes an expression of the artificial selection pressure applied by the farmer.

The ewes are dipped one day at the end of October and then about November 20th the group are brought in for tupping. Mating of the ewe-lambs is prevented by sewing a piece of cloth into the wool across their tails (traditionally known as 'breekin'). This allows the farmer to keep the ewe-lambs on the hill throughout the period of tupping and thus save on the cost of off-wintering. The group are generally kept in the in-bye field with the ram for about the length of one oestrous cycle (17 days). They are then released back onto the hill with the rams in attendance. This second period can be very variable in length depending on weather conditions. In 1981-82 it was not possible to remove the rams from the hill until the second week in January.

From the time that the sheep are released back onto the hill with the rams they are fed a feedblock. Feedblocks contain minerals, a source of energy such as molasses and urea (see Chapter 6 for a fuller description of the use feedblocks). The urea has the effect of increasing the animal's appetite for roughage and facilitating its digestion. The sheep are fed feedblock until they cease to show interest in it, usually sometime in the middle to end of April.

The group are left on the hill until just prior to lambing when they are gathered to be treated for parasites. Any ewes in poor condition at this time are retained in the field and fed a diet of concentrates.

The group lamb on the hill through the latter part of April and much of May. During lambing they are inspected twice daily by the farmer. This is in contrast to the rest of the year when the sheep are rarely disturbed by shepherding. This lack of a strict shepherding regime during most of the year allows the expression of natural movement patterns by the group.

The group are gathered up several times in the summer. Firstly in the middle of June to castrate the male lambs and shear the ewe-lambs; secondly in the middle of July to shear the adult ewes; thirdly in the first week of August to wean the best of the wether lambs; and finally about the 20th of August to wean all other lambs apart from the replacement ewe-lambs.

2:4 SAMPLING METHODS

2:4:1 <u>The Scan Samples</u>

Much of the research effort in this project was designed around a system of instantaneous sampling (Lehner 1979) where several individuals are 'scanned' at predetermined points in time.

For the purposes of this thesis the scanning technique was developed into a form of census similar to that used by Clutton-Brock et al. (1982). Each scan was designed to gather data on the location and activity of each individual in the group. In addition the size and composition of the sub-group to which each ewe was attached was recorded. Time of day and weather data were also collected.

See Appendix 4 for further details of sampling methods.

1 The sample seasons

Data was collected in the following seasons:

a)Summer 1981. This period ran from 21/05/81 to 19/08/81 (i.e. from lambing to artificial weaning). Ninety scans (or 90 observations/animal) were carried out during this period over a total of 31 days.

b)Post weaning 1981. This short period ran from 27/08/81 to 16/09/81 (i.e. from artificial weaning to culling). Twenty-four scans were performed in 8 days during this period.

c)Autumn 1981. This sample period ran from 13/10/81 to 17/11/81 (i.e. from culling to tupping). Sixty scans were completed over 21 days.

d)Winter 1982. This period ran from 02/02/82 to 05/04/82 (i.e. from the end of tupping to lambing). Seventy-eight scans were performed over 26 days.

e)Summer 1982. This period ran from 04/05/82 to 23/08/82 (i.e. from lambing to weaning). Eighty-four scans were completed over 28 days.

f)Post weaning 1982. This final period ran from 30/08/82 to 17/09/82 (i.e. weaning to culling). Thirty scans were carried out over 10 days.

2 <u>The sample area</u>

An initial problem was to decide on the size of area that should be covered by the scan to be certain of finding most or all of the group. Initial observations indicated that the farmer´s description of the upward movement of the sheep was correct. Observations therefore did not extend beyond the sweep road or the top of the SW spur of the Black Hill. In addition to sampling the area originally described by the farmer as being that used a by the Howlet group, it was decided initially to include the top and SE slopes of the Gask Hill. Latterly it was decided to exclude the Gask from the sample area as members of the group were only very rarely seen there.

Observations commenced at the end of April 1981 and it quickly became apparent that many of the Howlet group could be found on the south side of the reservoir. Consequently the sides of Carnethy Hill were included in the scan. Animals were also found in the in-bye field, which was therefore also included in the sample area.

3 <u>The grid method for location of individuals</u>

In order to locate sheep the map of the area was divided into 100m x 100m (hectare) grid squares. Conspicuous landmarks such as trees and large stones were found in each grid sqare and their positions marked onto the map. An animal could therefore be allocated to a grid square by judging its position relative to these landmarks.

The grid map that was used during observations is shown in Figure 2.3. The following points should be noted:

a)The top and bottom line of grid squares are not equivalent to one hectare.. Values in these grid squares indicates that an animal or animals have gone beyond the "grid system" in that general location. This inaccuracy could be tolerated due to the low number of occurrences of sheep in these grids squares.

b)The grid squares which have been added to the eastern border of the map as in a) do not represent hectare grid squares. The more western of the top pair of grids represents the easterly continuation of the road and Logan burn, from the edge of the map to the start of the in-bye field. The eastern grid square represents the field. The single grid square lower down represents a specific patch of Agrostis/Festuca species poor sward that Howlet animals grazed, again off the edge of the map.

c)The thicker black line surrounds the farmer's original estimate of the area used by the Howlet sheep. It is important to note that within this area in Summer 1981 the locations of all animals, marked or unmarked, were noted. Outside this line only the locations of marked animals were recorded.

4 Measures of sub-grouping

Initial observations showed that the group readily split into sub-groups or temporary sub-divisions. Following the precedence of a number of workers(e.g. Kummer 1968; Grant 1973; Croft 1981; and recently Clutton-Brock et al. 1982) it was decided to adopt a fixed distance within which individuals could be said to be in the same sub-group.

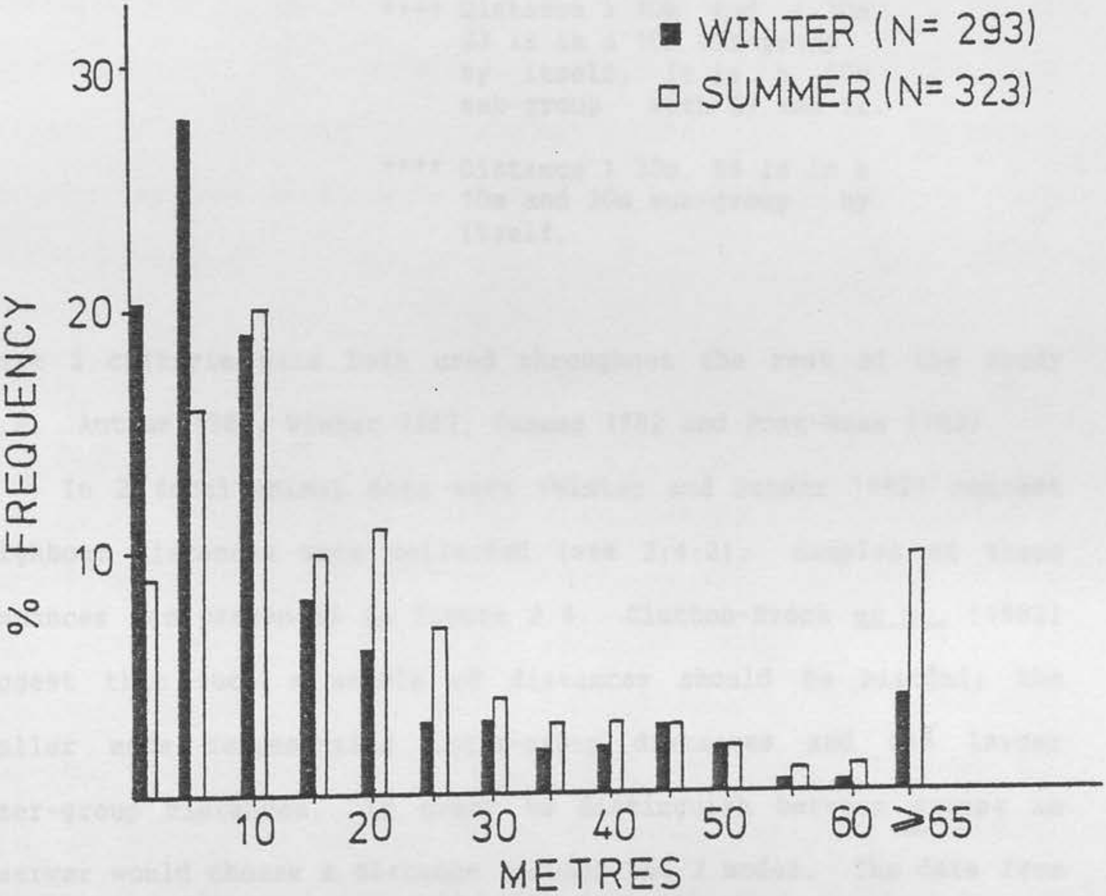
Prior to starting observations in Summer 1981 some distances between apparently separate sub-groups were measured. In many cases it was found that distances in excess of 30m separated these sub-groupings of animals. Thirty metres was therefore used in Summer 1981 as a measure to distinguish between sub-groups,(i.e. animals within 30m of each other were said to be in the same sub-group). However in Autumn 1981, due to a general increase in the number of

FIGURE 2.4

FREQUENCY HISTOGRAM (%) OF NEAREST NEIGHBOUR DISTANCES

IN WINTER 1982 AND SUMMER 1982.

This figure shows the distribution of nearest neighbour distances collected during the focal animal samples in Winter 1982 and Summer 1982.



WINTER (N= 293)
SUMMER (N= 323)
% FREQUENCY
30
20
10
10
20
30
40
50
60
≥65
METRES

animals found within 30m of one another, it was decided to employ a secondary distance of 10m in addition to the original 30m distance. The diagram below illustrates the use of these two distance criteria:

```
     S1-----S2****************** S4
             +
             +
             +
             +          ---- Distance ≤ 10m. S1 and S2
             +               are in a 10m  sub-group.
            S3
                        ++++ Distance > 10m  and  ≤ 30m.
                             S3 is in a 10m sub-group
                             by  itself.  It is  a  30m
                             sub-group   with S1 and S2.
                        **** Distance > 30m. S4 is in a
                             10m and 30m sub-group   by
                             itself.
```

These 2 criteria were both used throughout the rest of the study (i.e. Autumn 1981, Winter 1982, Summer 1982 and Post-Wean 1982).

In 2 focal animal data sets (Winter and Summer 1982) nearest neighbour distances were collected (see 2:4:2). Samples of these distances are presented in Figure 2.4. Clutton-Brock <u>et al.</u> (1982) suggest that such a sample of distances should be bimodal; the smaller mode representing intra-group distances and the larger inter-group distances. In order to distinguish between groups an observer would choose a distance between the 2 modes. The data from the present study is however probably not bimodal, the greater than 65m class being a concatenation of the small frequencies of larger distances. Therefore no clear choice of a distance, separating sub-groups decisively under all conditions, could be made from this data.

If these data are a true representation of nearest neighbour distance in these sheep then the use of a 10m distance criterion has in both situations separated the substantial number of small distances from the medium to long distances. This could provide evidence for the existence of permanent close social bonds between sheep, if they exist.

Using the larger 30m distance criterion, it would appear that sampling was occurring at slightly different points of the frequency distribution of distances in the different seasons. In winter 86% of the observations are less than 30m and it may have been that some distinct sub-groups were not separated by the criterion. In summer the opposite may have occurred and certain sub-groups were not separated that ought to have been.

5 Time samples

It was decided to sample the same time period throughout the year; between 600 hours GMT and 1800 hours GMT. One scan of the sample area took approximately 2 hours. The following timetable of scans was observed: 600-800 hours; 800-1000 hours; 1000-1200 hours; 1200-1400 hours; 1400-1600 hours and 1600-1800 hours. The day was split in two; from 600-1200 hours (morning) and 1200-1800 hours (afternoon). Morning and afternoon sessions were carried out on different days. Normally 3 or 4 sessions were performed each week. In order to avoid bias in the data by always starting the scan at the same point and sampling in the same direction, the route for a scan was randomly selected from a choice of 12 standard routes.

Data obtained in different scans were treated as being independent, a procedure justified by the extensive movements that could occur in 2 hours.

The same time period was sampled throughout the year to allow comparisons between seasons. It should be noted, however, that this period represented a varying proprtion of the daylight hours.

6 Weather samples

At the start of each scan the temperature was taken using an ordinary air thermometer and the wind speed and direction were estimated by eye. A record was also taken of cloud cover and whether or not it was raining, snowing or misty.

7 Activity samples

In order to assess the behavioural activity of individual sheep during a scan, a sub-set of the ethogram used in the focal animal sampling method was drawn up.

2:4:2 The Focal Animal Samples

A focal animal sampling method was employed mainly to give more detailed information on the social relationships between different age classes of sheep. Two data sets were collected, in Winter and Summer 1982.

See Appendix 4 for further details of sampling methods.

1 The Winter 1982 focal animal samples

From January to April 1982 70 hours of focal animal data was collected. Those interactions used in analysis can be found in Appendix 1.

Nearest neighbour distances were collected at the start of the sample and at the end of every sample. Time of day, location of the focal animal and weather conditions were also noted.

Eight focal animals were chosen at random from the 3 age classes ewes, gimmers and ewe-lambs. Each focal animal was sampled 5 times from January to April.

The choice of focal animal on any one day was made by selection from a list of random numbers. To reduce wasteful seaching for animals the animals to be observed on the day were sampled in the order in which they were found.

2 The Summer 1982 focal animal samples

During the months April to October 1982 167 hours of focal animal data were collected. The same ethogram was used as previously.

In this period 8 ewes and 4 gimmers were sampled. Only those animals who had single female lambs were observed. Each animal and its lamb were sampled seperately, twice in each sample week (i.e. each mother-daughter pair was sampled 4 times in each sample week). The animals were observed in the 1st, 3rd, 5th, 8th, 14th, 18th, 22nd and 25th weeks of the lambs life. The samples were designed to be compatible with those taken in the winter period. In addition to nearest neighbour distances being collected the distance between the mother and her lamb was also recorded every 2 minutes.

Further to these observations 6 ewe-lambs were sampled for a total of 12 hours as a comparison to the observations made of them during winter.

CHAPTER 3 SEASONAL CHANGES IN HOME RANGE BEHAVIOUR

3:1 INTRODUCTION

It is well established that under hilly or montane conditions free ranging female domestic sheep form home range groups (Hunter and Davies 1963; Hunter and Milner 1963; Hunter 1964; Lynch 1967; Griffiths 1970; Hewson and Wilson 1979). The term home range was first described by Burt (1943) and restated by Jewell (1966) as "the area over which an animal normally travels in pursuit of its routine activities." A home range group contains a number of individuals that share similar home ranges and restrict their movements without any obvious need to do so (Hunter and Milner 1963).

Hunter and Milner (1963) initially demonstrated the existence of home range groups by individually tagging Cheviot hill ewes grazing a 251 acre ring fenced "heft". (A heft is a term that describes both the area of ground and the flock of sheep that customarily grazes it). The home range maps of certain of these individuals looked sufficiently different for them to be designated as belonging to separate home range groups within the same heft. Hunter and Milner also qualitatively illustrated that seasonal changes in social behaviour occurred. They described how the flock in summer tended to disperse into small sub-groups. In winter they occurred in much larger groups.

Hunter (1964) tagged all the members of Alderhope heft at Sourhope in the Cheviot hills in south-east Scotland. He illustrated that on the basis of their home range behaviour individuals could be assigned to separate home range groups. It is worth emphasizing that assignment of ewes to home range groups in both these studies was on the basis of how similar their home range maps appeared to the investigator. Hunter (1964) described the difficulty he experienced in assigning some sheep to a particular home range group.

Chadwick (1978) found no evidence for the existence of home range groups in a study of Blackface sheep in Stirlingshire. From her description it would seem that the management system was responsible for the lack of social organization. Thus ,it seems, the existence of home range groups can not be taken for granted in domestic flocks where management systems may destroy bonding to areas and to other sheep.

In addition to this work on the home range behaviour of domestic sheep there are two detailed accounts of similar behaviour in feral Soay sheep (Grubb and Jewell 1966; 1974). In this study rams were present throughout the year. In domestic sheep flocks, in general, rams are only introduced to females at mating. Boyd et al. (1964) had already illustrated that Soay ewes kept to particular parts of the study area known as the Village. Grubb and Jewell (1966) therefore assumed that sheep of the same home range group would tend to graze with one another on a daily basis. When large sub-groups became isolated from other sheep the members of these sub-groups were identified and assumed to be members of a home range group. The reality of this grouping was subsequently verified and the ewes in the Village study site were classified into 10 groups. Unlike Hunter (1964), Grubb and Jewell chose to illustrate the home range of the group by presenting the data for one representative individual. They reasoned that individuals behaviour would be similar to the behaviour of other members of the group.

The results from this work showed that the situation in Soay sheep was similar to that described by Hunter. The presence of rams had not disrupted the social organization of the ewe groups. The ranges of groups overlapped but it seemed evident that a group of ewes occupying a home range in some way deterred intrusion by other sheep. Individual variation in home range behaviour between ewes in the same home range group was again apparent as it had been in Hunter's work. Grubb and Jewell made no attempt to record this individual variation in detail but gave examples of ewes apparently preferring different areas within the group range. They suggested that the nature of the individual home range in relation to that of the group required further examination. Grubb and Jewell also provide the only description so far of the relationships between ewe home range groups. Generally there was little reaction to ewes from other groups if they were encountered reasonably frequently. On occasions when strange ewes did stray onto another group's area they did evoke a response; varying from investigative sniffing to front kicking and butting.

Geist (1971) has provided evidence that wild bighorn sheep living in the Rocky Mountains in Canada also form home range groups. His evidence is less complete in some senses than the preceding studies; for example he presents no home range maps. This was due to the difficulties he faced in identifying animals and following their movements in extremely rugged terrain. He found that although the home range phenomenon was apparent in the bighorn that it was not as simple as the situation described by Hunter and Grubb and Jewell. This was because his study animals occupied seasonal home ranges between which they migrated. Thus females lived in more than one home range group. It seems from his account that they might share each with different individuals.

Other studies of home range behaviour in bighorn (Mills 1937; Davies 1938; Woolf et al. 1970) suggest that in some populations the migration between ranges would be more properly regarded as a seasonal drift or an extension of the winter range during the summer months. In other populations the seasonal ranges could be regarded as being separate and distinct.

In this chapter evidence will be presented to show the existence of a) the Howlet home range group; b) seasonal variation in the home range behaviour of the group; c) considerable individual variation in relation to the group home range.

3:2 MATERIALS AND METHODS.

The scan sampling technique described in chapter 2 provided the data on home range behaviour. The data on social interactions between the Howlet home range group and other animals was obtained from the Winter and Summer 1982 focal animal data.

3:2:1 Extent of Sub-Grouping Between Animals from Different Groups

To test the validity of classifying particular sheep as the 'Howlet home range group', the degree to which they formed exclusive sub-groups rather than sub-groups with sheep from adjacent groups was analysed within an area peripheral to the main Howlet area (Area 2, see 3:2:2). Within this area ewes from other groups caused more than 10% of the observations. Also within Area 2 all sheep (irrespective of their group of origin) were recorded during the scan. It is therefore possible to calculate the proportion of observations due to either Howlet or non-Howlet animals within that area. It is also possible to calculate the probability of finding sub-groups of purely Howlet animals, and the probability of finding mixed sub-groups of members of different home range groups, based on the overall number of sheep from different groups found in Area 2. The probabilities of finding pure Howlet sub-groups and mixed sub-groups alter depending on the size of the sub-group. It is however necessary only to consider sub-groups of 2 animals. This is because the probability of finding pure Howlet sub-groups decreases as the sub-group size increases (from 0.53 for sub-groups of 2 to 0.30 for sub-groups of 3). The raw data contain a sample of many different sub-group sizes.

If the observed frequency of pure Howlet sub-groups, derived from these data, is significantly greater than the expected frequency, then this will be a conservative estimate of the significance of the effect.

The binomial test (Siegel 1956) was used as a test of significance. The binomial distribution tends towards the normal as sample size increases. Siegel (1956) presents a formula to calculate ´z´ which can be used to estimate significance levels.

3:2:2 <u>Methods of Analysis of the Howlet Group´s Home Range Behaviour</u>

1 <u>Analysis of the group home hange</u>

The home range of the group can be presented as a series of distribution maps similar to that used by Hunter (1964). In the analysis of the distribution of the group the area has been subdivided into 4 areas (see Figures 2.3 and 3.4).

Area 1 : the grid squares within the farmer´s original description of the area used by the group (see 2:4:2) where unmarked animals caused less than 10% of the observations. This could be defined as a core area or to use the terminology of Grubb and Jewell (1966), a monopolised zone.

Area 2 : the remaining grid squares within the original estimate of the group´s area where unmarked animals caused more than 10% of the observations. Within both Areas 1 and 2 the numbers of marked and unmarked animals are known. Areas 1 and

2 if summed together cover 56 ha and will also be referred to as the Howlet area.

Area 3 : the remaining grid squares in the study site on the N, NW and NE sides of the reservoir outside the original estimate of the group area. Area 3 is 52 ha in size.

Area 4 : all those grid squares on the south side of the reservoir and the south side of the road and the Logan Burn, including the in-bye field. Within Areas 3 and 4 only the numbers of marked animals are known. Area 4 covers 54 ha.

2 <u>Analysis of the relationship between individuals´ home ranges</u>

The analysis of the relationship between individuals home ranges required multivariate analysis. The number of dimensions present in the data can be expressed as 2xN, the home range map of each individual being in 2 dimensions; N being the number of sheep in the group.

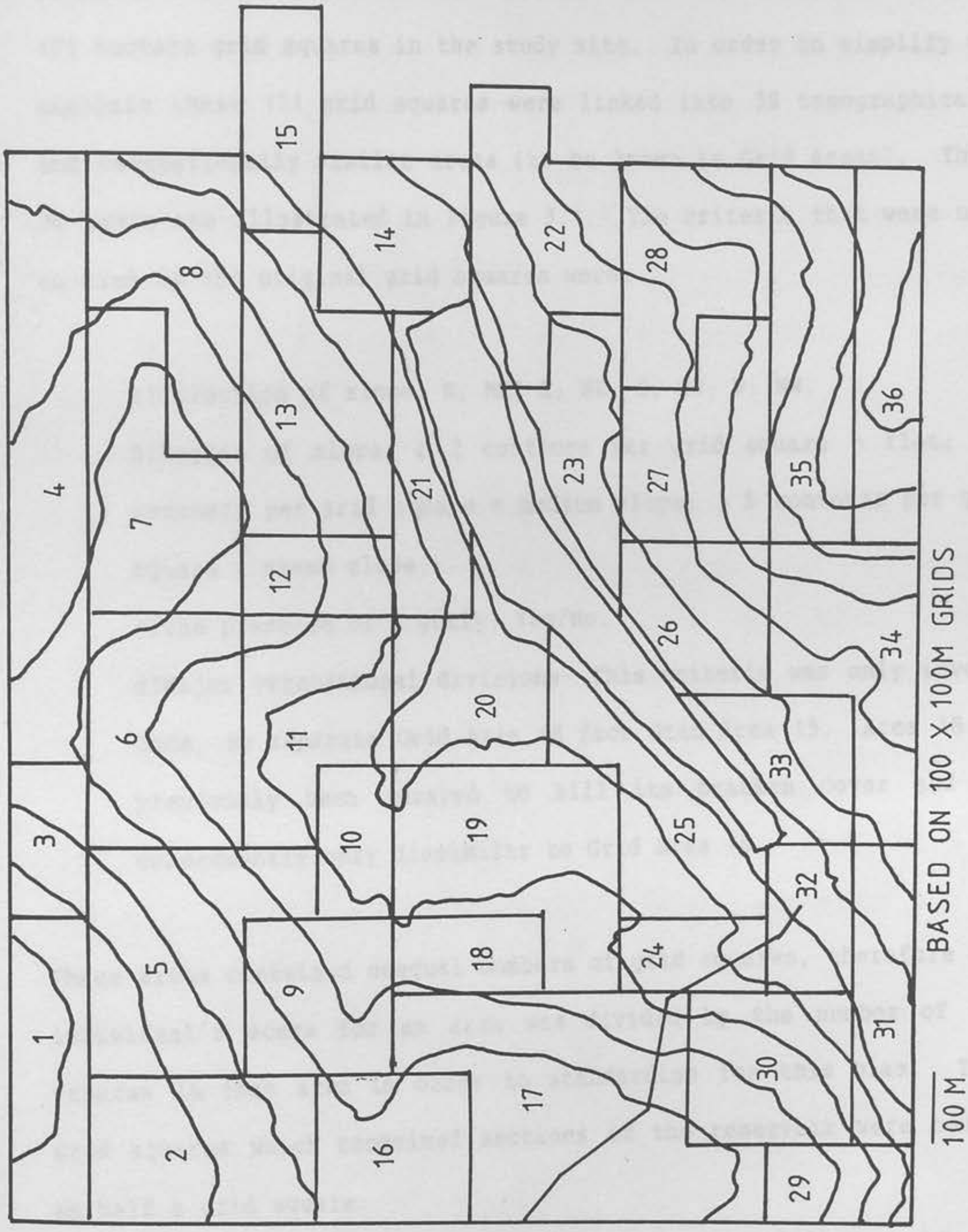
Cluster analysis is a multivariate technique that has found wide biological application (see Altmann 1968; Morgan <u>et al.</u> 1974; Lehner 1979). It makes fewer assumptions than other multivariate techniques and is often easier to interpret (Morgan <u>et al.</u> 1974). Cluster analysis assumes no underlying statistical model and its results therefore cannot be interpreted as probabilities of events occurring. According to Gordon (1981) cluster analyses have often been regarded as forms of exploratory data analysis useful as ´hypothesis generators´.

FIGURE 3.1

MAP OF THE 36 TOPOGRAPHICALLY AND VEGETATIONALLY

SIMILAR GRID AREAS USED IN THE CLUSTER ANALYSIS IN THIS CHAPTER.

See 3:2:2 part 1 for a full description of the criteria by which the original grids were linked into these 36 grid areas.



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36
BASED ON 100 X 100M GRIDS
100 M

The home range data were arranged in a NxMN matrix, where N were the entities to be clustered (in this case the individual sheep) and MN were the variables, depending on the value of which the entities were to be clustered. In this case the variables were the 171 hectare grid squares in the study site. In order to simplify the analysis these 171 grid squares were linked into 36 topographically and vegetationally similar areas (to be known as Grid Areas). These 36 areas are illustrated in Figure 3.1. The criteria that were used to link up the original grid squares were:

a)Direction of slope: N; NE; E; SE; S; SW; W; NW.

b)Degree of slope: ≤ 2 contours per grid square = flat; 3-4 contours per grid square = medium slope; ≥ 5 contours per grid square = steep slope.

c)The presence of a gully: Yes/No.

d)Major vegetational divisions: This criteria was only invoked once, to separate Grid Area 18 from Grid Area 19. Area 18 had previously been sprayed to kill its bracken cover and was consequently very dissimilar to Grid Area 19.

These areas contained unequal numbers of grid squares, therefore each individual´s score for an area was divided by the number of grid squares in that area in order to standardise for this bias. Those grid squares which contained sections of the reservoir were counted as half a grid square.

Some authors (e.g. Everitt 1974; Gordon 1981) suggest that continuous variables ought to be standardized as results could be biased towards those variables with high variances. It would seem in this case that standardization is not applicable. Standardization is most applicable where the variables have different scales of measurement (e.g. weight and height); the problem is to determine the correct weighting to give each variable; dividing variables by their standard deviations reduces all variables to unit variance. However the data used in this chapter consist of variables which are all measured on the same scale of measurement (see above); to standardize to unit variance would be to accord equal weight to all areas. This would dilute real differences between individuals and give undue weighting to outlying areas that were infrequently used. For these reasons the data were not standardized.

Cluster analysis techniques begin with a matrix of similarities, or dissimilarities. A dissimilarity matrix is a triangular array of N(N-1)/2 coefficients such that each element measures the dissimilarity between two individuals. These dissimilarities are computed from the NxMN matrix of entities and variables.

The measure of dissimilarity used in the analyses in this chapter was Euclidean distance. If the variables are x_1 to x_p the Euclidean distance between individuals A and B is expressed as:

$$d^2(A,B)=\sum_{i=1}^{p}(x_{iA}-x_{iB})^2 .$$

For example if the data set is:

	variable x_1	variable x_2
Individual A	0.8	1.8
Individual B	1.1	1.6

the Euclidean distance between A and B is 0.13.

There are many different types of cluster analysis ranging from the simple hierarchial method of single linkage to much more sophisticated methods such as relocation (see Everitt 1974). Wishart (1978) recommends the use of Ward's Error Sum of Squares Method as it is probably the best of the hierarchial techniques.

Initially in the analysis each individual constitutes a group; there are n single member groups. At each step in the analysis union of every possible pair of clusters whose fusion results in the minimum increase in the error sum of squares are combined.

If for a simple example we have 4 sheep who have values for Grid Area X so:

	Grid Area X
Individual A	3
Individual B	4
Individual C	7
Individual D	9

The error sum of squares is given by:

$$\sum_{i=1}^{n} x_i^2 - \frac{1}{n}\left(\sum x_i\right)^2$$

In this case the total error sum of squares is 22.5. The two individuals (or clusters) who would contribute least if fused are A and B and the error sum of squares becomes 0.5. Next C and D are fused and add 2.0 to the sum of squares which becomes 2.5. Finally the two groups are fused together to bring the error sum of squares to 22.5.

The algorithm which computes the error sum of squares method from the dissimilarity matrix was found by Wishart (1969). This is available in the Clustan suite of programmes (Wishart 1978). The Clustan version of Ward's method was used to analyse the data in this chapter.

The results of cluster analyses are often presented in the form of dendrograms. Dendrograms are graphic representations of cluster analyses. One is used here to illustrate the simple example given earlier:

```
22.5       -------------
           I           I
        ++++++++++++++++++++ 2
           I           I
           I           I
           I           I
           I           I
 2.5       I        -------
        +++++++++++++++++++++ 3
 0.5    -------     I     I
        I     I     I     I
        I     I     I     I

        A     B     C     D
```

If the dendrogram is sectioned at certain dissimilarities then a level of clustering is obtained at that dissimilarity (e.g. the highest level gives 2 clusters and the lower level gives 3 clusters). The basic features of a dendrogram are then, that the most similar individuals are fused at the bottom of the dendrogram and that the dendrogram is hierarchial (i.e. at higher levels of dissimilarity (further up the dendrogram) less similar individuals are fused into larger clusters).

Clustan (Wishart 1978) also performs principal components analysis (PCA) onthe NxMN matrix. Principal components are useful where a matrix contains a number of variables some of which may correlated. Principal components are uncorrelated linear functions of the original variables (Kendall 1980). The function of PCA this thesis is to provide another method for displaying the results of the cluster analysis (see Chapter 6). Individuals are plotted relative to the first 2 principal components. The clusters as computed by Ward´s Method are then enclosed by a polygon connecting the outermost individuals in the cluster.

As mentioned previously there are many different types of cluster analyses. Some authors (e.g. Gordon 1981) suggest that more than one method should be used to examine the robustness of the analysis. It was decided to compare the results using Ward´s Method on the Summer 1981 data with those produced by an iterative relocation algorithm available on Clustan. In this algorithm the initial classification into clusters is modified by moving individuals from one cluster to another if this movement will reduce the sum of squares. It is therefore a method for attempting to improve upon the original classification. It was firstly used to classify a random assortment of individuals and secondly to improve upon the classification produced by Ward´s Method.

3 Analysis of cluster compositional stability between seasons

If there is no relationship in the composition of clusters between 2 seasons, ´a´ and ´b´, then the numbers of animals recruited into any one cluster in the next season (´b´) from each of the clusters in the previous season (´a´) should be in direct proportion to the total size of each of the clusters in ´a´. In other words if there is no relationship in the assortment of animals into clusters on the basis of their home range behaviour between one season to the next, then the composition of any cluster in 'b' would be a random assortment of animals from the clusters in the preceding season.

In this analysis the expected theoretical number of animals from a cluster in 'a' being found in a cluster in 'b' was calculated thus:

$$\frac{\text{Number in cluster 'x' in season 'a'}}{\text{Total number of animals in season 'a'}} \times \text{Number of animals in cluster 'y' in season 'b'}$$

The calculation then proceeds as for a one sample chi-square test (Siegel, 1956). For the one sample case degrees of freedom (df) = k - 1 where k stands for the number of categories in the classification.

For this calculation clusters do not require to be numbered in the same order in different seasons and were left in the order chosen by the computer. The accepted rule with chi-square is that the expected frequencies should in general be at least 5. Everitt (1977) however indicates that this criteria is probably too stringent. He states that in the majority of cases the chi-square test may be used with expected frequencies as low as 0.5 in the smallest cell. In the present study this test was only applied in circumstances where this criterion was met.

Only the animals present from the start of observations in Summer 1981 are used in this analysis. They are obviously the only sheep which can occur in particular clusters throughout the entire length of the study.

4 Analysis of inter-cluster variability

To examine the extent to which the clusters produced by cluster analysis were separated by "real distance" on a map of the study site it was decided to use a modification of the probability ellipse (Jennrich and Turner 1969; Koeppl et al. 1975).

The problem of deciding what level of clustering to examine was solved by arbitrarily dividing the dendrogram at the level of 5 clusters. Where possible 5 members of a cluster were chosen at random. In some cases where clusters contained less than 5 members all the group were included. A centre of activity was estimated for the pooled data of the members from each cluster. The centre of activity is the mathematical centre of the distribution of sightings and can be represented:

$$\bar{x} = \sum x_i / n \qquad \text{and} \qquad \bar{y} = \sum y_i / n .$$

The rows (x axis) and columns (y axis) of the grid square map are weighted by their respective row or column number and the number of sightings in each row or column are multiplied by their respective weightings. The totals for all the rows and all the columns are divided by the total number of sightings to give the statistical mean of the animal's activity.

Koeppl et al. (1975) suggest a method for calculating confidence ellipses around this centre of activity which takes into account the covariance of the x and y coordinates; in other words the axes of the ellipse are orientated in line with the activity of the animal and not with the arbitrary axes of the map. In the modification of the method used in this paper 1 standard deviation was calculated on either side of the centre of activity along both the x and the y axes. An ellipse was then drawn to enclose this estimate of the standard deviation. The resulting ellipse could be said to represent an area within which approximately 68% of the sightings of the animals from that cluster should be found; provided the original data was normally distributed. However this formula, for ease of computation, takes no account of the 'true axes' of variation; the orientation of the ellipse being controlled by the axes of the original grid square system. The main purpose of presenting the data in this form is to help illustrate inter-cluster variability, but these ellipses can also be regarded as giving a reasonably accurate description of the home range activity of animals in a cluster.

5 Analysis of consistency of home range behaviour

In order to examine how consistent animals were over the two summer seasons in their home range behaviour the home range data sets for Summers 1981 and 1982 were combined in one cluster analysis. Obviously only those animals present in both summers were included. The proximity of sheep to themselves in the resulting dendrogram gives an indication of consistency of home range behaviour. As with all cluster analyses the results can be viewed at a variety of cluster levels; in this case allowing some estimation of the strength of the effect. These dendrograms were analysed at the levels of 2, 5 and 10 clusters. The lower the level of clustering analysed (lower being nearer to the bottom of the dendrogram) the more detailed the analysis of the similarity of an animal's home range behaviour in the 2 summer seasons.

In the analyses to follow much emphasis is laid on seasonal comparisons. Ordinarily direct comparison of dendrograms is qualitative. Here, however, the use of Ward's Method has allowed some quantitative comparison of seasonal variation using the total error sum of squares for each season.

3:3 RESULTS

3:3:1 The Group Home Range

1 Sampling efficiency of the group.

A measure of the fact that the animals gathered by the farmer from the Howlet area constituted a home range group, would be the success with which they were found during scans of the study site. In all seasons a high percentage of marked animals were seen each scan (Table 3.1). The majority of animals were well sampled, especially in Autumn 1981, Winter 1982 and Summer 1982 (Figure 3.2). Individual animals were not regularly missed during scans except for a few exceptions. These, as already stated, included ewe-lambs who temporarily left the group in Autumn 1981 and certain individuals in Summer 1981 who assumed home range patterns rather different to those of the rest of the group.

The possibility that the location of an animal's home range might influence the number of times it was seen, was explored by analysing the number of times animals which frequented Area 4 (see 3:2:2) were sampled in Summer 1981 when variation in sampling was greatest. Area 4 is probably the most likely area to have influenced sampling (see below). Animals were discriminated as using this area by cluster analysis (see 3:3:2). The number of sheep which used Area 4 and were sampled less than the group median, were compared with the number of animals that used this area, and were sampled more than the group median. There was no association between the use of Area 4 and the number of times an animal was sampled in relation to the group average, (χ^2 one-sample test; χ^2 =1.8, df=1, NS).

TABLE 3.1

SUMMARY OF SAMPLING INFORMATION FOR THE DIFFERENT SEASONS.

The values in parenthesis show the average numbers of sheep in the group seen each scan.

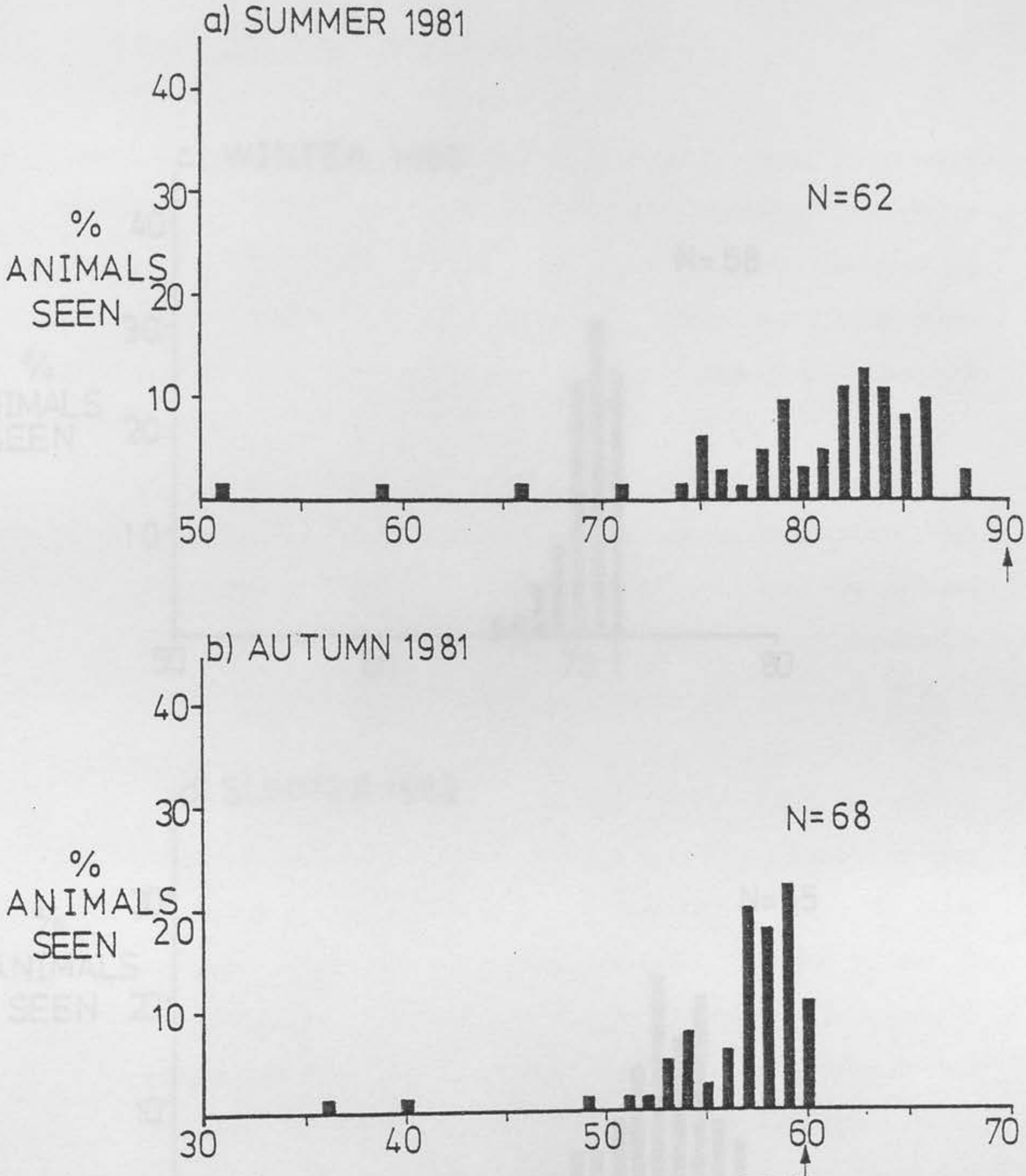
	SCANS	ANIMALS IN GROUP	AVERAGE NUMBER SEEN
Summer 1981	90	62	56 (90%)
Autumn 1981	60	68	64 (94%)
Winter 1982	78	68	66 (97%)
Summer 1982	84	65	62 (95%)

FIGURE 3.2

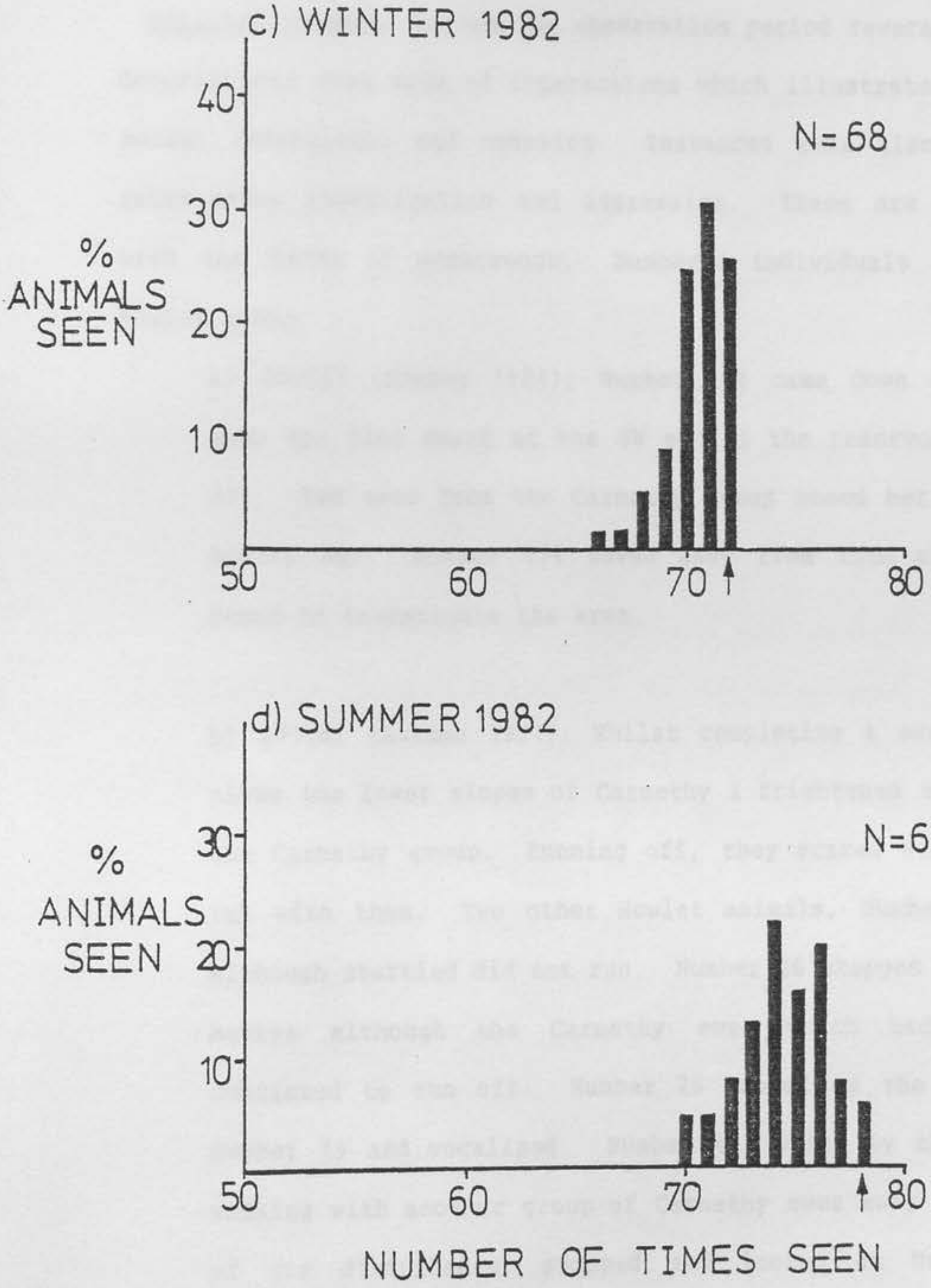
HISTOGRAMS OF THE FREQUENCY WITH WHICH INDIVIDUAL

SHEEP WERE OBSERVED IN DIFFERENT SEASONS.

N is the number of individuals present in any one season. The arrows indicate the maximum number of times an individual could be seen in any season.



a) SUMMER 1981
N=62
% ANIMALS SEEN
40
30
20
10
50
60
70
80
90
b) AUTUMN 1981
N=68
% ANIMALS SEEN
40
30
20
10
30
40
50
60
70
NUMBER OF TIMES SEEN


c) WINTER 1982
N=68
%
ANIMALS
SEEN
40
30
20
10
50
60
70
80
d) SUMMER 1982
N=65
%
ANIMALS
SEEN
30
20
10
50
60
70
80
NUMBER OF TIMES SEEN

2 <u>The relationship between home range groups</u>

Qualitative data: During the observation period several qualitative descriptions were made of interactions which illustrated intra-group social recognition and cohesion. Instances were also recorded of inter-group investigation and aggression. These are listed below with the dates of occurrence. Numbered individuals are from the Howlet group.

a) 080581 (Summer 1981): Number 114 came down Carnethy Hill onto the flat sward at the SW end of the reservoir (Grid Area 31). Two ewes from the Carnethy group nosed her; one of them butted her. Number 114 moved away from them and apparently began to investigate the area.

b) 241081 (Autumn 1981): Whilst completing a scan by walking along the lower slopes of Carnethy I frightened some ewes from the Carnethy group. Running off, they scared Number 26 which ran with them. Two other Howlet animals, Numbers 15 and 49 although startled did not run. Number 26 stopped after some 50 metres although the Carnethy ewes which had scared her continued to run off. Number 26 looked in the direction of Number 49 and vocalised. Number 49, which by this stage was walking with another group of Carnethy ewes away from the area of the disturbance, stopped and looked at Number 26 and vocalised to her. Number 26 then began to walk towards Number 49 which subsequently began walking towards Number 26. Having met they walked off together and soon after commenced grazing.

c) 030281 (Winter 1982): Number 12 attempted to feed off Carnethy group´s feedblock (see 2:3) in amongst some Carnethy ewes. The block was placed on the sward at the SW end of the reservoir (Grid Area 31). Repeatedly Number 12 would approach the block with her head in a very low position. As she moved near to the block she would be approached by a Carnethy ewe. In response Number 12 would turn away from the other ewe, keeping her head low. She would only finally raise her head when she stood with her back to the strange ewe. As she attempted to return to the block she would turn around and lower her head again.

d) 050382 (Winter 1982): Number 4 attempted to feed off the Carnethy group´s feedblock. As she moved near the block she was approached by 3 Carnethy ewes in succession. As she turned away from them she kept her head low. One of the Carnethy ewes attempted to come round to Number 4´s head; another ewe butted her on the side. Number 4 continued to circle around the block attempting to feed off it but was constantly being approached by Carnethy ewes and hence was prevented from doing so.

e) 180382 (Winter 1982): Number 48 attempted to feed off the Carnethy group´s feedblock ......Number 48 feeding off the block was displaced by a Carnethy ewe. Number 48 left the block and approached another Carnethy ewe which walked away from her. The Carnethy ewe which had originally approached

Number 48 again approached her. Number 48 urinated.....A Carnethy ewe approached Number 48 and butted her on the side of the head; Number 48 ran away with her head down. Number 48 stood with her back to the Carnethy ewe and defecated.

f) 200382 (Summer 1982): Number 77 (a ewe-lamb) was locked overnight on the wrong side of a gate that was shut at lambing to prevent passage of ewes between the Howlet area and the neighbouring farm. On being let through the gate she lay down ruminating on the flat sward at the SW end of the reservoir. About 20 ewes from the Carnethy group and one Howlet animal (Number 45) were grazing the sward at that time. About half an hour later Number 45, at least 30 metres from Number 77 walked off along the south side of the reservoir (i.e. the lower slopes of Carnethy). Number 77 immediately got up and walked through the grazing Carnethy ewes to follow Number 45 along the path.

g) 220682 (Summer 1982): Number 69 (a ewe-lamb) grazing in the in-bye field was left behind by the ewes that had accompanied her there in the morning. As she left the field by herself she was surrounded by a large group of Gask ewes. A Gask ewe approached her; Number 69 ducked her head and keeping it low walked away. Another Gask ewe approached her and Number 69 responded by butting the ewe. There then followed a series of 5 approaches by Gask ewes during which Number 69 was nosed, front kicked and butted. She began to show some distress by baaing continuously; she eventually walked back to the Howlet

TABLE 3.2

TYPES OF 30M SUB-GROUPS OBSERVED IN AREA 2 IN 3 SEASONS.

See 3:2:2 for a description of Area 2. The binomial test is used to test for significance.

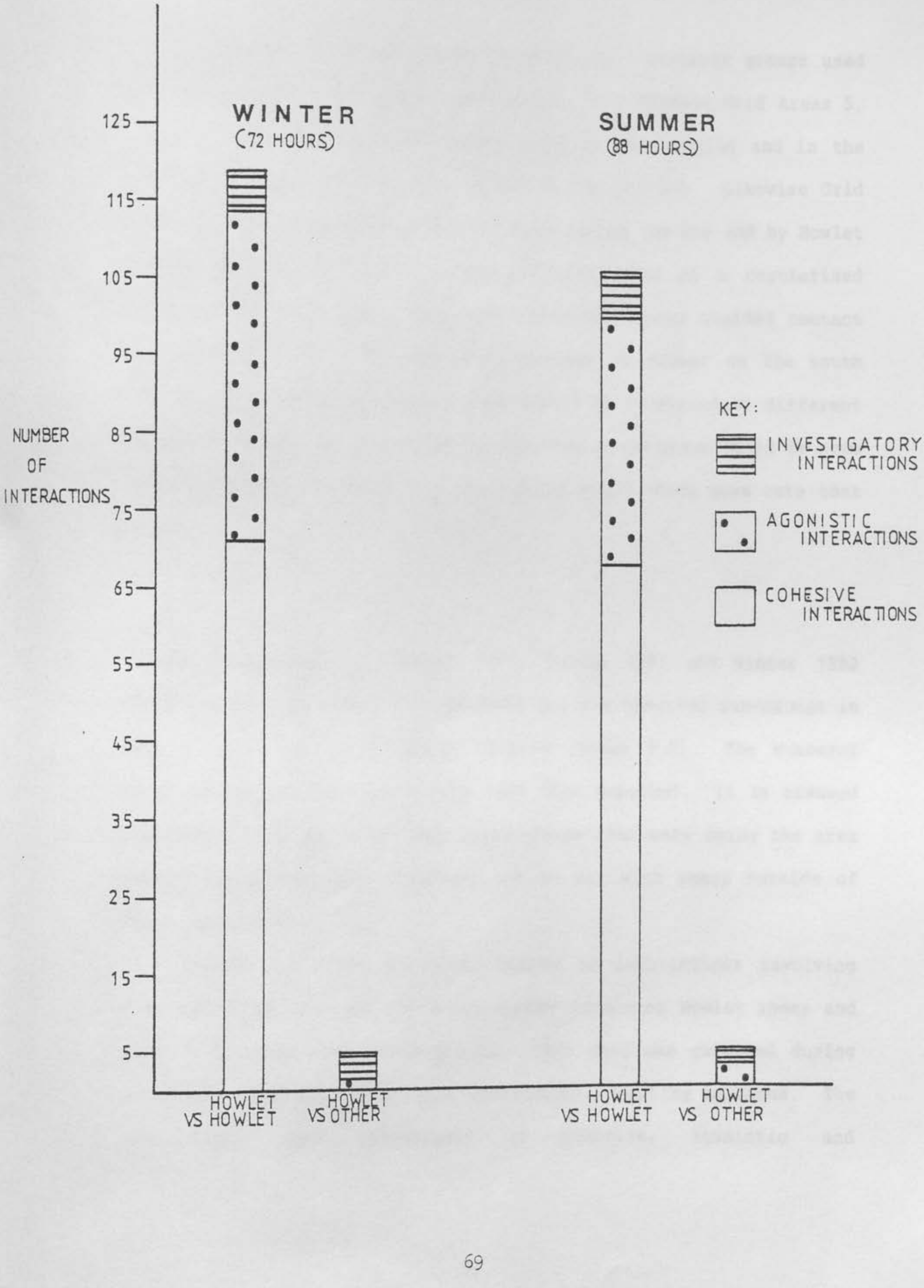
	OBSERVATIONS OF HOWLET SHEEP IN AREA 2	NUMBER OF HOWLET SUB-GROUPS IN AREA 2	NUMBER OF MIXED SUB-GROUPS IN AREA 2
Summer 1981	64%	83	14 z=6.4 p <0.001
Autumn 1981	53%	158	14 z=9.65 p <0.001
Winter 1982	63%	114	30 z=6.203 p <0.001

FIGURE 3.3

FREQUENCY OF INTERACTIONS BETWEEN HOWLET ANIMALS AND

BETWEEN HOWLET ANIMALS AND ANIMALS FROM OTHER GROUPS.

The data were taken from the Winter and Summer focal animal samples. See Chapter 5 for a description of the types of interactions.


WINTER
(72 HOURS)
SUMMER
(88 HOURS)
NUMBER OF INTERACTIONS
125
115
105
95
85
75
65
55
45
35
25
15
5
KEY:
INVESTIGATORY INTERACTIONS
AGONISTIC INTERACTIONS
COHESIVE INTERACTIONS
HOWLET VS HOWLET
HOWLET VS OTHER
HOWLET VS HOWLET
HOWLET VS OTHER

by herself.

There was also qualitative evidence that different groups used the same areas at different times of day. For example Grid Areas 5, 6 and 9 were used by Howlet sheep early in the morning and in the evening but were used by other groups during the day. Likewise Grid Areas 6 and 11 were used by other groups during the day and by Howlet animals during the evening. The impression was of a regularised mosaic of movement where sheep from different groups avoided contact with other groups. This was most apparent in summer on the south side of the reservoir; an area that tended to be shared by different groups of sheep. As sub-groups of one home range group could be seen leaving an area, sheep from another group would often move onto that area.

Quantitative data: In Summer 1981, Autumn 1981 and Winter 1982 there was a large significant tendency for the observed sub-groups in Area 2 to be purely of Howlet animals (Table 3.2). The numberof mixed sub-groups was always much less than expected. It is assumed that sheep from the other home range groups that were using the area showed a similar strong tendency not to mix with sheep outside of their own groups.

Figure 3.3 shows the total number of interactions involving only Howlet animals and the total number involving Howlet sheep and sheep from other home range groups. This data was gathered during the Winter 1982 and Summer 1982 focal animal sampling sessions. The interactions were categorised as cohesive, agonistic and investigatory. A detailed description of these interaction types is contained elsewhere (see 5:2:6).

Few interactions occurred between Howlet animals and sheep from other groups (Figure 3.3). In 160 hours of observation only 10 interactions with ewes from other groups were recorded as opposed to 224 between members of the Howlet group. The other major difference is that in the many interactions involving only Howlet sheep, large numbers of these interactions were cohesive grazing movements. There were no occurrences of these movements in the mixed group interactions. In Winter 1982 4 out of the 5 interactions, between sheep from different groups involved investigatory behaviour, the other being aggressive; in Summer 1981 2 out of the 5 were investigatory and the other 3 were aggressive.

3 The distribution of the group

The distribution maps for the locations of the group in the different seasons are shown in Figures 3.4, 3.5, 3.6 and 3.7. The largest trend in the data, obvious from both the distribution maps and the summary of this data in Figure 3.8 is the difference in the proportion of observations which occur in Area 1 and Area 4 in the different seasons. In Winter 1982, 79% of observations occurred in Area 1, the core area. This is in contrast to 69% in Autumn 1981 and 61% and 57% in Summers 1981 and 1982 respectively. In Winter 1982, 2% and in Autumn 1981, 7% of observations occurred in Area 4, the south side of the reservoir; in contrast 28% and 33% occurred here in

FIGURE 3.4

THE DISTRIBUTION OF THE HOWLET GROUP IN SUMMER 1981.

This figure shows the distribution of the Howlet group in Summer 1981 (● ⩽ 30 observations). It also shows the distribution of sheep from other groups within Areas 1 and 2 (▲ ⩽ 30 observations). The outermost thick black line surrounds the farmer's original estimate of the area occupied by the Howlet group and within this line occurrences of all sheep were recorded. The innermost thicker black line indicates the boundaries of Area 2. North of this inner line and south of the outer line sheep from other groups formed more than 10% of the observations; this area can be regarded as being "shared" by sheep from more than one group. South of the inner line but within the outer line, sheep from other groups formed less than 10% of the observations; this is Area 1, the core area, or to use Grubb and Jewell's term the monopolized zone. Area 3 contains the remaining grids on the north side of the reservoir outside of the outermost black line. Area 4 contains all the grids on the south side of the reservoir (see 3:2:2 part 1 for a fuller description).

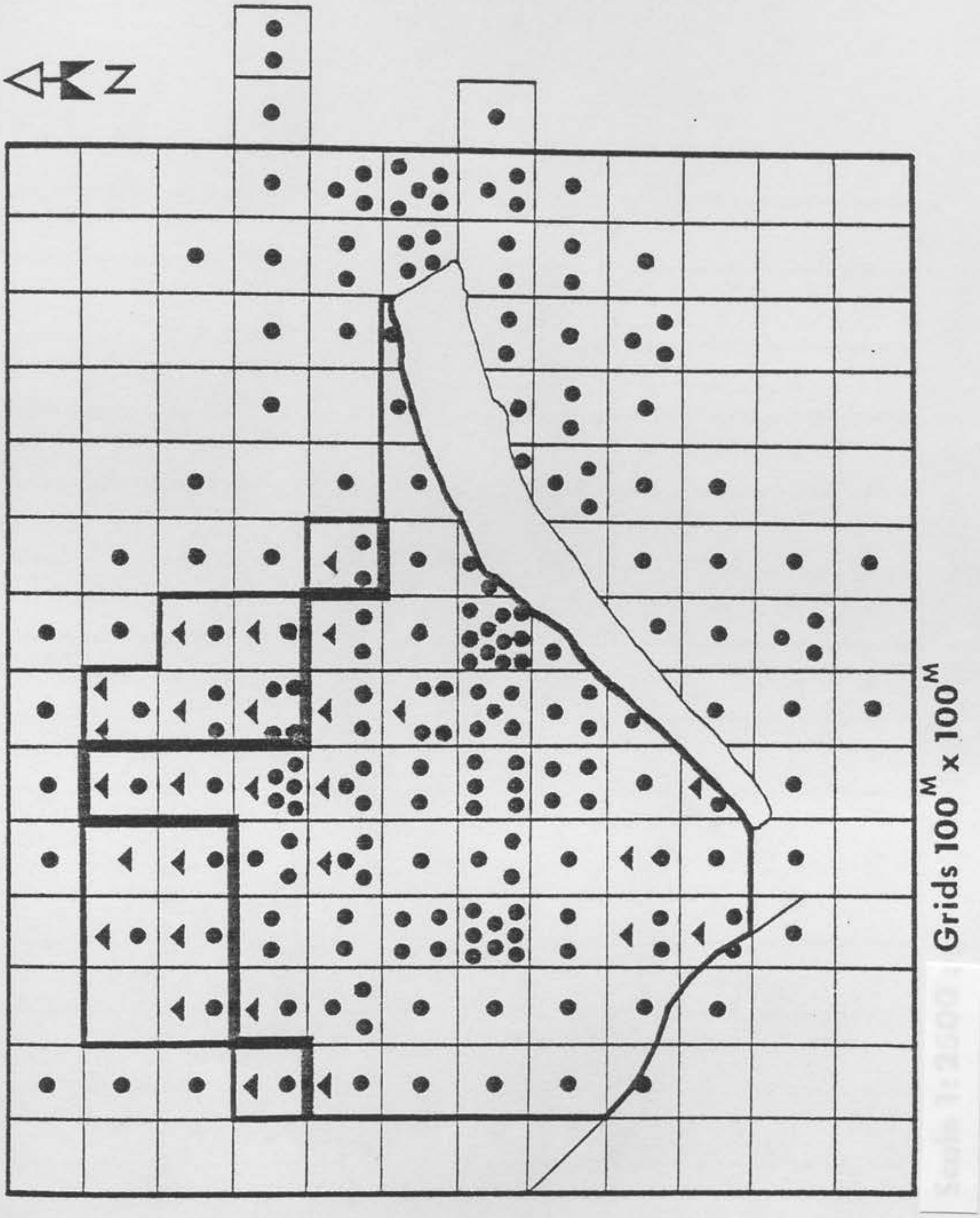

N
Grids 100M x 100M
Scale 1:2500

FIGURE 3.5

THE DISTRIBUTION OF THE HOWLET GROUP IN AUTUMN 1981.

See Figure 3.4 for a description of this figure.

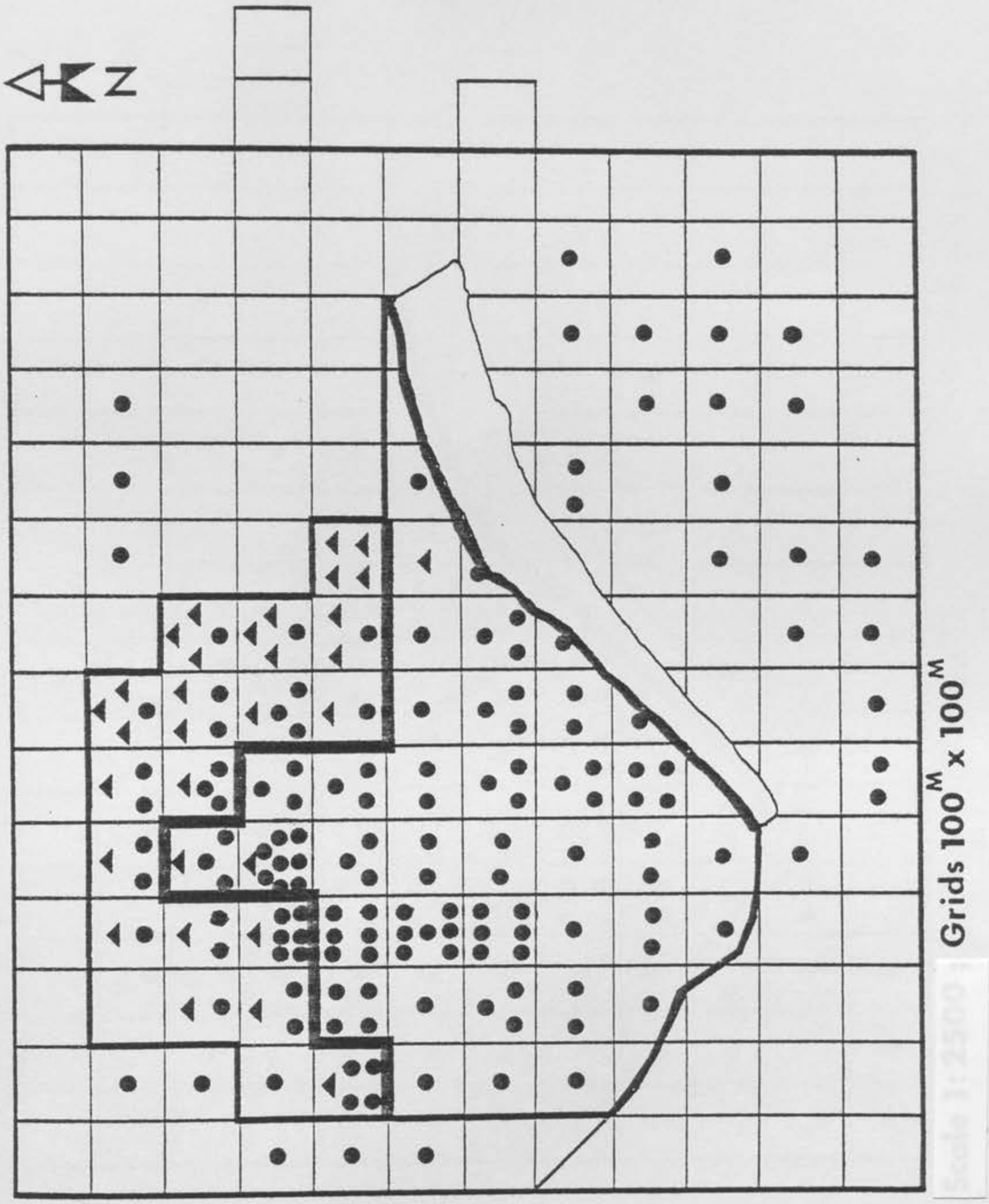
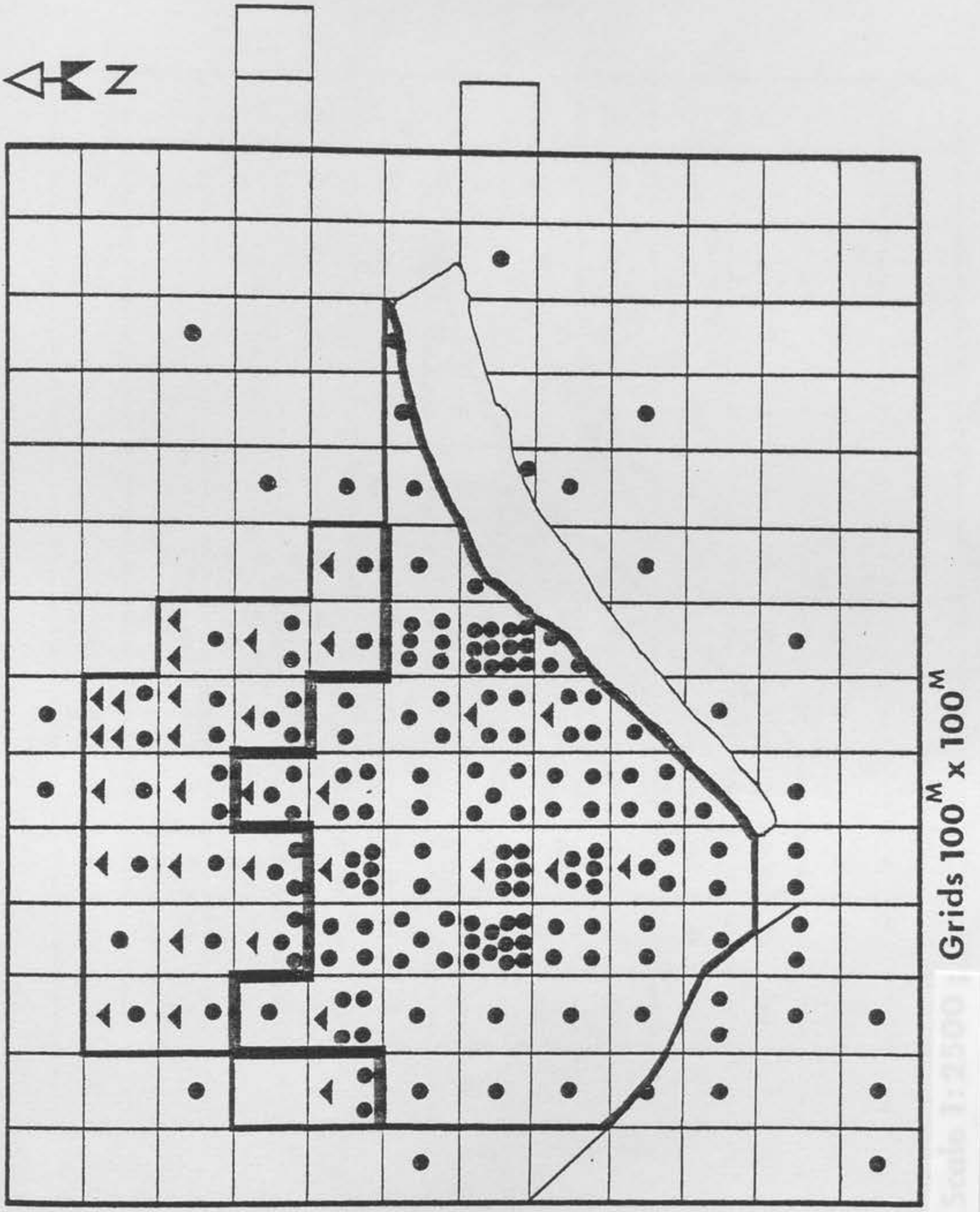

N
Grids 100M x 100M
Scale 1:2500

FIGURE 3.6

THE DISTRIBUTION OF THE HOWLET GROUP IN WINTER 1982.

See Figure 3.4 for a description of this figure.



Grids 100M x 100M

FIGURE 3.7

THE DISTRIBUTION OF THE HOWLET GROUP IN SUMMER 1982.

See Figure 3.4 for a description of this figure.

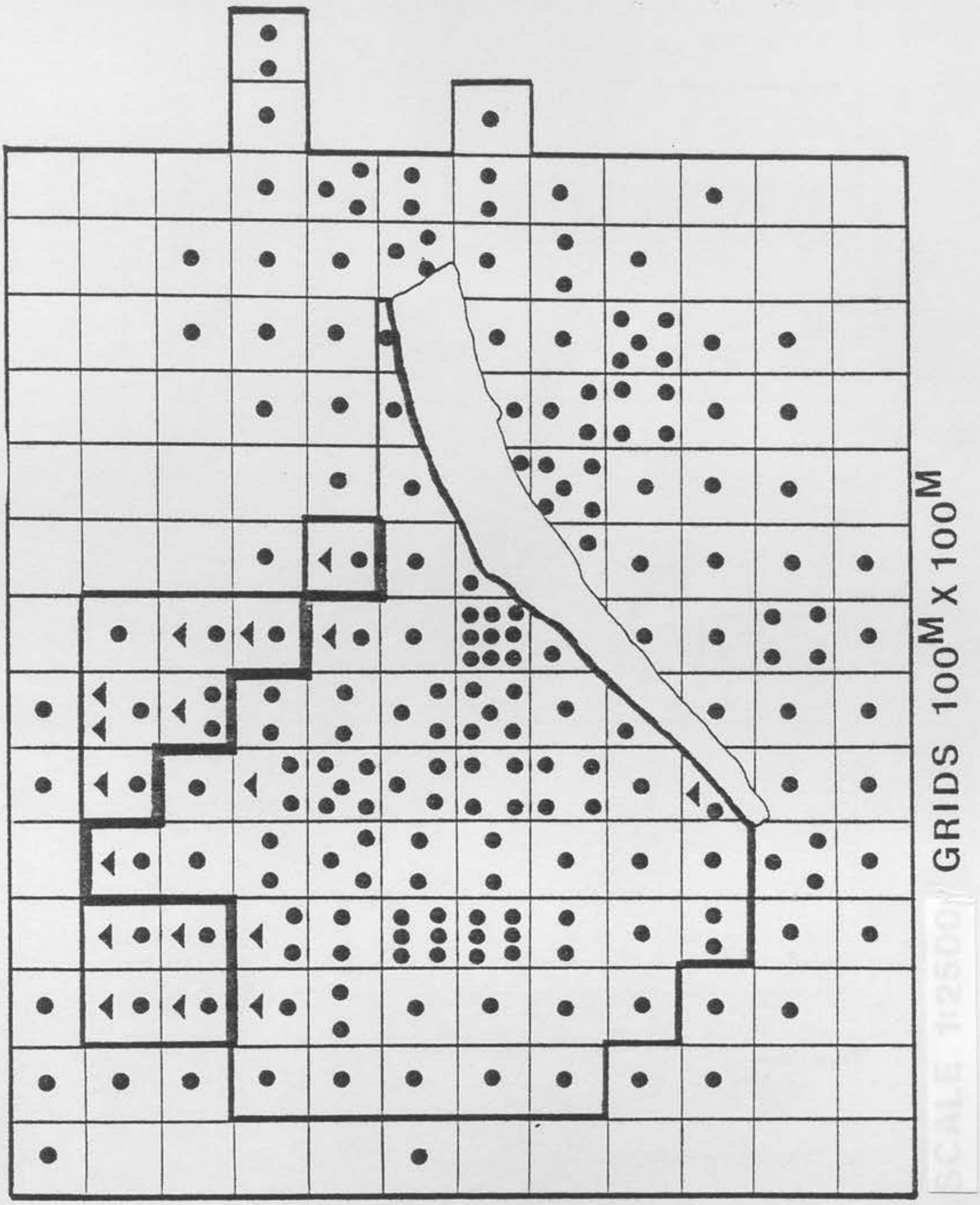
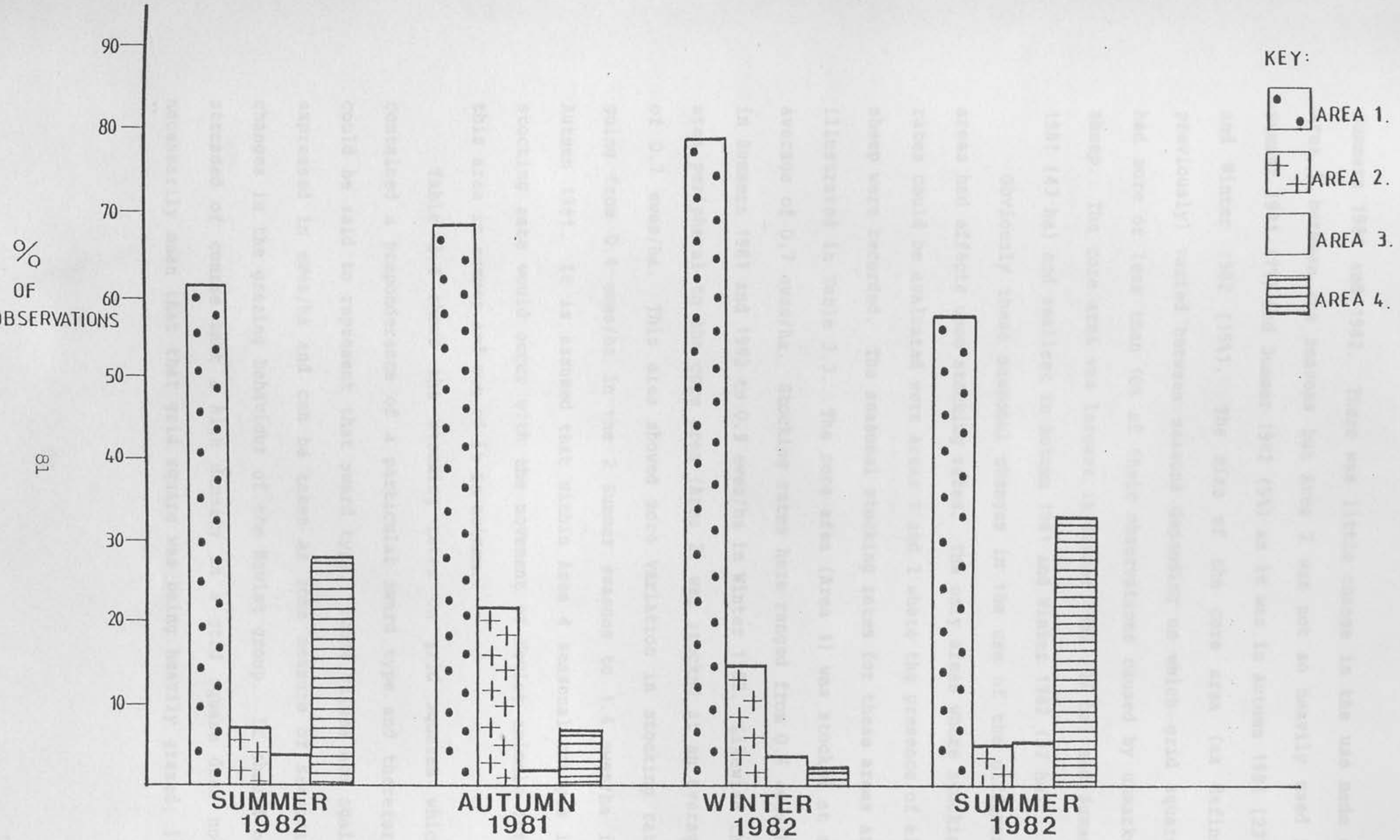

GRIDS 100M X 100M
SCALE 1:2500

FIGURE 3.8

THE SEASONAL CHANGES IN THE DISTRIBUTION OF THE HOWLET GROUP IN AREAS 1, 2, 3, AND 4.



%
OF
OBSERVATIONS
90
80
70
60
50
40
30
20
10
SUMMER 1982
AUTUMN 1981
WINTER 1982
SUMMER 1982
KEY:
AREA 1.
AREA 2.
AREA 3.
AREA 4.

Summers 1981 and 1982. There was little change in the use made of Area 3 between the seasons but Area 2 was not so heavily used in Summer 1981 (7%) and Summer 1982 (5%) as it was in Autumn 1981 (23%) and Winter 1982 (15%). The size of the core area (as defined previously) varied between seasons depending on which grid squares had more or less than 10% of their observations caused by unmarked sheep. The core area was largest in Summer 1982 (46 ha) and Summer 1981 (43 ha) and smallest in Autumn 1981 and Winter 1982 (37 ha).

Obviously these seasonal changes in the use of the different areas had effects upon stocking rates. The only areas where stocking rates could be evaluated were Areas 1 and 2 where the presence of all sheep were recorded. The seasonal stocking rates for these areas are illustrated in Table 3.3. The core area (Area 1) was stocked at an average of 0.7 ewes/ha. Stocking rates here ranged from 0.6 ewes/ha in Summers 1981 and 1982 to 0.9 ewes/ha in Winter 1982. Likewise the area peripheral to the core area (Area 2) was stocked at an average of 0.7 ewes/ha. This area showed more variation in stocking rate going from 0.4 ewes/ha in the 2 Summer seasons to 1.4 ewes/ha in Autumn 1981. It is assumed that within Area 4 seasonal changes in stocking rate would occur with the movement of Howlet animals into this area in summer and out of it in autumn.

Table 3.4 shows the stocking rates on grid squares which contained a preponderance of a particular sward type and therefore could be said to represent that sward type. These values are again expressed in ewes/ha and can be taken as some measure of seasonal changes in the grazing behaviour of the Howlet group. It should be stressed of course that a high density in a grid square does not necessarily mean that that grid square was being heavily grazed; it

TABLE 3.3

STOCKING RATES IN AREAS 1 AND 2.

This table illustrates the seasonal changes in stocking rate within Areas 1 and 2. The stocking rate was calculated by dividing the total numbers of ewes found in an area within a season by the total number of grid squares in that area. The unit of measurement is therefore ewes/ha.

	AREA 1 (core area)	AREA 2 (peripheral area)
SUMMER 1981	0.6	0.4
AUTUMN 1981	0.7	1.4
WINTER 1981	0.9	0.8
SUMMER 1981	0.6	0.4

TABLE 3.4

STOCKING RATES ON DIFFERENT SWARD TYPES IN AREA 1.

This table shows the stocking rate on grid squares which, because of the preponderance of a particular sward type, could be said to represent that sward type. The stocking rate on these grid squares is therefore some measure of the grazing preferences of the Howlet group in different seasons. An indication is also given of the altitude of the grid square (see 2:2 for a full description of the sward types). The unit of measurement is ewes/ha.

GRID SQUARE	VEGETATIONAL TYPE	SUMMER 1981	SUMMER 1982	AUTUMN 1981	WINTER 1982
D0405	*Agrostis*/ *Festuca* spp rich, (low).	3.45	3.00	1.5	4.3
B1005	*Agrostis*/ *Festuca* spp poor, (high).	2.7	2.6	3.4	4.0
D0104	Old *Calluna* (low).	0.2	0.1	0.5	2.2
B0908	Old *Calluna* (high).	0.3	0.4	1.1	0.3
D0108	Young *Calluna* (high).	0.9	0.9	4.1	1.3
D0203	Bracken sward (low).	0.5	0.2	2.0	1.8
B0904	Bracken sward (high).	0.3	0.3	1.0	0.4

could for example have been used expressly for shelter. Where possible vegetation types are represented by 2 grid squares, one occupying a low altitude and one occupying a high altitude. These grid squares were all situated in Area 1 (the core area) and were therefore only used by Howlet animals.

The first point to note is the high degree of similarity between the 2 summer seasons and concomitantly the lack of similarity between summer and the other 2 seasons. Autumn and winter also show some differences to one another. The stocking rates on the *Agrostis/Festuca* species rich grid square were highest in summer and winter and lowest in autumn. The *Agrostis/Festuca* species poor grid square however was grazed least in summer and most in autumn and winter. It should be noted that the species rich grid square was situated at a low altitude whilst the species poor grid square was at a high altitude. The low old *Calluna* grid square was most heavily used in winter, whilst the high old *Calluna* grid square was used most in autumn. The high old *Calluna* grid square was never as heavily used as the low grid square. Also the young *Calluna* grid square, situated at a high altitude had a very high stocking rate in autumn. It was in general more heavily used than the old *Calluna* grid squares. The low bracken grid square was used equally heavily in autumn and winter compared to the situation in summer. The high bracken grid square was used most in autumn. Again the high bracken grid square was never as heavily used as the low grid square.

Table 3.5 illustrates the stocking rates on 2 other high young *Calluna* grid squares. These 2 grid squares were found in Area 2 and were used by both Howlet animals and by animals from other groups. There is general agreement between the stocking rates for these grid

TABLE 3.5

STOCKING RATES FOR 2 GRID SQUARES IN AREA 2.

The data in this table shows the stocking rates in ewes/ha for 2 grid squares in Area 2 that were used by both Howlet sheep and sheep from other groups.

GRID SQUARE	VEGETATIONAL TYPE	SUMMER 1981	SUMMER 1982	AUTUMN 19881	WINTER 1981
B1008	Young <u>Calluna</u> (high)	0.6	0.8	3.4	1.76
D0507	Young <u>Calluna</u> (high)	0.7	0.8	2.1	0.8

TABLE 3.6

VARIANCE IN HOME RANGE BEHAVIOUR.

The variances in this table were arrived at by dividing the error sum of squares for a season (as calculated by Ward's Method) by the number of observations in that season. The values are therefore a measure of the variation in home range behaviour within the Howlet group in different seasons. The values in parenthesis are the error sum of squares for each season.

SEASON	VARIANCE (error sum of squares/ number of observations)
SUMMER 1981	0.272 (24.567)
AUTUMN 1981	0.101 (6.099)
WINTER 1982	0.178 (12.822)
SUMMER 1982	0.293 (23.476)

squares and the young Calluna grid square illustrated in Table 3.4 despite them being used by animals from more than one group.

3:3:2 The Relationship Between Individuals' Home Ranges

As mentioned previously (see 3:2:2) Cluster Analysis was used to classify animals on the basis of their different grid square area scores.

1 Summer 1981

Figure 3.9 presents the dendrogram produced from the home range data for Summer 1981 by Ward's Method of Cluster Analysis. The animals are represented along the bottom of the dendrogram and the dissimilarity coefficient (error sum of squares) is shown on the y axis. Those animals who are most similar to one another are linked at the base of the dendrogram. As the dissimilarity coefficient increases so more dissimilar animals are fused to form clusters. The initial impression is that 2 major clusters exist. Below this level there exist several other major clusters and below that a large number of much smaller clusters.

A measure of the total variance in the home range data is given by the total error sum of squares at the fusion of the final 2 clusters (24.6). If this value is divided by n-1 (where n equals the number of observations in a season) then it is a measure of variance in which sample size is accounted for. The total variance in the Summer 1981 dendrogram is 0.272 (see Table 3.6).

FIGURE 3.9

THE DENDROGRAM PRODUCED BY WARD'S METHOD OF CLUSTER ANALYSIS

FROM THE SUMMER 1981 HOME RANGE DATA.

The sheep are represented by their identification numbers along the base of the dendrogram. The most similar animals are fused first at the base of the dendrogram. Less similar animals are fused progressively towards the top of the dendrogram. The dissimilarity coefficient (error sum of squares) is shown on the y axis. The dendrogram has been divided at the level of 5 clusters as shown by the dotted line. The clusters are numbered in the same order as they will be referred to in the text (ie Cluster 1 in this dendrogram is C1/Sum81).

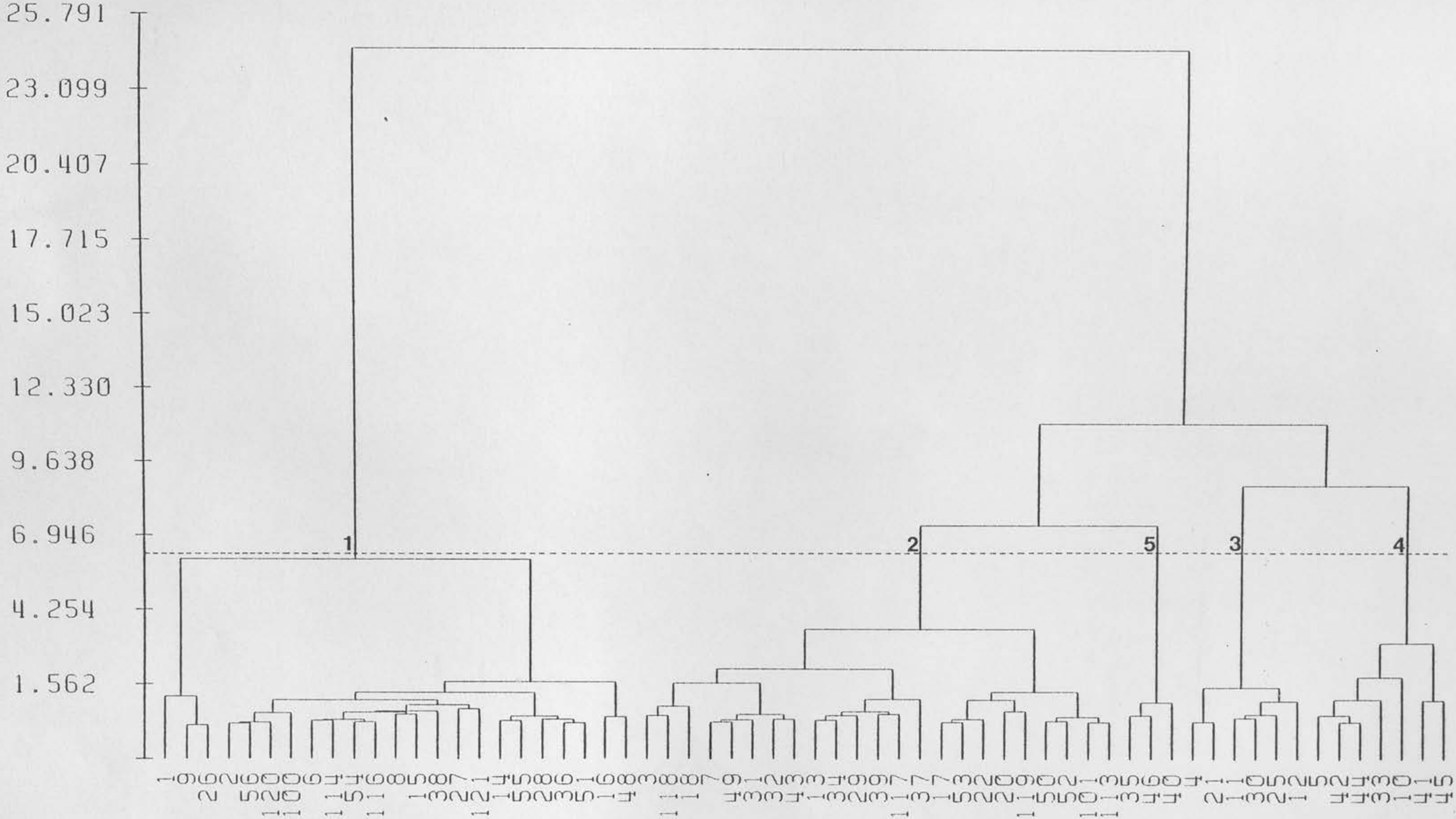
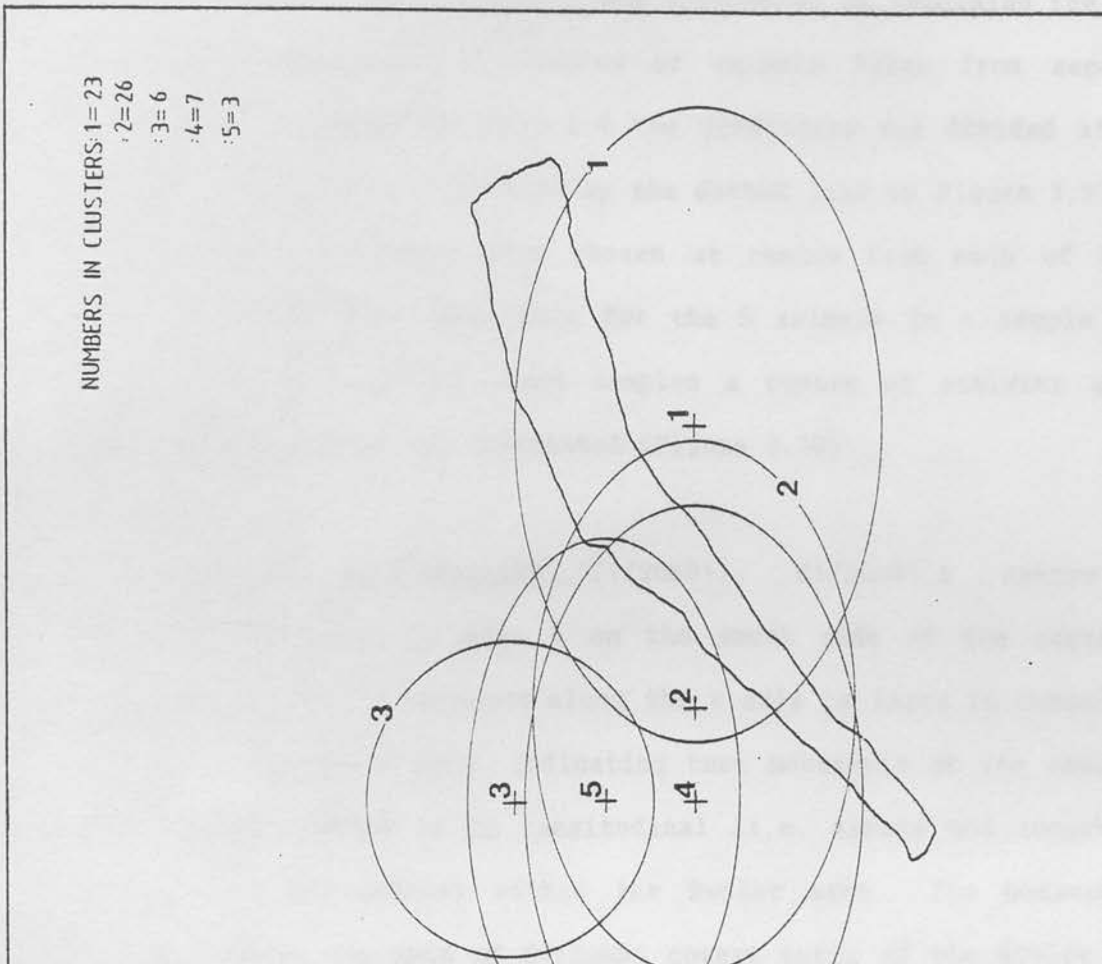

25.791
23.099
20.407
17.715
15.023
12.330
9.638
6.946
4.254
1.562
1
2
5
3
4

FIGURE 3.10

CENTRES OF ACTIVITY AND MEASURES OF VARIANCE FOR 5 CLUSTERS IN SUMMER 1981.

This figure shows the centres of activity and measures of variance (one standard deviation along the x and the y axis) as calculated for samples of animals from 5 clusters in Summer 1981. The numbers of sheep found in each cluster are given in the top right hand corner. Again clusters are numbered in the same order as they are referred to in the text (ie Cluster 1 in this diagram is C1/Sum81).


NUMBERS IN CLUSTERS: 1=23
:2=26
:3=6
:4=7
:5=3
BASED ON 100M X 100M GRIDS

Age was found to have no effect upon the composition of clusters in Summer 1981 (Kruskal-Wallis one way ANOVA, H =1.797, df=4, NS).

An understanding of the biological significance underlying the results of the cluster analysis was arrived at by examining the mean home range behaviour of samples of animals taken from separate clusters. As explained in 3:2:4 the dendrogram was divided at the level of 5 clusters (indicated by the dotted line on Figure 3.9) and if available 5 animals were chosen at random from each of these clusters. The home range data for the 5 animals in a sample were summed and for each of these samples a centre of activity and a measure of variance was calculated (Figure 3.10).

Cluster 1 in Summer 1981 (C1/Sum81): C1/Sum81's centre of activity was found in Area 4 on the south side of the reservoir (Figure 3.10). The variance along the x axis is large in comparison to that along the y axis, indicating that movements of the sheep in this cluster tended to be longitudinal (i.e. around the reservoir) rather than altitudinal within the Hwolet area. The measure of variance about the mean of C1/Sum81 covers parts of the Howlet area as well as covering large parts of the south side of the reservoir that sheep from other clusters did not use. Examination of the home range maps of individuals in C1/Sum81 support this analysis showing that sheep from C1/Sum81 largely used areas around the dam front (Grid Areas 14 and 15; see Figure 3.1) and on the south side of the reservoir (Grid Areas 22, 23, 26, 27, 28, 34). These animals were also found in the Howlet area for small amounts of time. From observational notes it is known that many of these animals would spend days (in some cases up to 2 or 3 weeks) without returning to the Howlet area.

Cluster 2 in Summer 1981 (C2/Sum81): Cluster 2 had a centre of activity situated near the water on the Howlet side of the reservoir. The variance along the x axis is again larger than along the y axis and includes areas on both sides of the reservoir. Home range maps of individuals in this cluster reveal it to contain basically 2 types of individual.

Firstly there are those members that made numerous visits to the dam front. Some of these ranged quite extensively on the south side of the reservoir. Notes taken at the time show that these sheep tended to visit the dam front on a daily basis returning to the Howlet on the same day. Some were however known to spend some nights on the south side of the reservoir.

Secondly there are individuals who rarely, if at all, left the Howlet area. These animals tended to have extensive ranges in the Howlet; some without seeming to have a strong preference for any area whilst others showed some preference for the centrally situated lower lying areas (Grid Areas 19 and 20).

Cluster 3 in Summer 1981 (C3/Sum81): This cluster had a centre of activity situated at a high altitude in the Howlet area. The variance around the centre of activity was circular. This cluster contains individuals that had small contained ranges with movements concentrated in the central and north-eastern parts of the Howlet (Grid Areas 6, 10, 11, 19, 20).

Cluster 4 in Summer 1981 (C4/Sum81): C4/Sum81 had a centre of activity in the Howlet that was further to the west than that of C2/Sum81. The home range maps of the animals in this cluster showed them to have a preference for western parts of the Howlet (Grid Areas 16, 17, 19 and 24). They also used the flat grassy sward at the SW end of the reservoir (Grid Area 32) and made use of the land to the west of the fence, on the neighbouring farm (Grid Area 30).

Cluster 5 in Summer 1981 (C5/Sum81): This cluster had a centre of activity centrally situated in the Howlet. The variance along the x axis was again large. This was a small cluster of 3 animals that concentrated their movements heavily on the 2 grid squares which had previously been sprayed for bracken (Grid Area 18) and the low lying area at the mouth of the Howlet burn (Grid Area 20)

2 Autumn 1981

As described in 2:3 the farmer at this time of year had removed approximately one-fifth of the old ewes and replaced them with an equivalent number of ewe-lamb. In the dendrogram for Autumn 1981 (Figure 3.11) the adults present in both Summer 1981 and Autumn 1981 are indicated. The other animals in the dendrogram are therefore the ewe lambs born in Summer 1981. As in Summer 1981 two main clusters are apparent but in this case one of these is a very small cluster of 6. Examination of the composition of the clusters however reveals little similarity to the situation in the previous summer (see below).

FIGURE 3.11

DENDROGRAM PRODUCED BY WARD'S METHOD

FROM THE AUTUMN 1981 HOME RANGE DATA.

The animals present in both this analysis and the analysis of the Summer 1981 home range data are indicated by dots. The unmarked animals are the ewe-lambs "added" to the group in August 1981. See Figure 3.9 for a full description of this figure.

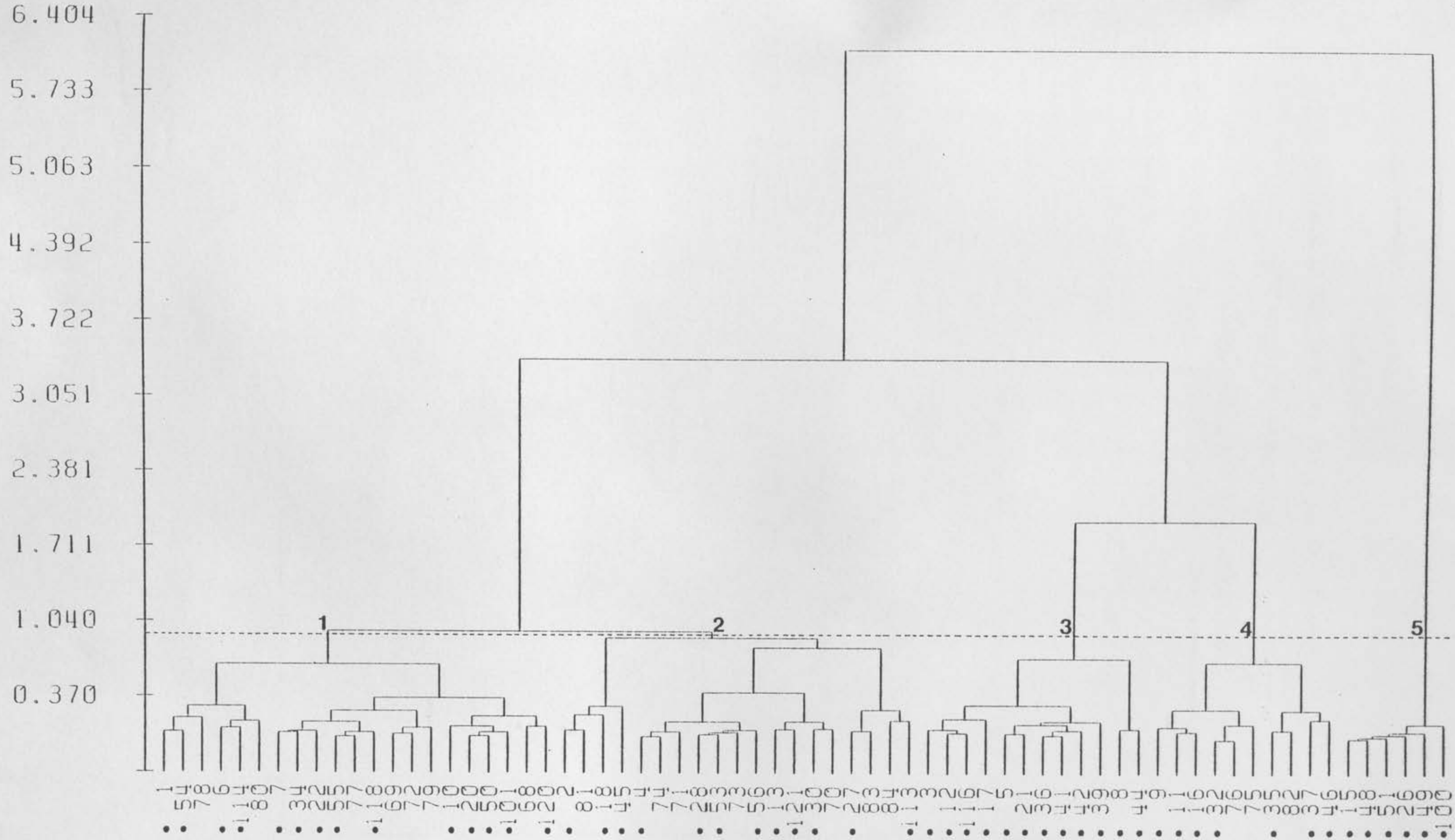
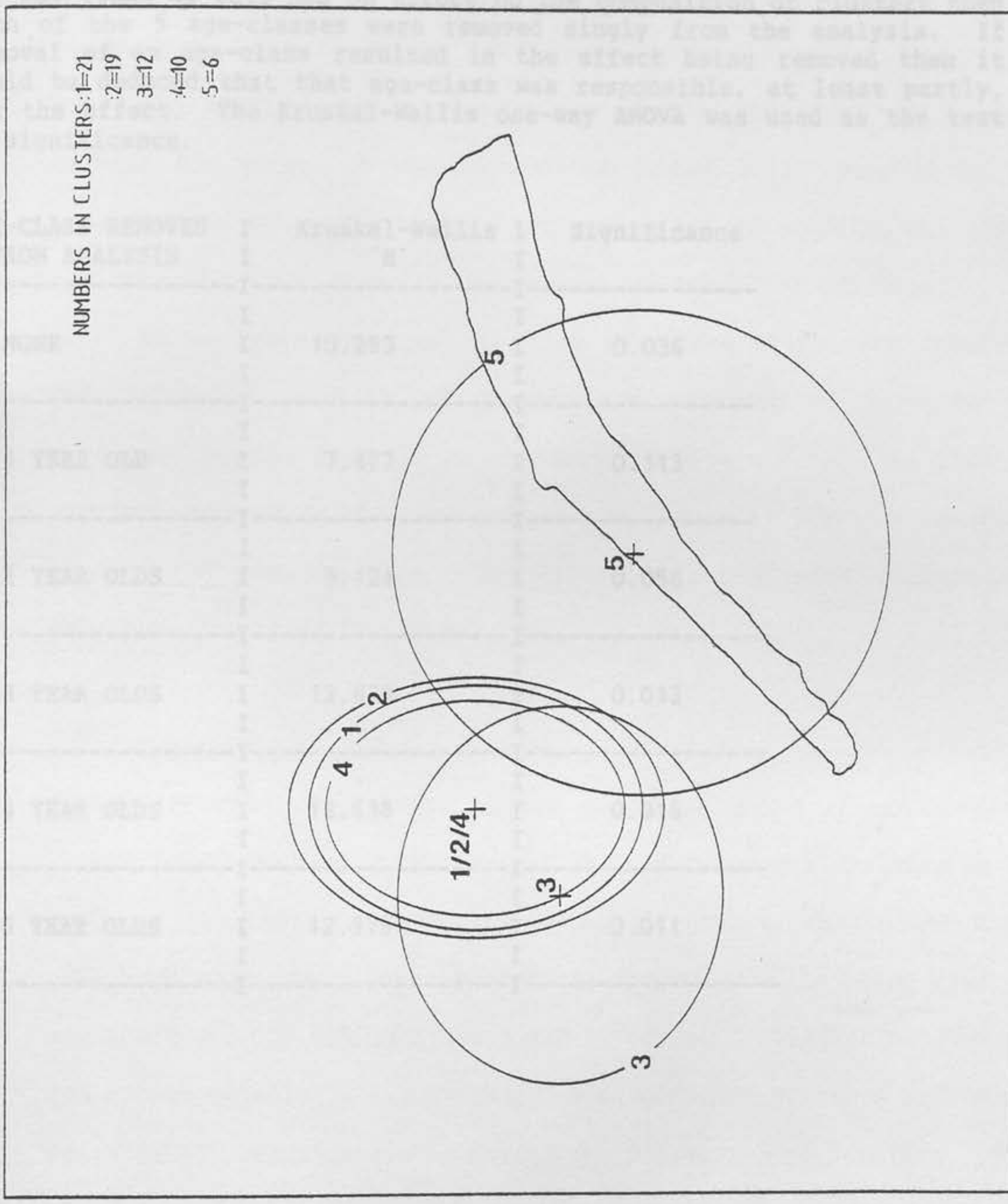

6.404
5.733
5.063
4.392
3.722
3.051
2.381
1.711
1.040
0.370
1
2
3
4
5

FIGURE 3.12

CENTRES OF ACTIVITY AND MEASURES OF VARIANCE FOR 5 CLUSTERS IN AUTUMN 1981.

See Figure 3.10 for a description of this figure.



BASED ON 100M X 100 GRIDS

<u>TABLE 3.7</u>

THE EFFECT OF AGE ON THE COMPOSITION OF CLUSTERS IN AUTUMN 1981.

Initially the analysis was performed with all age-classes present. If age was found to have had an effect on the composition of clusters then each of the 5 age-classes were removed singly from the analysis. If removal of an age-class resulted in the effect being removed then it could be deduced that that age-class was responsible, at least partly, for the effect. The Kruskal-Wallis one-way ANOVA was used as the test of significance.

AGE-CLASS REMOVED FROM ANALYSIS	Kruskal-Wallis ´H´	Significance
NONE	10.253	0.036
< 1 YEAR OLD	7.477	0.113
2 YEAR OLDS	9.124	0.058
3 YEAR OLDS	12.638	0.013
4 YEAR OLDS	12.638	0.016
5 YEAR OLDS	12.975	0.011

The total variance in the Autumn 1981 home range data was 0.101 (see Table 3.6).

Age had some effect upon the composition of clusters in Autumn 1981 (Kruskal-Wallis one-way ANOVA, H =10.252, df=4, $p<0.05$). In order to examine which age classes were largely responsible each age class was removed singly and the analysis recalculated. The ewe-lambs appear largely responsible for the effect as after their removal the effect is greatly reduced (Table 3.7). Removal of the gimmers from the analysis was less successful at reducing the effect and removal of the other 3 age-classes was even less effective.

An analysis identical to that described previously involving calculation of centres of gravity and measures of variance was performed on this data and is presented in Figure 3.12. The clusters are not numbered in the same order as in Summer 1981 but in the order produced by the computer. The situation has altered considerably from that described for Summer 1981.

<u>Clusters 1, 2 and 4 in Autumn 1981</u>(C1/Aut81, C2/Aut81/, C4/Aut81): These 3 clusters shared a common centre of activity and almost identical variances situated in a high central position in the Howlet. The variance along the y axis is greater than along the x axis indicating that most movement by the animals in these clusters was altitudinally within Areas 1 and 2. These 3 clusters account for 73% of the animals in the group. The composition of these 3 clusters bears little relationship to any of the 5 Summer 1981 clusters. This is illustrated in Table 3.8 where the results of the analysis of cluster compositional stability between these 2 seasons are displayed. (As previously stated only animals present from the start

TABLE 3.8

ANALYSIS OF CLUSTER COMPOSITIONAL STABILITY BETWEEN SUMMER 1981 AND AUTUMN 1981.

This table shows the numbers of animals from the 5 Summer 1981 clusters that would be expected to be found in the clusters in Autumn 1981 (see 3:2:2 part 4 for an explanation as to how the expected values were derived). The expected values are compared to the observed values. The values marked by an asterisk are those where there was a large departure from the expected (i.e. where the residual was > 2.0). The one-sample test was used in situations where none of the expected values were less than 0.5.

AUTUMN 1981 CLUSTERS		NUMBERS FROM SUMMER 1981 CLUSTERS OBSERVED AND EXPECTED IN CLUSTERS IN AUTUMN 1981.					
		C1/Sum81	C2/Sum81	C3/Sum81	C4/Sum81	C5/Sum81	
C1/Aut81	Expected:	5.19	5.19	1.3	1.5	0.67	χ^2= 2.88
	Observed:	6	7	0	1	0	df= 4, NS
C2/Aut81	E :	4.45	4.45	1.16	1.35	0.58	χ^2= 1.37
	O :	5	4	2	1	0	df= 4, NS
C3/Aut81	E :	4.45	4.45	1.16	1.35	0.58	χ^2= 7.32
	O :	3	3	2	4*	0	df= 4, NS
C4/Aut81	E :	2.5	2.5	0.67	0.79	0.33	(not
	O :	2	2	1	0	2*	tested)
C5/Aut81	E :	2.2	2.2	0.58	0.67	0.29	(not
	O :	5*	1	0	0	0	tested)

of observations in Summer 1981 are included in this analysis). C1/Aut81 and C2/Aut81 (50% of the animals analysed) showed no significant tendency to recruit more sheep than expected from any one cluster in Summer 1981. In other words they contain a random assortment of animals from the 5 Summer 1981 clusters. Both these Autumn 1981 clusters contain sheep from C1/Sum81, C2/Sum81 and C4/Sum81. C4/Aut81 could not be tested for cluster compositional stability, due to a small expected value, but it similarly showed little tendency to deviate from the expected except in the recruitment of 2 of the 3 sheep from C5/Sum81.

Examination of the home range maps of these 3 clusters reveals no consistent difference between them that is obvious on inspection by eye. They all had reasonably extensive home ranges within the Howlet that showed no strong preference for any one area. Some of the sheep that had spent time on the south side of this reservoir in Summer 1981 still had a few observations there.

Cluster 3 in Autumn 1981 (C3/Aut81): This cluster has a centre of activity to the west of C1/Aut81, C2/Aut81 and C4/Aut81. Table 3.8 shows it to contain 4 out of 7 members of C4/Sum81 that tended to use the western parts of the Howlet. This deviation from the expected, results in a high but non-significant chi-square. The other sheep in the cluster were recruited as expected from C1/Sum81, C2/Sum81 and C3/Sum81. The home range maps of the animals in C3/Aut81 reveal a slight tendency for these sheep to have used the lower and western parts of the Howlet more than other animals and not to have ranged as far east as sheep from C1/Aut81, C2/Aut81 and C4/Aut81. It must be said that by eye it would have been difficult to have discerned this as a separate grouping.

Cluster 5 in Autumn 1981 (C5/Aut81): C5/Aut81 has a centre of activity on the Howlet side of the reservoir at the water's side. This cluster consists of 5 members of C1/Sum81 and one member of C2/Sum81. These 6 sheep were still heavily using the south side of the reservoir in Autumn 1981. It seems that C5/Aut81 can be regarded as a remnant of C1/Sum81; it however could not be tested for cluster compositional stability due to a low expected value (see Table 3.8). The home range maps of this group reveal an extensive use of the south side of the reservoir and also some use of the higher parts of the Howlet area (Grid Areas 5, 6 and 9). This combination of use of both sides of the reservoir has resulted in the centre of activity being at the water's side.

Observational notes reveal that whilst on the south side of the reservoir this group of 6 generally were very coordinated in their movements and were rarely separated from one another. They were joined at various times by other members of the Howlet group.

During this period the farmer twice rounded up Carnethy with the following results:

a) 291081: Four of the 6 (Numbers 15, 48, 49 and 51) were rounded up with Carnethy ewes for the winter dip. Numbers 26 and 100 were left on the south side of the reservoir. The next day the 4 which had been rounded up had returned to the south side along with some members of C1/Aut81 and C3/Aut81 (Numbers 6, 80, 114 and 120). These 8 were also joined by Number 100 but Number 26 returned to the Howlet.

FIGURE 3.13

THE DENDROGRAM PRODUCED BY WARD´S METHOD

FROM THE WINTER 1982 HOME RANGE DATA.

All animals present in the Autumn 1981 analysis are present in this analysis. The animals present since Summer 1981 are again indicated by dots. See Figure 3.9 for a full description of this figure.

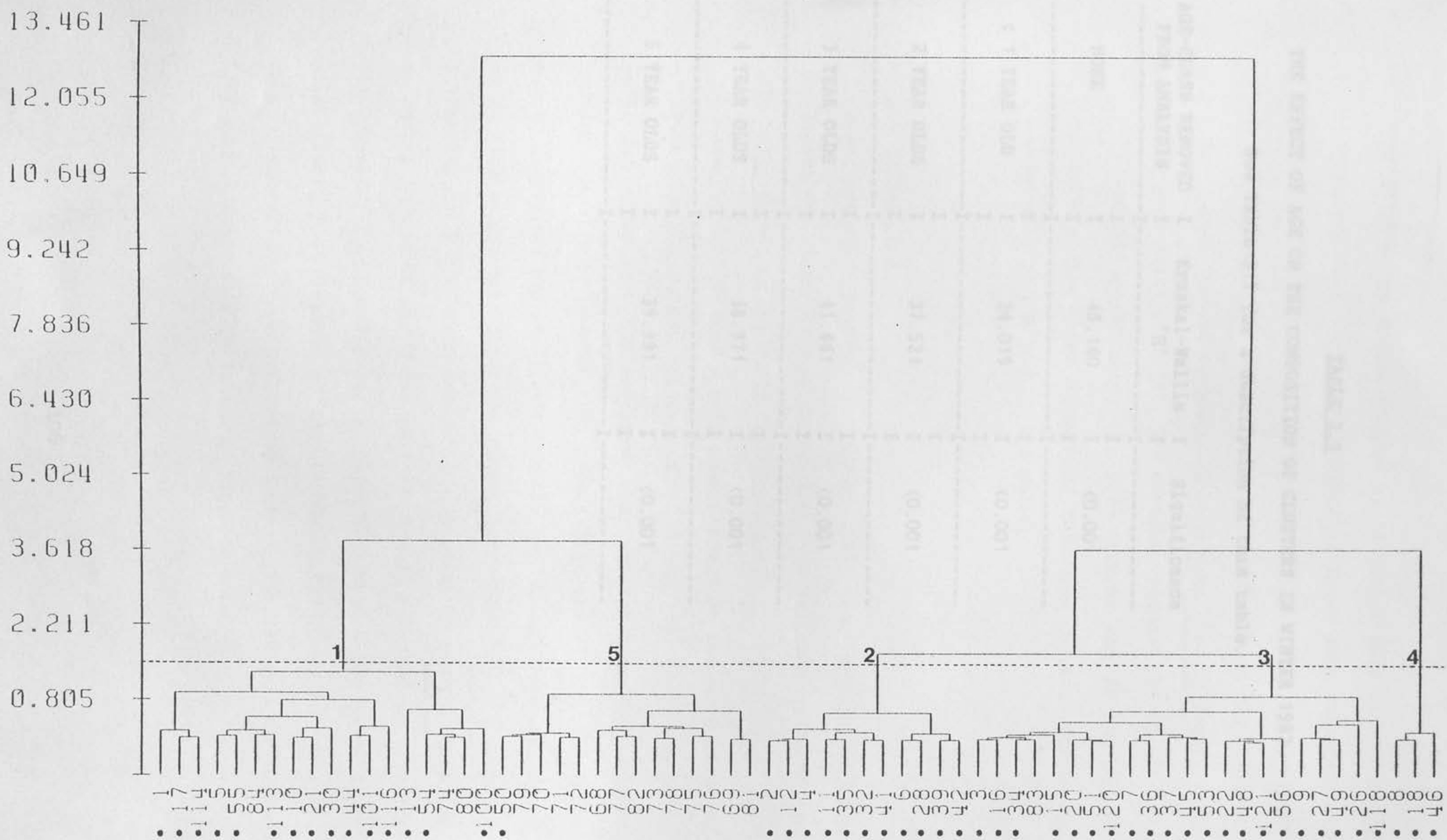

13.461
12.055
10.649
9.242
7.836
6.430
5.024
3.618
2.211
0.805
1
5
2
3
4

TABLE 3.9

THE EFFECT OF AGE ON THE COMPOSITION OF CLUSTERS IN WINTER 1982.

See Table 3.7 for a description of this table.

AGE-CLASS REMOVED FROM ANALYSIS	Kruskal-Wallis 'H'	Significance
NONE	45.140	<0.001
< 1 YEAR OLD	24.019	<0.001
2 YEAR OLDS	37.521	<0.001
3 YEAR OLDS	41.461	<0.001
4 YEAR OLDS	38.771	<0.001
5 YEAR OLDS	39.391	<0.001

b) 041181: The farmer rounded up 13 Howlet ewes with Carnethy ewes including the 6 from C5/Aut81. These were released with the Carnethy ewes but all returned to the Howlet on their own accord. From this point onward the south side of the reservoir was rarely visited by Howlet sheep before the end Autumn 1981. Two days later (061181), for example, Numbers 15, 26, 36, 49, 77 and 114 moved along the road towards the SW end of the reservoir (the first movement of this type for some weeks) but eventually turned back to the Howlet.

3 Winter 1982

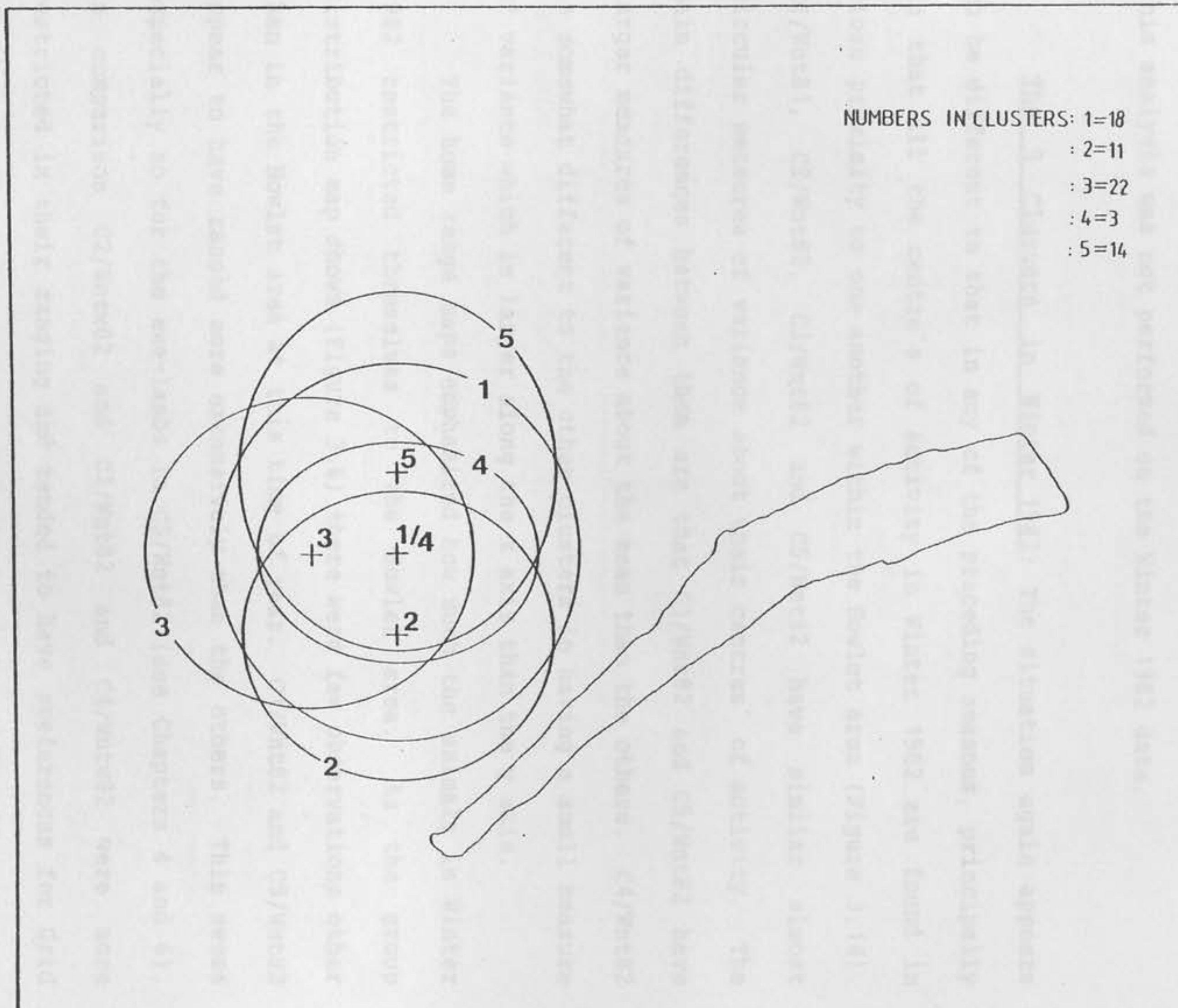
All animals present in Autumn 1981 are present in the dendrogram for Winter 1982 (Figure 3.13). The variance in the Winter 1982 home range data was 0.178 (see Table 3.6).

Age was seen to have a very strong effect on the composition of clusters (Kruskal-Wallis one-way ANOVA, H =45.140, df=4, $p<0.001$). Table 3.9 shows that the ewe-lambs when removed from the analysis reduced the effect; however even after their removal the effect of age on clustering was still substantial. No one age-class was found to be wholly responsible for the effect (see Table 3.9). Clusters 1 (C1/Wnt82) and 5 (C5/Wnt82) contain the majority of animals up to and including 3 years of age (Binomial Test, z=3.3, $p<0.001$) and Clusters 2 (C2/Wnt82), 3 (C3/Wnt82) and 4 (C4/Wnt82) contain the majority of animals more than 3 years of age (Binomial Test, z=3.3, $p<0.001$). This effect of age upon the composition of the clusters in Winter 1982 will be dealt with in detail in Chapters 4 and 6.

FIGURE 3.14

CENTRES OF ACTIVITY AND MEASURES OF VARIANCE FOR 5 CLUSTERS IN WINTER 1982.

See Figure 3.10 for a description of this figure.



BASED ON 100M X 100M GRIDS.

The composition of the Winter 1982 clusters bears little relationship to clusters formed in previous seasons due to the strength of this age effect. It was felt therefore that the clusters in Winter 1982 would not afford a useful comparison for examining the compositional stability of clusters between seasons. Consequently this analysis was not performed on the Winter 1982 data.

The 5 Clusters in Winter 1982: The situation again appears to be different to that in any of the preceding seasons, principally in that all the centre's of activity in Winter 1982 are found in close proximity to one another within the Howlet area (Figure 3.14). C1/Wnt81, C2/Wnt82, C3/Wnt82 and C5/Wnt82 have similar almost circular measures of variance about their centres' of activity. The main differences between them are that C1/Wnt82 and C5/Wnt82 have larger measures of variance about the mean than the others. C4/Wnt82 is somewhat different to the other clusters in having a small measure of variance which is larger along the x axis than the y axis.

The home range maps emphasized how much the animals in Winter 1982 restricted themselves to the Howlet area. As the group distribution map shows (Figure 3.6) there were few observations other than in the Howlet area at this time of year. C1/Wnt82 and C5/Wnt82 appear to have ranged more extensively than the others. This seems especially so for the ewe-lambs in C5/Wnt82 (see Chapters 4 and 6). In comparison C2/Wntw82 and C3/Wnt82 and C4/Wntw82 were more restricted in their ranging and tended to have preferences for Grid Areas 18, 19 and 20. This is particularly so for C4/Wntw82.

Toward the end of Winter 1982 observational notes show that the animals began to move down towards the dam front:

TABLE 3.10

THE EFFECT OF AGE ON THE COMPOSITION OF CLUSTERS IN SUMMER 1982

See Table 3.7 for a description of this table.

AGE-CLASS REMOVED FROM ANALYSIS	Kruskal-Wallis 'H'	Significance
NONE	14.071	0.007
1 YEAR OLD	4.997	0.28
2 YEAR OLDS	16.217	0.003
3 YEAR OLDS	13.402	0.009
4 YEAR OLDS	15.050	0.005
5 YEAR OLDS	11.114	0.025

a) 020482: Numbers 9, 48, 49, 51 and 81 made the first recorded journey onto the dam front since Autumn 1981.

b) 050482: Numbers 34, 48, 49, 51 and 100 were found on the south side of the reservoir. They were grazing near to a group of Carnethy ewes when the shepherd on the neighbouring farm disturbed them by shouting and whistling at his dog. The Carnethy ewes remained stationary whilst the Howlet animals ran away from the disturbance and eventually made their way back to the Howlet.

4 Summer 1982

The total variance present in the Summer 1982 home range data was 0.293 (Table 3.6).

Age had a strong effect upon the composition of clusters in Summer 1982 (Kruskal-Wallis one-way ANOVA, H =14.071, df=4, $p<0.01$) (Table 3.10). This seems wholly attributable to the ewe-lambs as their removal from the analysis removed the effect; removal of the other age classes did not remove the effect.

The centres of activity and measures of variance for the 5 clusters in Summer 1982 bear a strong resemblance to the comparable figure for Summer 1981 (Figures 3.10 and 3.16).

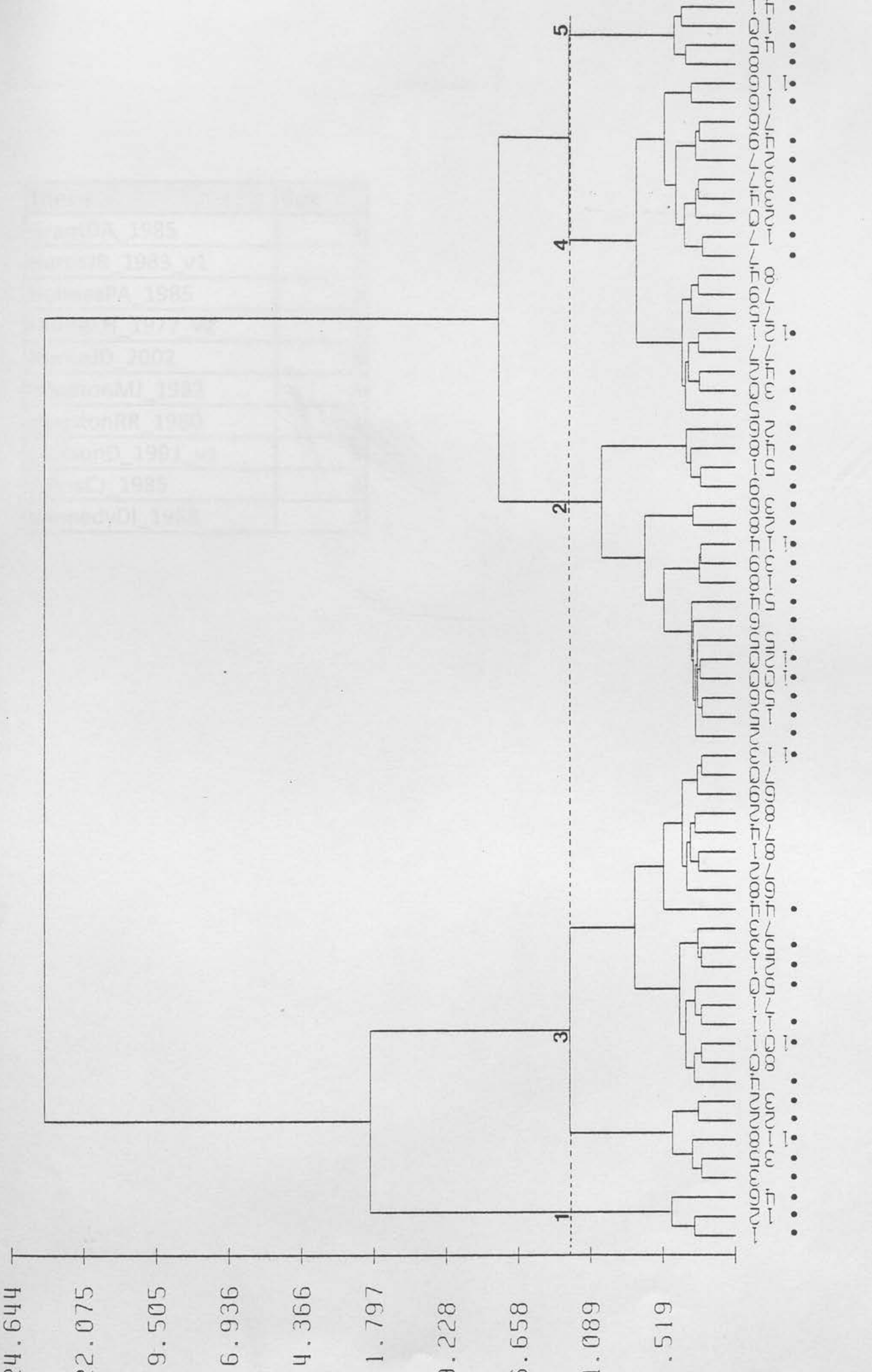
Cluster 2 in Summer 1982 (C2/Sum82): This cluster occupied an almost identical position to that of C1/Sum81 on the south side of the reservoir. The analysis of cluster compositional stability between Summers 1981 and 1982 Table 3.11 shows that C2/Sum82

FIGURE 3.15

THE DENDROGRAM PRODUCED BY WARD'S METHOD

FROM THE SUMMER 1982 HOME RANGE DATA.

See Figure 3.9 for a description of this figure.



24.644
22.075
19.505
16.936
14.366
11.797
9.228
6.658
4.089
1.519
1
2
3
4
5

FIGURE 3.16

CENTRES OF ACTIVITY AND MEASURES OF VARIANCE FOR

5 CLUSTERS IN SUMMER 1982.

See Figure 3.10 for a description of this figure.

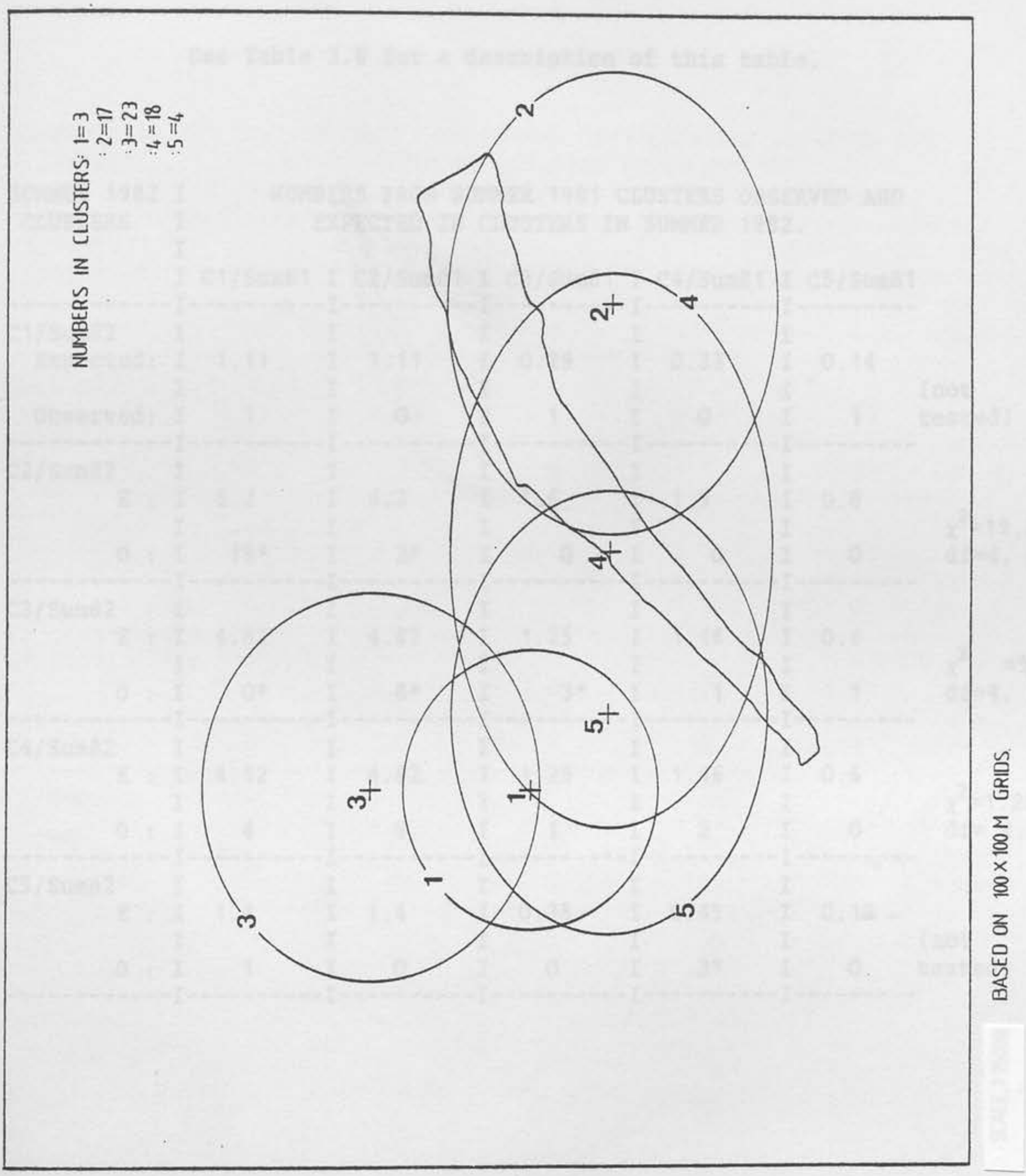

NUMBERS IN CLUSTERS: 1=3
: 2=17
: 3=23
: 4=18
: 5=4
BASED ON 100 X 100 M GRIDS
1
2
3
4
5

TABLE 3.11

ANALYSIS OF CLUSTER COMPOSITIONAL STABILITY BETWEEN

SUMMER 1981 AND SUMMER 1982.

See Table 3.8 for a description of this table.

SUMMER 1982 CLUSTERS	NUMBERS FROM SUMMER 1981 CLUSTERS OBSERVED AND EXPECTED IN CLUSTERS IN SUMMER 1982.					
	C1/Sum81	C2/Sum81	C3/Sum81	C4/Sum81	C5/Sum81	
C1/Sum82 Expected:	1.11	1.11	0.29	0.33	0.14	
Observed:	1	0	1	0	1	(not tested)
C2/Sum82 E :	6.3	6.3	1.6	1.9	0.8	
O :	15*	2*	0	0	0	χ^2=19.3 df=4, p<0.001
C3/Sum82 E :	4.82	4.82	1.25	1.46	0.6	
O :	0*	8*	3*	1	1	χ^2 =9.76 df=4, p<0.05
C4/Sum82 E :	4.82	4.82	1.25	1.46	0.6	
O :	4	6	1	2	0	χ^2=1.25 df= 4, NS
C5/Sum82 E :	1.4	1.4	0.38	0.45	0.19	
O :	1	0	0	3*	0	(not tested)

<u>TABLE 3.12</u>

ANALYSIS OF CLUSTER COMPOSITIONAL STABILITY BETWEEN

AUTUMN 1981 AND SUMMER 1982.

See Table 3.8 for a description of this table.

SUMMER 1982 CLUSTERS	NUMBERS FROM AUTUMN 1981 CLUSTERS OBSERVED AND EXPECTED IN CLUSTERS IN SUMMER 1982.					
	C1/Aut81	C2/Aut81	C3/Aut81	C4/Aut81	C5/Aut81	
C1/Sum82						
Expected:	0.82	0.70	0.70	0.41	0.35	(not
Observed:	1	0	1	1	0	tested)
C2/Sum82						
E :	4.59	3.99	3.99	2.33	1.99	χ^2= 6.32
O :	5	4	2	1	5*	df= 4, NS
C3/Sum82						
E :	3.5	3.05	3.05	1.78	1.52	χ^2= 2.42
O :	4	3	3	3	0	df= 4, NS
C4/Sum82						
E :	3.5	3.05	3.05	1.78	1.52	χ^2= 0.637
O :	3	3	4	2	1	df= 4, NS
C5/Sum82						
E :	1.09	0.94	0.94	0.54	0.47	(not
O	1	1	2	0	0	tested)

recruited a large and significant number of animals from C1/Sum81 and a significantly small number of animals from the other clusters. In other words C2/sum82 was very similar to C1/Sum81 both in terms of cluster composition and area preference.

Table 3.12 illustrates the results of cluster compositional stability between Autumn 1981 and Summer 1982. C2/Sum82 recruited no more than expected from any of the Autumn 1981 clusters. However 5 members (out of 6) of C5/Aut81 (the small cluster that exhibited a strong preference for the south side of the reservoir) showed a large (but non-significant) deviation from expected in joining C2/Sum82.

Observational notes and home range maps reveal that the behaviour of the animals in C2/Sum82 was very similar to that of C1/Sum81. They ranged extensively on the south side of the reservoir (using Grid Areas 14, 15 22, 23, 27, 28 and 34 particularly heavily), perhaps having even fewer observations in the Howlet than in the previous year. They would spend many days, sometimes weeks without returning to the Howlet.

Cluster 4 in Summer 1982 (C4/Sum82): C4/Sum82 occupied a very similar position to that of C2/Sum81. The variance covers large areas of both the Howlet and the south side of the reservoir.

The analysis of cluster compositional stability between Summer 1981 and Summer 1982 (see Table 3.11) shows that C4/Sum82 did not recruit significant numbers from any of Summer 1981 clusters. C4/Sum82 contains a selection from 4 of the Summer 1981 clusters, the majority coming from C1/Sum81 and C2/Sum81. Table 3.12 reveals that C4/Sum82 also did not recruit more than expected from the Autumn 1981 clusters.

Home range maps and observational notes reveal that similarly to C2/Sum81, C4/Sum82 contained a variety of home range types. The basic distinction made between animals in C2/Sum81 of those which visited the dam front and the south side of the reservoir on a daily basis, and those which never or rarely left the Howlet still existed. Those animals from C2/Sum81 which had visited the south side of the reservoir continued to do so, as did 4 animals from C1/Sum81. As in Summer 1981 they often travelled back to the Howlet on the same day although on some occasions they would remain on the south side continuously for 2 or 3 days. Those animals from C2/Sum81 that did not visit the south side, along with one animal from C4/Sum81, continued to range extensively in the Howlet with some bias towards Grid Areas 5, 9, 16, 17, 18 and 24. They also extended their ranging somewhat into Grid Areas 13, 14, 15 and 21 (i.e. towards the dam front).

C4/Sum82 also contained 5 ewe-lambs all of which visited the south side of the reservoir on a regular basis.

Cluster 3 in Summer 1982 (C3/Sum82): This cluster occupied a similar position to C3/Sum81. Again the variance was almost circular about the centre of activity, being somewhat larger in Summer 1982 than in Summer 1981.

Table 3.11 illustrates that this cluster recruited significantly large numbers from C2/Sum81 and C3/Sum81. It is basically a fusion of some of those animals in C2/Sum82 whose activity was centred in the Howlet and 3 (out of 6) ewes from C3/Sum81 that used north-eastern parts of the Howlet. Table 3.12 shows that this cluster again bore no relationship to clusters in

Autumn 1981.

Home range maps show that at least 2 basic types of animal can be distinquished in C3/Sum82. Firstly a small group of 5 older ewes (4 from C2/Sum81) which tended to concentrate their movements in the central lower parts of the Howlet (Grid Areas 18, 19 and 20) and made a very small number of visits to the dam front. Secondly a much larger group containing the 3 animals from C3/Sum81 plus 4 two year olds from C2/Sum81 and 10 ewe-lambs. This group showed preference for northeastern and central parts of the Howlet.

Cluster 5 in Summer 1982 (C5/Sum82): This cluster occupied a similar position to C4/Sum81. Table 3.11 shows that 3 of the 7 members of C4/Sum81 are found in this cluster along with one member of C1/Sum81. This cluster again bore little relationship to clusters in Autumn 1981 (see Table 3.12).

The animals in C5/Sum82 (similarly to C4/Sum81) used south and north western parts of the Howlet preferentially, especially Grid Areas 24, 25 and 32. This group also sometimes ranged on the south side of the reservoir.

Cluster 1 in Summer 1982 (C1/Sum82): C1/Sum82 occupied a central position similar to that occupied by C5/Sum81. Table 3.11 shows that the 3 animals in this cluster were recruited at random from the Summer 1981 clusters. One of them came from the C5/Sum81. The cluster again bore little relationship to Autumn 1981 clusters (see Table 3.12). The animals in this cluster had very small home ranges which were concentrated heavily on Grid Areas 18 and 20.

FIGURE 3.17

THE CONSISTENCY OF HOME RANGE BEHAVIOUR IN DIFFERENT AGE-CLASSES OVER SUCCESSIVE SUMMERS

This diagram illustrates how consistent the 3 age-classes; ewe-lambs, gimmers and 3 year old ewes, and 4 year old ewes were in their home range behaviour over 2 successive summers, 1981 and 1982. The results were arrived at by clustering the 2 summer data sets together using Ward's Error Sum of Squares Method. Thus individuals that were found in the same cluster could be said to have had similar home range behaviour in the 2 summers. Ewe-lambs in Summer 1982 were compared to their mothers in Summer 1981, as direct data was not available for them in their first summer of life. The resulting dendrograms were analysed at different levels of clustering; the lower the level (ie the 10 cluster level is lower than the 5 cluster level) the finer the scale of the measurement. The numbers of individuals in an age-class found in the same cluster as themselves were summed and expressed as a percentage. See also Table 3.13.

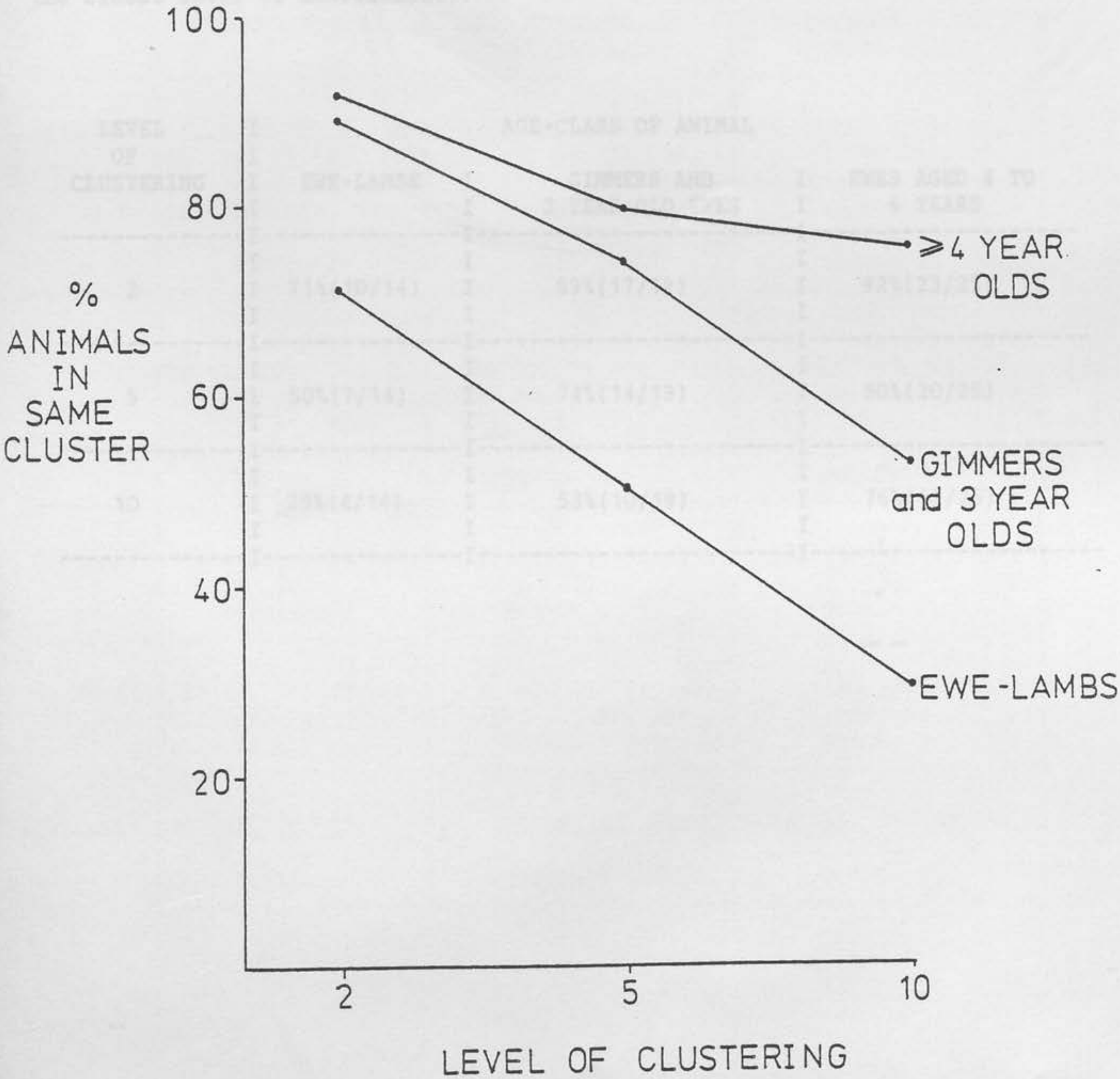

100
80
60
40
20
%
ANIMALS
IN
SAME
CLUSTER
≥4 YEAR
OLDS
GIMMERS
and 3 YEAR
OLDS
EWE-LAMBS
2
5
10
LEVEL OF CLUSTERING

TABLE 3.13

WARD′ CLUSTER ANALYSIS OF CONSISTENCY IN HOME RANGE PATTERNS

OVER SUMMERS 1981 AND 1982.

This table shows the percentage of animals in each age class occuring in the same cluster as themselves when the 2 summer season home range data are analysed singly; it is therefore a measure of how similar individual animals′ home range behaviour was over the 2 summers. The ewe-lamb data was obtained by comparing their behaviour in Summer 1982 with that of their mother in Summer 1981 (the ewe-lambs first summer of life). The dendrograms were divided at different levels to analyse the strength of the effect at finer levels of similarity (i.e. the 10 cluster level is the finest level of measurement).

LEVEL OF CLUSTERING	AGE-CLASS OF ANIMAL		
	EWE-LAMBS	GIMMERS AND 3 YEAR OLD EWES	EWES AGED 4 TO 6 YEARS
2	71%(10/14)	89%(17/19)	92%(23/25)
5	50%(7/14)	74%(14/19)	80%(20/25)
10	29%(4/14)	53%(10/19)	76%(19/25)

TABLE 3.14

COMPOSITION OF 5 CLUSTERS IN SUMMER 1981

AS ESTIMATED BY 3 METHODS OF CLUSTERS ANALYSIS.

The high degree of conformity across the methods, with regard to the composition of the clusters, shows that the results obtained with Ward´s Method can be regarded with some confidence.

CLUSTER	COMPOSITION OF CLUSTERS USING :		
	WARD´S METHOD; USED IN THE PRESENT STUDY.	RELOCATION TECHNIQUE USING WARD´S METHOD TO GENERATE THE INITIAL ARRAY.	RELOCATION TECHNIQUE USING A RANDOM ASSORTMENT AS THE INITIAL ARRAY.
C1/Sum81	1, 2, 6, 8, 9, 14, 15, 16, 26, 27, 28, 36, 38, 48, 51, 54, 56, 100, 114, 116, 120, 121. TOTAL= 23	1, 2, 6, 8, 9, 14, 15, 16, 26, 27, 28, 36, 38, 45, 48, 51, 54, 55, 56, 100, 114, 116, 120, 121. TOTAL= 24	1, 2, 6, 8, 9, 14, 15, 16, 26, 27, 28, 36, 45, 48, 51, 54, 55, 56, 100, 114, 116, 120, 121. TOTAL= 24
C2/Sum81	3, 7, 13, 17, 18, 20, 22, 29, 31, 32, 34, 37, 39, 43, 49, 50, 52, 53, 101, 113, 117, 118, 119. TOTAL= 23	3, 7, 13, 17, 18, 20, 22, 29, 31, 34, 37, 39, 43, 53, 113, 117, 118, 119. TOTAL= 19	3, 7, 13, 17, 20 22, 29, 31, 34, 37, 39, 49, 52, 53, 101, 113, 117, 118, 119. TOTAL=19
C3/Sum81	4, 11, 12, 21, 25, 30. TOTAL= 6	4, 11, 12, 21, 25, 30. TOTAL= 6	4, 11, 12, 21, 25, 30. TOTAL= 6
C4/Sum81	5, 10, 33, 41, 42, 44, 45. TOTAL= 7	5, 10, 33, 41, 42, 44, 50, 52, 101. TOTAL= 9	5, 10, 33, 41, 42, 44, 50. TOTAL= 7
C5/Sum81	35, 40, 46. TOTAL= 3	32, 35, 40, 46. TOTAL= 4	18, 32, 35, 40, 43, 46. TOTAL= 6

5 Analysis of consistency of home range behaviour:

Table 3.13 and Figure 3.17 show the results of cluster analyses to determine the consistency of individuals´ home range behaviour over 2 summer seasons. The data was separated into 3 age-classes: ewe-lambs, gimmers and 3 year old ewes and finally ewes aged 4 years and over. The data for ewe-lambs was obtained by comparing their home range behaviour in Summer 1982 with that of their mother in Summer 1981. Lambs were not included in scans until artificial weaning in August; it was assumed that in their first summer they would have identical behaviour to that of their mothers.

At the grossest level of clustering (i.e. the 2 cluster level) all 3 age-classes appeared consistent in their home range behaviour across 2 summers, although the effect clearly strengthened with age. At the finer levels of similarity the ewe-lambs were less consistent than the older age-classes. In addition the difference between the gimmers and 3 year old ewes and the older ewes increased at the level of 10 clusters, when the older animals were still very consistent.

6 Analysis of the "efficiency" of Ward´s Method:

It is not possible to state that the solution produced by a clustering technique is ´correct´ or ´significant´. However the solution can be compared to that achieved by other methods. An iterative relocation technique was used to attempt to improve upon the classification produced by Ward´s Method and also to classify an initially random assortment of individuals (see 3:2:2). The results of these 3 analyses are shown in Table 3.14. In all, 88% of the animals are found in the same cluster across the 3 methods. This degree of accord between these analyses increases confidence in the solutions produced by Ward's Method on the home range data sets.

3:4 DISCUSSION

3:4:1 Do the Sheep Occupying The Howlet Area Constitute a Home Range Group?

Following reports of the existence of home range groups in hill sheep (Hunter and Milner 1963; Hunter 1964) the intention of this study was to examine the behaviour of members of a home range group in detail. The choice of which group to study was facilitated by discussions with the farmer and it was he who rounded up the sheep with dogs for marking. It is therefore only possible to provide indirect proof that the sheep found in the Howlet are a home range group.

At the start of observations in May 1981, 7 unmarked animals were found to spend considerable amounts of time in the study site. They were consequently included in the scans as marked animals. At future times when Howlet animals were gathered in, a proportion of the animals, but never consistently the same animals, eluded the dogs, as these 7 animals apparently had in February at the first marking of the group.

The success with which marked animals were found in the study site was always high. On average at least 89% of marked animals were sighted each scan (see Table 3.1). It seems that such a success at locating marked animals within the study site, could not have occurred without an underlying home range structure as appears typical of hill sheep flocks (Hunter, 1964). The existence of a home range group structure in the sheep occupying the Howlet area is therefore indicated.

The possibility does exist of course that certain individuals were consistently missed during scans. As Figure 3.2 shows in general most individuals were sighted approximately the same number of times. It is worth pointing out that the success with which individuals were found increased with the experience of the observer. The quite large spread in the number of times that individuals were seen in the first summer was due more it seems to the inexperience of the observer than to the fact that the animals with low scores belonged to different groups.

The qualitative descriptions of interactions between marked and unmarked animals (see 3:3:1 part 2) indicate a strong ability in these sheep to recognize group members. In examples b) and f) Howlet animals apparently recognized other Howlet animals visually from considerable distances. In examples a) and g) Howlet animals were investigated and butted by non-Howlet animals whilst away from the Howlet area. In examples c), d) and e) Howlet animals attempting to feed off another group's feedblock were recognized and prevented from doing so. It seemed subjectively that the number of times that Howlet animals were prevented from feeding was higher than that with which non-Howlet were prevented. It was interesting to note the behaviour of Number 48, (example e), an animal who was very successful in interactions at the Howlet feedblock. It seemed that her advantage was lost when attempting to feed off another group's block.

The analysis of 30m sub-groups within Area 2 (see Table 3.2) illustrates that even in areas of considerable overlap of use, sheep from different home range groups very rarely came into close proximity to one another. Such an effect could be produced by different groups using the same area at different times of day, or different groups simultaneously using the same area, but recognizing and not approaching one another. As described in the results the first of these situations occurred regularly. On occasions as members of one home range group left an area, members of another would move to that area. In other situations areas would be used by one group at one time of day and by another group at other times of day. This is similar to the situation described in Soay sheep (Grubb and Jewell (1974).

Where sheep from different groups did use the same area at the same time there may well have continued to be avoidance between them. There is no direct evidence for this except that it was by no means rare for sheep from different groups to graze the same area. Recognition and avoidance of non-group members would have contributed both to the low number of mixed sub-groups and to the low number of interactions between the Howlet animals and sheep from other groups. In addition there is evidence of quantitative differences between the interactions involving solely Howlet animals and those involving sheep from different groups. In the very small number of interactions that occurred between Howlet animals and sheep from other groups none of these were of the type described as cohesive grazing movements, a type of interaction that was very common between Howlet animals; all of them involved either investigatory or aggressive acts (see Figure 3.3). Therefore sheep from different groups may have avoided one another partly by adopting differing movement patterns. In addition, when in close proximity animals almost certainly recognized, avoided and showed little or no cohesive behaviour towards non-group sheep.

This evidence suggests strongly that the Howlet sheep can be regarded as a home range group, in that they confine their movements to a limited area of the hill and do not mix indiscriminately with sheep from other groups.

3:4:2 <u>The Home Range Behaviour of the Howlet Group</u>

The seasonal changes in the distribution of the Howlet home range group were very striking. In the 2 summer seasons the group expanded the area over which they ranged and spent large amounts of time on the south side of the reservoir (Area 4). In Autumn 1981 and Winter 1982 the south side of the reservoir was rarely used and the majority of observations occurred in the core area (Area 1) and the area peripheral to the core area (Area 2), (see Figures 3.4 to 3.8).

It is important here to illustrate the difference between measuring the total size of a home range and measuring the distribution of use within a home range. Jewell (1966) describes some of the inadequacies of regarding home range as a bounded area (see Chapter 6). In 3:3:1 part 3 it was illustrated that the overall size of the group home range did not show as large seasonal variation as did the use of different areas (the distribution of use). In this discussion we will be largely concerned with changes in distribution rather than changes in size of home range which will be dealt with in Chapter 6.

In previous work on home range behaviour in Scottish hill sheep seasonal changes in the distribution of home range groups have not been described (Hunter and Milner 1963; Hunter 1964; Griffiths 1970; Hewson and Wilson; 1979). However Hunter and Milner (1963) did illustrate seasonal changes in dispersion in their study whereby grid squares contained higher densities of sheep in winter than in summer. They described the sheep as forming larger sub-groups in winter than summer. It seems that in fact there could be 2 components involved in the seasonal changes in dispersion which they describe. The first of these is the social factor; that animals tended to flock more in winter would obviously have affected dispersion. The second factor is any seasonal change that might have occurred in the distribution of use of the home range groups in their study. If their animals had extended their winter range to make use of a larger summer range (as seems to be the case in this study) this would also have affected dispersion. The fence surrounding the area could not alone it seems have prevented expansion into larger summer ranges as the area enclosed by it was substantial.

Hunter (1964) described in detail the existence of home range groups within a ring fenced area. He used data collected between May and November, at least 70% of these observations coming from the period May to August. He did not provide a comparison between the situation in summer and that in autumn and winter. It is again conceivable that the home range groups he described also showed seasonal changes in their distribution (see also 3:4:3 part 4).

Grubb and Jewell (1966) illustrated that individual Soay sheep ranged further in the period September to January than in May. They do not supply information on the total size and distribution of use of group home ranges but imply that group home ranges would be larger in winter than in summer. This would apparently be contrary to the situation in the present study. However they base this assumption on data from one sheep in the 2 seasons. As is illustrated in Chapter 6 although the group home range size expands in summer, individual home range sizes do not necessarily follow the same pattern. The reasons for this are explained in the next section (3:4:3).

Several studies (Mills 1937; Davies 1939; Woolf et al. (1970) provide evidence of seasonal changes, similar to those found in the present study, in the home range behaviour of bighorn sheep. In these studies some groups underwent seasonal migrations from one area to another whilst other groups could only be said to show an extension of the winter range during the summer months.

It seems therefore reasonable to suggest that the summer expansion of the group home range found in this study is not unique to the Howlet group. The strong possibility exists that early workers on home range behaviour in domestic sheep overlooked these seasonal changes by not examining in detail seasonal effects upon the distribution of individual home range groups.

3:4:3 The Relationship Between the Home Ranges of Individual Sheep

1 The use of cluster analysis

It has been possible using cluster analysis to illustrate the seasonal changes in the relationship between the home ranges of individuals in great detail. This has been achieved by arbitrarily defining a level of clustering and analysing the composition and locations of these clusters in different seasons. At this stage however there may exist some confusion as to the biological interpretation to place on the cluster analysis. Can, for example, the 5 clusters chosen to exemplify seasonal changes in this chapter be regarded as biologically meaningful groups?

Most certainly the clusters cannot a priori be regarded as 'natural' groupings. They can at this stage only be said to represent sheep with similar home range behaviour patterns. Biologically meaningful groupings of sheep may be found at many levels of clustering. This is easy to illustrate. At the highest level of clustering when all sheep are fused to form one cluster they constitute a home range group which is distinquishable from other home range groups (see 3:4:1). At subsequent levels various biological interpretations may be found as explanations for the clustering such as age or use of preferred areas. At the finest level there may exist preference by some animals for specific partners. Even after illustrating that the animals in a cluster show a degree of similarity in their home range behaviour it is still necessary to describe and explain the social forces, if any, that are acting between them. For example although 2 animals may use the same area they may not do so simultaneously. The social relationships between individuals found in the same cluster will be dealt with in

Chapter 5.

The 5 cluster level which has been used repeatedly in this chapter was chosen then as an explorative tool to examine various properties of home range behaviour in the Howlet group. The biological differences such as age and use of preferred areas which have been found to exist between clusters can be used to generate further hypotheses regarding the nature of group behaviour in domestic sheep.

2 <u>The effect of age on the composition of clusters</u>

Summers 1981 and 1982 and Autumn 1981 were broadly similar in that where age had a significant effect on the composition of clusters it was always almost wholly attributable to the 1 year old ewe-lambs (ie the other age-classes showed little or no age-class segregation). In Winter 1982 no one age class was responsible for the large effect that age was found to have and it seems that this was partly attributable to the use of feedblock at this time of year, and partly to the stage of social development of the ewe-lambs (see Chapters 4 and 6). Seasonal variation therefore seems particularly strong between winter and the other seasons.

3 <u>Seasonal variation in the relationship between clusters</u>

<u>Autumn 1981</u>:

Following the analysis of seasonal changes in the home range behaviour of the group (see 3:3:1), the Howlet area (Areas 1 and 2) shall be known as the winter range. The term summer range will refer to both the winter range and Area 4 (the south side of the reservoir). In Autumn 1981 the majority of animals were found in clusters within the Howlet area that were similar both in their location and their axes of variation. The home range maps of 4 of the clusters were virtually indistinguishable from one another by eye. The total variance for the home range behaviour of the group in Autumn 1981, as calculated by Ward´s Method, was the lowest of all the seasons. It would seem therefore that during this period the home range group tended to act as a single unit in terms of the home range behaviour of its members.

The major exception to the rule was a cluster of 6 animals that persisted in their occupation of the summer range long after the majority of the animals had returned to the Howlet area. This cluster was interesting in that such a small number of animals could appear to form a cohesive and close knit group. The possibility exists that if they had not been disturbed by the farmer on 2 occasions, they might have remained on the south side of the reservoir over winter.

<u>Winter 1982</u>: The situation in Winter 1982 bore some resemblance to that in Autumn 1981. All animals at this time occupied the winter range. However despite the fact that no animals occupied the south side of the reservoir the total variance in this data set was larger than in Autumn. Whereas in Autumn 73% of animals had shared the same centre of activity and had almost identical measures of variance only 2 of the clusters in Winter 1982 shared centres of activity and the

measures of variance were quite variable in size and shape. In fact, as mentioned previously there was a large age segregation of the group at this time partly brought about about by the use of feedblock (see Chapters 4 and 6).

Summers 1981 and 1982: It is the contrast between Autumn 1981 and Winter 1982 and the 2 summer seasons that is most striking. The expansion of the winter range into the larger summer range could have been brought about by all animals possessing larger ranges in summer or by certain animals only moving into the summer range. This study clearly shows the latter to be the case. If the 2 cluster level had been analysed, one cluster in each summer would have been seen to rarely if ever visit the summer range, whilst most animals in the other cluster would have spent considerable amounts of time there. This rough division however would have failed to illustrate the fact that between these 2 extremes there was a range of animals with quite different home range behaviour.

These types were described in some detail in the results sections 3:3:2 part 1 and part 4. It was in fact impossible to adequately describe the variation in home range behaviour that existed in summer without entering into tremendous detail. Whereas in Autumn 1981 and Winter 1982 the use of the 5 cluster level adequately described the different types of home range behaviour that existed within the group, in the summer seasons it would have required a much lower level of clustering, sometimes at the level of individual sheep to describe fully the different types. The locations of the centres of activity and the shape and extent of the measures of variance indicate that the sheep arranged themselves in a continuum of home range types. These ranged from those animals that used various parts of the Howlet, to those that used parts of the Howlet and also parts of the summer range, to those that spent large amounts of time on the summer range.

As a result of the large differences in home range behaviour that existed between individuals the total variance in home range behaviour within the group (as measured by Ward's Method) was larger in the 2 summer seasons than at the other times of year.

The large degree of similarity between the 2 summer seasons in the general locations of the 5 clusters is interesting. This result was not necessarily to be expected if one considers that between these 2 seasons a number of older animals had been culled and a number of ewe-lambs added to the group.

The similarity in the locations of the clusters between the 2 seasons suggest that the clusters in each season may have been composed largely of the same animals. Although there was a significant tendency for 2 of the 3 large clusters to have broadly the same composition in 1982 as they did in 1981, only one of these occupied exactly the same location in both seasons (C1/Sum81; C2/Sum82). C3/Sum82 was composed of significant numbers of animals from C2/sum81 and C3/Sum81. Its location was similar to that occupied by C3/Sum81. Although C4/Sum82 occupied a similar position to C2/Sum81, it did not have a similar composition to any 1981 cluster. The same is true for the small C1/Sum82 that occupied a similar position to C5/Sum81. Finally C5/Sum82 occupied a similar position to that of C4/Sum81 and contained 3 of C4/Sum81's members, but was too small to test for stability of cluster composition.

Therefore several situations were seen to arise in Summer 1982:

a) The same sheep were found in the same cluster using the same area in 1981 and 1982.

b) Significant numbers of sheep from 2 separate clusters in 1981 fused and were found in the same cluster in 1982. The area used in 1982 was broadly similar to that used by the 2 separate 1981 clusters.

c) Sheep were found in clusters that compositionally bore little relationship to clusters in 1981. These clusters used areas previously occupied by other clusters.

Despite the tendency for there to be consistency of cluster composition between the 2 summers there was no such relationship between the clusters formed in Autumn 1981 or Winter 1982 and the 2 summer seasons.

As one might predict from the above there was an overall tendency for individual sheep to have similar home range patterns in successive summers (Table 3.13; Figure 3.17). The results indicated that this was especially so at the level of 2 clusters representing the tendency to use, or not to use the south side of the reservoir. The tendency for this effect to strengthen with age will be discussed in Chapters 4 and 7. The fact that the clusters in Summer 1982 were not seen to match exactly those in 1981 in terms of location and composition may have been due to:

a) The lack of absolutely rigid movement patterns in certain animals especially younger sheep.

b) The changes in the composition of the Howlet home range group, as brought about by the management system.

c) The 2 seasons not matching one another exactly in terms of weather and herbage production.

d) Inadequacies in attempting to describe the variability in summer home range behaviour in terms of just 5 basic types.

4 Are the Howlet an exceptional group of sheep?

The literature on domestic sheep suggests that the seasonal changes in home range behaviour described in this chapter are not peculiar to this group of sheep.

The results of this chapter can be regarded as a more extensive description of the seasonal changes in dispersion which Hunter and Milner (1963) present. At the time of year when they described sheep being found in large sub-groups (i.e. autumn and winter), in the present study there were large changes in the group's distribution. These changes have been interpreted as a move by all the members of the group to a winter range. In summer, a time of year during which the sheep in Hunter and Milner's study dispersed, in the present study saw the Howlet group again make large changes in their distribution. These changes were brought about by certain group members only moving to summer areas and consequently expanding the area covered by the group as a whole.

As mentioned previously (see 3:4:2) Hunter (1964) illustrated the apparent existence of separate home range groups within a ring fenced area using data largely gathered between May and August (the equivalent of the summer seasons in this study). It is tempting to suggest that these apparently separate groups might have had an overall larger group structure which would only have become apparent in autumn or winter when the whole group had fully returned to the winter range. There is in fact some evidence in the paper that this might be so for at least 2 of the groups; the Middle and the Bottom (56% of the animals in the study). Hunter describes that he had some difficulty in separating these 2 groups. He writes that it would have been possible to have treated them as one large group composed of a series of partially overlapping distributions or to have split it into 4 sub-groups. Furthermore he qualitatively noted that in winter these 2 groups tended to merge. It does seem likely therefore that these animals were in reality one home range group some members of which had dispersed into a summer range.

There is also some evidence from Grubb and Jewell (1966) that a similar situation could have occurred in their study. They found that the West village home range group could be sub-divided into smaller sub-groups with different ranges. These ranges however overlapped considerably and members of distinct sub-groups would often mix in grazing sub-groups. They also made observations of interchanges between members of the sub-groups in spring, which testified to the reality of a larger cohesive group. It again seems possible that these separate sub-groups were only formed in summer. The home range maps that they used to illustrate the differences between these sub-groups and the other home range groups in the Village Glen is data taken from May.

It is worth pointing out that they also supply the home range maps of 5 members of a home range group, again using data taken from May. The differences between these 5 sheep are small. It may be of course that other members of the group had more disparate home ranges. If however group members do differ as little in their home range behaviour as these 5 examples then it may be that the high densities that Soay sheep live at, not only limit the ranges of individuals (Grubb and Jewell 1974), but also limit the extent to which individuals can vary from one another. The result of this would be to make any summer increase in home range variability small and difficult to discern.

Woolf et al. (1970), in their description of the expansion of winter ranges into larger summer ranges in bighorn sheep, write that they observed incomplete migrations. These migrations were regarded as incomplete because some sheep moved to summer ranges, while others remained on winter ranges or returned to them at intervals throughout the summer. The description of these incomplete migrations bears a very strong resemblance to the situation in summer in the Howlet group and lends more weight to the view that the seasonal changes in behaviour shown by the Howlet group are not exceptional to that group but may find corollaries in other populations of domestic, feral and wild sheep living under similar ecological conditions.

SUMMARY:

a) As in other studies of sheep the Howlet home range group showed allegiance to a specific area. Members of the group rarely mixed with sheep from adjacent groups partly because their movement patterns were asynchronous, partly because they could apparently recognize non-group members from group members and may have avoided them and partly because they showed no cohesive movement patterns when in close proximity to non-group members.

b) The Howlet group occupied 2 distinct seasonal ranges. The winter range was occupied by the majority of animals from the middle of October to the end of March. This was the area that the group were by local farming tradition supposed to occupy. The summer range was an expansion of the winter range and consisted, in addition to the winter range, of areas to the south and southeast of the reservoir. There is evidence from other studies of domestic and wild sheep that occupation of winter and summer ranges is not a phenomenon confined to this group alone.

c) During the occupation of the winter range from October to the end of November (Autumn 1981) all members of the group tended to use all parts of the group home range to a similar extent. The period from the end of January to the end of March (Winter 1982) brought about some increase in the variability of home range behaviour in the group. Two factors, yet to be discussed, may have separately or interactively been responsible for this increase. Firstly the group were fed a feedblock at this time of year and secondly the group was largely age segregated.

d) The expansion of the group into the summer range was accompanied by a very large increase in the variability of home range behaviour within the group. In effect the animals formed a continuum ranging from those that remained on the winter range, through those that used the winter range and parts of the summer range, to those that spent most of their time on the summer range. All members revisited the winter range at some point during the summer.

It was possible using cluster analysis to identify 5 clusters of sheep, most members of which showed clear tendencies to graze the same preferred areas. Not all sheep fell neatly into these 5 categories. It was felt that a lower level of clustering might have helped more fully describe all the types of home range behaviour in the group.

Individual sheep tended to use similar home ranges in the 2 summers. Certain of the sheep which had been found in the same clusters in the first summer were again found in the same clusters in the second summer. These clusters were found to either occupy the same location as in the first summer, or a slightly different location. Other sheep in the second summer were found in clusters that were compositionally dissimilar to any of the previous summers clusters.

Despite the large and seasonally consistent differences that existed between different clusters in summer there was no evidence that on return to the winter range that these differences were maintained. The sheep mixed in Autumn 1981 at random with regard to the previous summer´s clusters.

e) It is suggested that previous workers on domestic sheep largely overlooked seasonal changes in home range behaviour. From the present study it is plain that the composition of a home range group can only be accurately defined by observation of it at its most contracted phase, during the late autumn and winter months. Evidence is found from work on domestic, semi-wild and wild sheep to support the view that these findings may be generally applicable to all sheep populations living under similar ecological conditions to the Howlet group.

CHAPTER 4 SOCIAL DEVELOPMENT OF THE EWE-LAMB

4:1 INTRODUCTION

The literature holds many references to the long-lasting nature of the ewe-daughter bond in domestic sheep and the importance of this bond in the formation of home range groups (Hunter and Milner 1963; Hunter 1964; Griffiths 1970; Squires 1975; Darling and Boyd 1977; Arnold and Dudzinski 1978; Craig 1981; Shillito Walser et al. 1982a).

The belief that the ewe-daughter bond persists until the death of either of the pair is founded on the work of Hunter and Milner (1963) and Hunter (1964). These workers suggested that ewe-lambs tended to graze the same areas of the hill as their mothers. They based this assumption on home range maps of ewe-daughter pairs. They proposed that the basis of the home range groups formed by domestic sheep was the continuing association of the daughter with its mother; home range groups being formed by matrilineal descent. An experiment conducted by Hunter and Davies (1963) apparently supported this view. In this experiment 2 groups of ewe-lambs were removed from the hill at different ages for periods of up to 41 weeks; controls were a group which were not removed from the hill, and a group removed for the relatively short period of 10 weeks. It was found that removal from the hill at a young age and for a lengthy period markedly affected the ewe-lambs' later home range behaviour and the associations they made with other sheep.

By contrast a recent study Arnold et al. (1981) found little evidence of permanent ewe-daughter bonds in 3 breeds of domestic sheep grazing in relatively small enclosures, associations being generally between sheep of the same age and sex. Similarly, in bighorn, Geist (1971) found that although ewe-lambs tended to stay in the group in which they were reared, they were not found in association with their mother after the age of 10 or 11 months. Lambs formed social bonds with old barren females, rams, and perhaps most commonly with peers. In Soay sheep Grubb (1974) also found that by the middle of the rut it was common for ewe-lambs to graze and rest together, apart from their dams but still within their home range group.

To explain the dichotomy between the work of Hunter and Milner (1963) and the findings of later workers on domestic, feral and wild sheep we can postulate that a) the nature of the ewe-daughter bond in Scottish hill sheep is of a more permanent form than in other sheep populations; or b) the assumption of early workers, that as the daughter remained in her natal group it maintained a permanent social bond with its mother, was incorrect.

The behaviour of the ewe at the birth of her lamb and in the immediate post-partum period is well documented (Smith et al. 1966; Poindron and Le Neindre 1975; Bareham 1976; see Wood Gush et al. 1984 for a recent review). However to date there has been little description of the longer term mother-lamb relationship under extensive Scottish hill conditions. This chapter will firstly describe qualitatively mother-infant interactions observed between birth and 25 weeks in the Howlet group. It will also re-examine the longer term nature of the ewe-daughter bond in Scottish hill sheep by analysing data obtained from the Howlet home range group. The development of other social bonds in ewe-lambs from the age of 6 to 18 months will also be described and analysed. Finally the development of home range behaviour in the ewe-lamb will be discussed.

4:2 MATERIALS AND METHODS

The scan sampling technique described in Chapter 2 supplied the data on associations. It should be noted that in this chapter only 30m sub-group data were considered. In addition to the above the focal animal samples collected in Winter and Summer 1982 were used to supply information on the frequency of interactions. The Summer 1982 focal animal samples were further used to provide a qualitative description of mother-lamb interactions in the field.

4:2:1 Measures of Association

In the analysis of seasonal changes in associations formed by ewe-lambs, measures of association for 11 ewe-lambs were computed. Six ewe-lambs were not considered in the analysis as 2 died in April 1982, 3 conceived and had lambs in April and May 1982, and one temporarily left the group in Autumn 1981 and so was rarely seen in that season. Likewise any other animal in the group that was seen infrequently, in one or more seasons, was discarded from the computation of the general group association index (see below). Animals were judged as being seen infrequently if they were observed in less than 75% of scans.

The 3 association indices that were computed were:

a) Mother Association Index (MAI):

$$\frac{a}{b}$$

where a is the number of times mother and daughter were seen within 30m of one another, and b is the total number of times that the daughter was seen.

b) Peer Association Index (PAI):

$$\frac{\sum_{i=2}^{n} p_i / n-1}{b}$$

where i=1 is the ewe-lamb for whom the association is being formed (and is therefore not included); p_i is the number of times the ewe-lamb in question was found within 30m of the ith peer and n is the number of peers.

c) Group Association Index (GAI):

$$\frac{\sum_{i=1}^{q} g_i / q}{b}$$

where g_i is the number of times the ewe-lamb in question was found within 30m of the ith member of the home range group (excluding its own mother and its peers) and q is the number of animals in the group (again excluding the peers and the mother of the ewe-lamb in question).

The denominator b was chosen as it yielded 3 comparable indices of association that expressed the proportion of time that a daughter spent either with its mother, with its peers or with other members of the group.

The 3 indices were computed for each of the 11 ewe-lambs in the 5 seasons Post-Weaning 1981, Autumn 1981, Winter 1982, Summer 1982, and Post-Weaning 1982 (see 2:4). As described in 2:2:3 daughters were not ascribed individual numbers or included in the scan until the farmer removed the majority of lambs in August. There is therefore no association data for the ewe-lambs in Summer 1981, their first summer. The 3 indices were also computed for the ewe-lambs born in Summer 1982 in the season Post-Weaning 1982.

4:2:2: <u>Strength of the Maternal Bond Under 'Fearful' Conditions</u>

In order to test the strength of the mother-daughter bond under conditions that could be regarded as fearful or stressful, the group was penned (on 31.3.82) and a person previously unknown to the sheep entered the enclosure from a randomly chosen direction (left or right). He walked through and around the animals before leaving the pen. After 30 seconds had elapsed the observer scanned the group in a randomly selected direction (left or right) and recorded which ewe-lamb was closest to which ewe. Twenty minutes were allowed to pass before the whole procedure was repeated. Fourteen replicates were carried out between 1100 and 1600 hours. Each mother received 14 scores indicating which ewe-lamb was her nearest neighbour after each trial. Ewe-lambs were not necessarily the nearest neighbour to any ewe or alternatively may have been the nearest neighbour to more than one ewe.

The binomial test was used to analyse results, as the chances of a mother being found with its daughter or another ewe-lamb as nearest ewe-lamb, ought to be distributed approximately binomially if no bond exists between mother and daughter. It can only be an approximation to the binomial, as no account is taken of any differences that might exist between ewe-lambs in their general sociability towards older ewes, or to differences in reactivity to human presence.

The mean number of times a mother would be expected to have her daughter as nearest ewe-lamb is kp where k is the sample size and p is the probability of the mother being found with the daughter. The variance about this mean is kpq where q is the probability of the mother being found with any other ewe-lamb than its daughter as nearest neighbour (Sokal and Rohlf 1981a).

If the data are arranged in a matrix with ewes and daughters placed along the diagonal the sum of the diagonal elements (St), the total number of times that all mothers had daughters as their nearest ewe-lambs, ought also be distributed approximately binomially. Again the expected mean and variance of the sample statistic, St, can be calculated.

To test the significance of the effect, a procedure was derived from Sokal and Rohlf (1981a, p. 174). It tests the significance of a deviation from a parameter for normally distributed statistics. As N increases the binomial tends towards the normal distribution (Siegel 1956) and therefore the deviation of the observed value, the statistic St, can be tested against the binomially derived mean by fitting it to the normal distribution. The procedure involves computation of the following ratio:

$$ns = \frac{St - Stp}{SdSt}$$

where St is the sample statistic, Stp is the parametric value against which the sample statistic is to be tested (in this case the expected mean) and SdSt is the standard deviation of Stp. The ratio ns (standard deviation units) is compared to a table of areas under the normal curve (Sokal and Rohlf 1981b). If for example the sample statistic (St) was found to lie 1.00 standard deviation from the parametric mean, the table would inform us that 0.3413 of items under the normal curve fall between the mean and 1 standard deviation on one side of the mean; or that 0.3174 of items lie outside 1 standard deviation on both sides of the mean. One would accept the null hypothesis therefore that the sample mean did not vary significantly from the parametric mean.

In this and the following chapters when non-parametric analyses of variance such as Friedman's 2-way Anova were used, it was often of interest, having shown there was an overall effect, to test a posteriori, which treatments were significantly different from one another. In the absence of non-parametric testing procedures for comparing means, pair-wise tests between treatments were performed using either the Wilcoxon Matched-Pairs Test or the Mann-Whitney U Test. A posteriori, or unplanned comparisons between treatments increase the possibilty of Type 1 error. However in the pair-wise tests in this chapter and the chapters to follow the number of comparisons made was never greater than 6. In addition , α was raised to the 1% level, results only being regarded as significant if

$p < 0.01$.

4:3 RESULTS.

4:3:1 Qualitative Description of Mother-Lamb Interactions Between Birth and Weaning

The behaviour of the mother at the birth of her lamb and in the immediate post-partum period was similar to that previously described in the literature (Smith et al. 1966; Bareham 1976). Within the first week, however, there was considerable inter-individual variation in what could be termed quality of mothering. This variability was expressed in a number of ways including the distance the mother allowed to exist between herself and her lamb; the attentiveness of the mother to the calls of her lamb; the latency between the lamb calling and the mother moving to the lamb; the frequency of maternal vocalisations directed at the lamb and the extent to which the ewe rejected nursing attempts by the lamb. In one case, Number 10, a 4 year old ewe failed to remain with her twins during the first day after birth, leading to the death of one twin and permanent separation from the other. In another case, Number 42, a 7 year old ewe did not clean her lamb properly at birth, allowed distances of up to 100m to exist between herself and her lamb during the first week, was inattentive to her lambs calls, and frequently rejected nursing attempts by the lamb. This behaviour persisted for some weeks and led to stunted growth of the lamb. Finally a gimmer, Number 101, an animal who was very reactive to humans, failed to allow her lamb to suck and had to be removed to a pen with the lamb to secure a bond between them. The effects of less extreme forms of maternal inattentiveness on lamb growth and development were difficult to assess. Subjectively it seemed that gimmers (primiparous mothers) were more attentive to their lambs than older ewes. The variability between mothers decreased from the middle of the second week and had largely disappeared by the third week.

In the first week ewes would generally allow lambs to approach and initiate nursing and mothers rarely terminated nursing bouts. When ewes did initiate nursing they did so by looking at, approaching and vocalising to their lambs, often doing so prior to lying down after a grazing bout. By the third week ewes would only rarely allow lambs to initiate nursing and to do so themselves, would look at their lamb, vocalise at it, but seldom approach it. Almost all nursing bouts at this stage were terminated by the mother stepping over the lamb as it sucked.

Beyond the third week ewes could initiate suckling simply by lifting their heads from the grazing position. On a number of occasions disturbance of the ewe would cause her to stop grazing and stand with her head raised in the Upright Attention Posture (UAtP) (Geist 1971), resulting in the lamb running to her and attempting to suckle. Ewes in this situation would either allow the lamb to suck, return to grazing thus preventing nursing, or walk away from the disturbance with the lamb at heel.

On 2 occasions known to the observer, lambs fell and became trapped in ditches where they were invisible except at close quarters. In the first instance, it was apparently some hours since the lamb had fallen in the ditch because the mother had ceased vocalising and was grazing some distance away when a hill walker passed close to the location of the trapped lamb. The ewe immediately stopped grazing and ran past, just behind the walker, and stood over her lamb vocalising. The hill walker walked on. When the observer, approximately 10 minutes later, took the same route as the walker, the ewe behaved in an identical manner. The observer, unaware at this stage that her lamb was trapped, walked to where the ewe was standing and discovered and retrieved her lamb. An almost identical sequence of events, a week later, led to the discovery of another lamb similarly trapped. The first of these died subsequent to being rescued probably due to chilling whilst in the ditch; another lamb, belonging to Number 116 was found drowned in a ditch.

Individual variation existed in the timing and nature of weaning. One mother, Number 2, developed a serious limp and she began aggressively rejecting nursing attempts by her lamb in the 14th week. The other focal mother-daughter pairs did not appear to commence weaning until the 22nd week; by this stage nursing was an exceptionally rare event. Apart from the case of Number 2 weaning was generally a gradual process, albeit more rapid in some pairs than others. Mothers and daughters would be found apart on one day and together the next. In most cases it appeared that daughters put most effort into maintaining the relationship, being found vocalising and apparently ´searching´ for their mothers. However this behaviour was only performed for short periods and if the lamb was unsuccessful in finding its mother it would commence grazing with other members of the group. In one incident, Number 16 and her daughter became separated on either side of the reservoir at a time when they were still commonly found in association. They vocalised at each other across the reservoir for 2 days, although they did not make any attempts to move round the reservoir to reach each other. After this time they were rarely seen together again.

By the 25th week all focal animal pairs were either partially or completely weaned. There were no records of vocalisations by

FIGURE 4.1

SEASONAL CHANGES IN THE 3 EWE-LAMB ASSOCIATION INDICES MAI, PAI AND GAI

Values shown are medians and inter-quartile ranges. Generally values in a season are significantly different if their inter-quartile ranges do not overlap, with the exception of the MAI and PAI in Autumn 1981 (see Table 4.4). The abscissa represents a monthly time-scale. Seasons are indicated by their median observation. See 4:2:1 for the derivation of the mother association index (MAI), the peer association index (PAI) and the group association index (GAI).

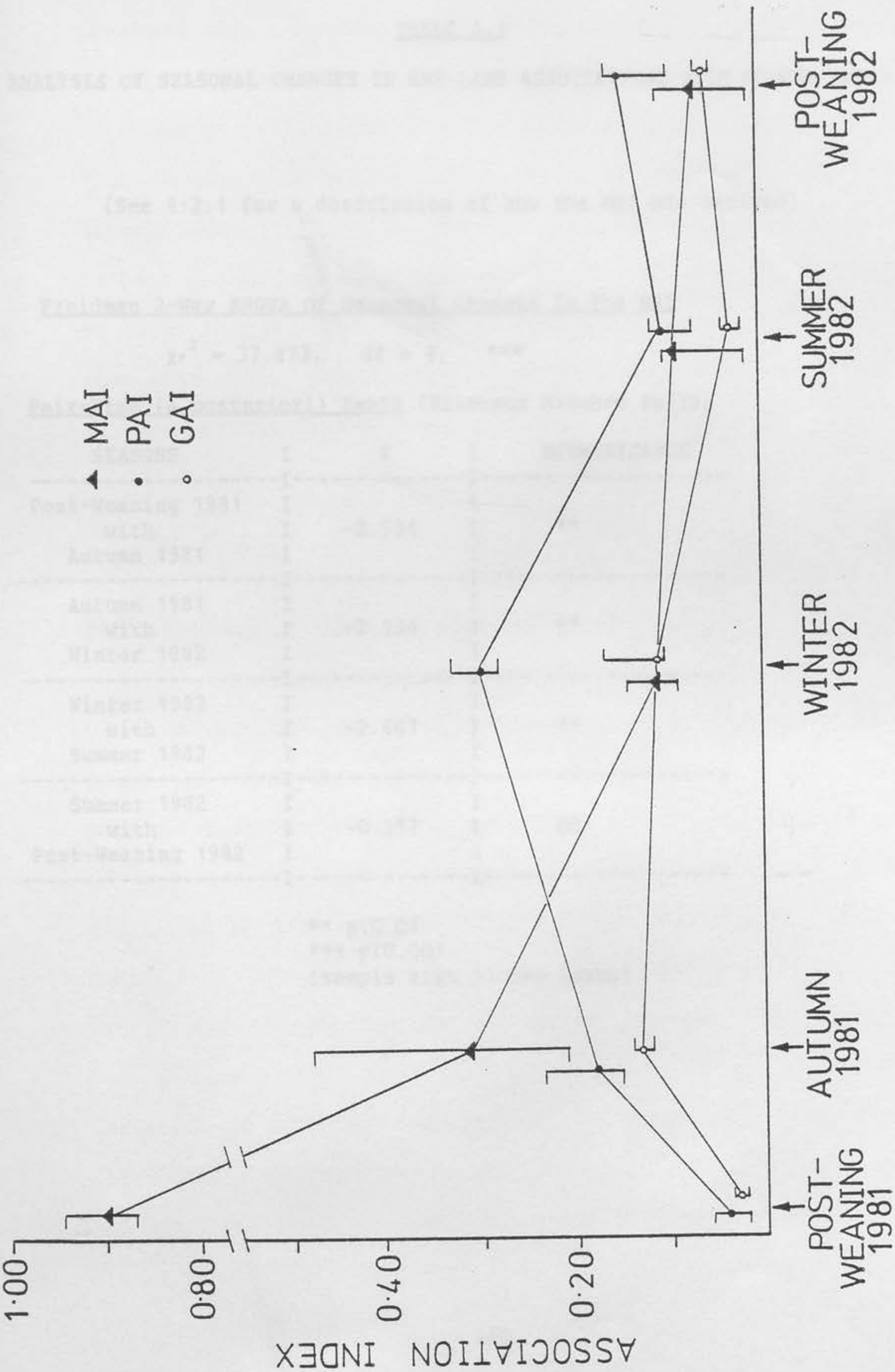

MAI
PAI
GAI
ASSOCIATION INDEX
1·00
0·80
0·40
0·20
POST-WEANING 1981
AUTUMN 1981
WINTER 1982
SUMMER 1982
POST-WEANING 1982

TABLE 4.1

ANALYSIS OF SEASONAL CHANGES IN EWE-LAMB ASSOCIATIONS WITH MOTHER (MAI)

(See 4:2:1 for a description of how the MAI was derived)

Freidman 2-Way ANOVA Of Seasonal Changes In The MAI

$\chi_r^2 = 37.873$, df = 4, ***

Pair-Wise (a posteriori) Tests (Wilcoxon Matched Pairs)

SEASONS	Z	SIGNIFICANCE
Post-Weaning 1981 with Autumn 1981	-2.934	**
Autumn 1981 with Winter 1982	-2.934	**
Winter 1982 with Summer 1982	-2.667	**
Summer 1982 with Post-Weaning 1982	-0.357	NS

** p<0.01
*** p<0.001
(sample size 11 ewe-lambs)

pairs at this time. The ewe-lambs were now found generally with the same sub-group of animals, and in the same area (north or south of the reservoir), as they and their mother had been prior to weaning. There was also a tendency for daughters to graze close to their peers whilst in sub-groups comprised of a variety of ages of animals.

Weaned lambs often showed distress when they became separated from grazing sub-groups. This occurred frequently, especially between January and March, when the ewe-lambs were found most often in peer groups (see 4:3:2 and Chapter 6). Lambs could be separated by up to 100m from the nearest sub-group before becoming distressed; then they would vocalise loudly and repeatedly and run towards the sub-group. Such behaviour was rarely seen in older ewes.

4:3:2 Seasonal Changes in Ewe-Lamb Associations From 7 to 18 Months of Age

The seasonal changes in associations of ewe-lambs with mothers, peers and other group members are illustrated in Figure 4.1. A measure of mother-daughter association (MAI), showed that the number of sightings of mother and lamb within 30m of one another declined significantly from September 1981 onwards (Table 4.1). Pair-wise comparisons of each season with the preceding season found significant changes in the MAI except between Summer 1982 and Post-Weaning 1982, when the effect levelled off. Individual variation in the MAI was highest in Autumn 1981 and declined thereafter. The MAI for ewe-lambs born in Summer 1982 was computed and there was found to be no significant difference between this MAI

TABLE 4.2

ANALYSIS OF SEASONAL CHANGES IN EWE-LAMB ASSOCIATIONS WITH PEERS (PAI)

(See 4:2:1 for a description of how the PAI was derived)

Freidman 2-Way ANOVA Of Seasonal Changes In The PAI

$\chi_r^2 = 42.473$, df = 4, ***

Pair-Wise (a posteriori) Tests (Wilcoxon Matched Pairs)

SEASONS	Z	SIGNIFICANCE
Post-Weaning 1981 with Autumn 1981	-2.973	**
Autumn 1981 with Winter 1982	-2.973	**
Winter 1982 with Summer 1982	-2.973	**
Summer 1982 with Post-Weaning 1982	-2.845	**

** p< 0.01
*** p<0.001
(sample size 11 ewe-lambs)

TABLE 4.3

ANALYSIS OF SEASONAL CHANGES IN EWE-LAMB ASSOCIATIONS WITH THE HOME RANGE GROUP (EXCLUDING MOTHERS AND PEERS) (GAI)

(See 4:2:1 for a description of how the PAI was derived)

Freidman 2-Way ANOVA Of Seasonal Changes In The GAI

$\chi_r^2 = 38.6$, df = 4, ***

Pair-Wise (a posteriori) Tests (Wilcoxon Matched Pairs)

SEASONS	Z	SIGNIFICANCE
Post-Weaning 1981 with Autumn 1981	-2.934	**
Autumn 1981 with Winter 1982	-0.561	NS
Winter 1982 with Summer 1982	-2.934	**
Summer 1982 with Post-Weaning 1982	-2.934	**

** p <0.01
*** p <0.001
(sample size 11 ewe-lambs)

and that for ewe-lambs born in Summer 1981 (Mann-Whitney U Test, n1 = 11, n2 = 13, U = 51, NS).

Similarly there was found to be a strong seasonal effect on ewe-lambs' associations with peers (PAI) (Figure 4.1; Table 4.2). The PAI rose from a median of 0.05 in Post-Weaning 1982 to a level of 0.30 in Winter 1982. Thereafter it declined to 0.09 in Summer 1982 and then rose again to 0.15 in Post-Weaning 1982. The PAI in each season was found to differ from that in the preceding season (Table 4.2). Individual variation in the PAI tended to be considerably smaller than that found in the MAI. The PAI computed for ewe-lambs born in Summer 1982 did not differ significantly from the PAI of those born in Summer 1981 (Mann-Whitney U Test: n1 = 11, n2 = 13, U = 66, NS).

Finally the ewe-lambs' associations with other members of the group, excluding mothers and peers (GAI), was also affected by season (Figure 4.1; Table 4.3). The GAI rose significantly from a median of 0.03 in Post-Weaning 1981 to a level of 0.14 in Autumn 1981. From Autumn 1981 to Winter 1982 it did not change significantly, but there was a subsequent drop to 0.04 in Summer 1982. From there it rose a small but significant amount to a median level of 0.06 in Post-Weaning 1982. The small amount of variation in the GAI was at its greatest in Winter 1982. Again there was no significant difference between the GAI computed for ewe-lambs born in Summer 1982 and that for ewe-lambs born in Summer 1981 (Mann-Whitney U Test: n1 = 11, n2 = 13, U = 41, NS).

Intra-seasonal variation between the 3 association indices was found to be significant in all seasons, the strongest effects being found in Post-Weaning 1981, Autumn 1981 and Winter 1982, the

TABLE 4.4

ANOVA IN 3 EWE-LAMB ASSOCIATIONS MAI, PAI AND GAI IN 5 DIFFERENT SEASONS.

Those values with the same suffix are not significantly different at p<0.01 (Wilcoxon Matched Pairs Test). Values shown are medians. The different seasons were analysed separately.

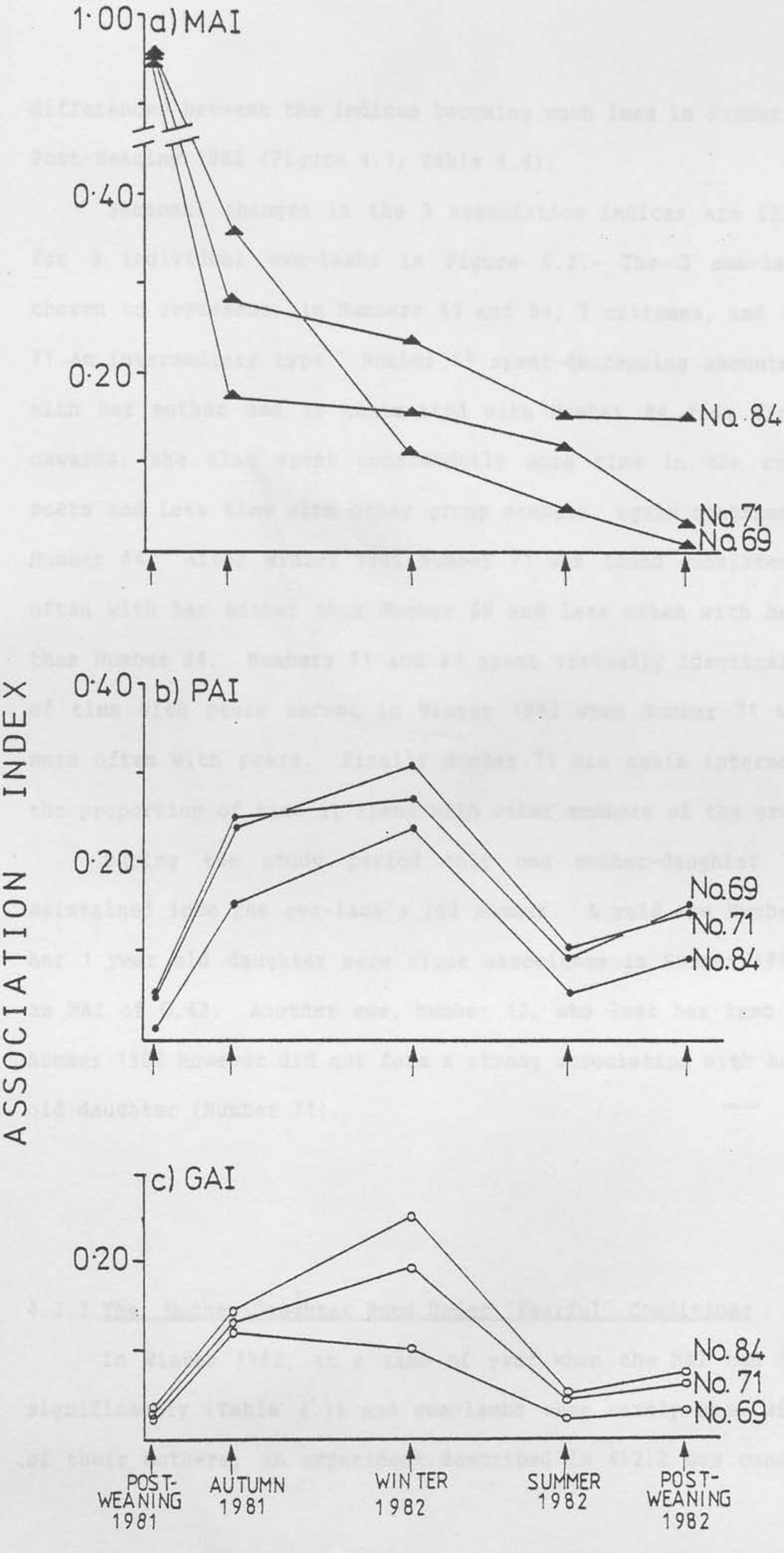
SEASON	ASSOCIATION INDEX MAI	PAI	GAI	Freidman χ_r^2
Post-Weaning 1981	0.90^{a}	0.04^{b}	0.04^{b}	17.636 ***
Autumn 1981	0.32^{a}	0.18^{b}	0.13^{c}	18.5 ***
Winter 1982	0.11^{a}	0.30^{b}	0.12^{a}	15.273 ***
Summer 1982	0.09^{ab}	0.10^{a}	0.04^{b}	6.682 *
Post-Weaning 1982	0.07^{ab}	0.15^{a}	0.06^{b}	10.346 **

* p<0.05 ** p<0.01 *** p<0.001 Sample size= 11 ewe-lambs

FIGURE 4.2

SEASONAL CHANGES IN THE 3 EWE-LAMB ASSOCIATION INDICES MAI, PAI AND GAI FOR 3 INDIVIDUAL EWE-LAMBS.

See Figure 4.1 for a description of this figure.



ASSOCIATION INDEX
1·00 a) MAI
0·40
0·20
No. 84
No. 71
No. 69
0·40 b) PAI
0·20
No. 69
No. 71
No. 84
c) GAI
0·20
No. 84
No. 71
No. 69
POST-WEANING 1981
AUTUMN 1981
WINTER 1982
SUMMER 1982
POST-WEANING 1982

differences between the indices becoming much less in Summer 1982 and Post-Weaning 1982 (Figure 4.1; Table 4.4).

Seasonal changes in the 3 association indices are illustrated for 3 individual ewe-lambs in Figure 6.2. The 3 ewe-lambs were chosen to represent, in Numbers 69 and 84, 2 extremes, and in Number 71 an intermediary type. Number 69 spent decreasing amounts of time with her mother and so contrasted with Number 84 from Winter 1982 onwards; she also spent consistently more time in the company of peers and less time with other group members, again contrasting with Number 84. After Winter 1982 Number 71 was found consistently more often with her mother than Number 69 and less often with her mother than Number 84. Numbers 71 and 69 spent virtually identical amounts of time with peers except in Winter 1982 when Number 71 was found more often with peers. Finally Number 71 was again intermediary in the proportion of time it spent with other members of the group.

During the study period only one mother-daughter bond was maintained into the ewe-lamb´s 2nd summer. A yeld ewe Number 31 and her 1 year old daughter were close associates in Summer 1981 having an MAI of 0.43. Another ewe, Number 12, who lost her lamb early in Summer 1982 however did not form a strong association with her 1 year old daughter (Number 71).

4:3:3 The Mother-Daughter Bond Under ´Fearful´ Conditions

In Winter 1982, at a time of year when the MAI had decreased significantly (Table 4.1) and ewe-lambs were rarely seen within 30m of their mothers, an experiment described in 4:2:2 was conducted to

FIGURE 4.3

RESULTS OF EXPERIMENT TO TEST STRENGTH OF THE EWE-LAMB BOND

See 4:2:3 for a description of the experiment. Mother-daughter pairs are situated along the diagonal. Those cells that contain half (ie 7) or more of the possible scores are circled. One ewe-lamb (No. 80) whose mother had been culled was inadvertently included in the data set.

DAUGHTERS

MOTHERS	68	71	72	83	74	76	77	78	79	81	84	80
3	3	2	1	2		1	1		1	1	1	1
12		(12)				1						1
17		1	1			3		1	2		3	2
27	1			(8)				2	1		1	1
28		1			(10)	1			1		1	1
32	1	1		1		4		1	2		1	3
34		1		1		1	(8)	1			1	1
35	1			1	1		1	(7)	2		1	
36									(12)	1	1	
45		1		2			2	2	1	3	1	2
116		1	1			2			1		(9)	

TABLE 4.5

ANALYSIS OF EXPERIMENT TO TEST STRENGTH OF MOTHER-DAUGHTER BOND

The results of the analysis of an experiment to test the strength of the ewe-daughter bond with ewe-lambs aged 11 months under 'fearful' conditions. The binomial distribution was used to derive the expected values (See also 4:2:3, and Figure 4.3).

EXPERIMENTAL- 11 mothers, 12 daughters, 14 replicates

RESULT- Observed sum of diagonal elements= 77

TEST-

1) Mean expected score per diagonal element = kp = 1.162

2) Expected variance = kpq = 1.079

3) Expected mean for sum of all diagonal elements = 12.78

4) Expected standard deviation = 3.54

5) Test for deviation of a normally distributed parameter = $\frac{77 - 12.78}{3.54}$

= 18.18 standard deviation units.

6) As no items fall beyond 4.9 standard deviation units of the normal curve $p<0.001$

k = sample size
p = probability of mother being found with daughter as nearest neighbour
q = probability of mother being found with ewe-lamb other than daughter as nearest neighbour.

test the mother-daughter bond under 'fearful' or 'stressful' conditions. The data collected from this experiment are illustrated in a matrix in Figure 4.3 with mother-daughter pairs arranged along the diagonal.

All the cells containing half or more of the possible scores are along the diagonal. In addition to this, only 1 mother-daughter pair (Numbers 17 and 72) have a score that is less than the expected mean value (see Table 4.9). The method of analysis described in 4:2:2 is illustrated in Table 4.9. There was a highly significant tendency for mothers to be found with their daughters as the nearest ewe-lamb to them. However it is worth noting the considerable individual variation, with pairs 3 and 68, 17 and 72, 32 and 76, and 45 and 81, having relatively low scores, and pairs 12 and 71, 28 and 77, and 36 and 79, having high scores of 10 or more. It was clear during the experiment that in those pairs with high scores, it was the daughters that sought out their mothers and not the converse.

4:3:4 Frequency of interactions between ewe-lambs, their mothers and other members of the group

In Winter 1982 the median frequency of interactions between ewe-lambs was 0.33/30 minutes compared to a median frequency of 0 /30 minutes between ewe-lambs and ewes. In Summer 1982 this difference had disappeared and the overall median frequency between ewe-lambs and between ewe-lambs and ewes was the same at 0.88/30 minutes.

In all focal animal samples in Winter and Summer 1982 only 3 interactions between ewe-lambs and mothers were observed. In Winter

1982 the only interaction between a mother-daughter pair was an investigatory one between Number 35 and her dughter Number 78. Of the 3 in Summer 1982, 2 of these occurred in the same sample and were between Number 11 and her daughter Number 70. One interaction was cohesive, the other aggressive.

4:3:5 The development of home range behaviour in ewe-lambs

As mentioned in 3:3:2 there was a broad similarity at the level of 2 clusters between the home range behaviour of the ewe-lamb in its second summer and that of its mother in its first summer (Figure 3.17 and Table 3.13).

In Autumn 1981 and Winter 1982, 3 ewe-lambs (Numbers 68, 75 and 80) temporarily could not be found in the study site. The facts were as follows:

a) Number 68 could not be found within the area covered by the scans between 311081 and 021181. Early in the morning of 311081 she was spotted with ewes from the Gask home range group at the dam front, but was not seen again until the morning of 031181, when she was found on the south side of the reservoir with a group of Howlet ewes. She was not sighted with this group on the previous night so must have joined them sometime between 1800 GMT on 021181 and 700 GMT on 031181. In doing this she must have left the group of strange ewes she had presumably been with and specifically moved to the Howlet ewes. On 041181 she was back on the winter range.

b) Number 75 could not be found between 020282 and 080282. There is no information as to where she was during this period.

c) Number 80 could not be found between 041181 and the start of Winter 1982 (020282) and no information is available on her whereabouts. Her leaving the group may have been related her mother (No. 40) being removed from the group in the annual cull in September 1981.

During the study period (18 months) only one ewe-lamb (Number 52) permanently left the group. She was found with the Black Hill group from 020781. On 290382 she was observed grazing with Black Hill ewes on Grid Area 5 of the Howlet winter range, within 30m of Howlet ewes. However by night fall she had moved back with the Black Hill ewes to their home range.

4:4 DISCUSSION

4:4:1 The Mother-Daughter Relationship

1 Individual differences in maternal behaviour

The individual variability in quality of mothering described in the first and second weeks after lambing may have had a number of underlying causes. Differences between breeds have been observed for a number of maternal characters such as nursing of twins (Purser and Young 1964; Stevens et al. 1982), maternal vocalisations (Shillito Walser et al. 1982b), and the strength of maternal behaviour at different stages of lamb development (Shillito Walser et al 1983). The existence of genetic variation in maternal behaviour within breeds therefore seems likely and further research would be of value.

Parity has been shown to have a large effect on maternal behaviour; primiparous ewes often show inappropriate behaviour at the birth of their lamb and this may prove detrimental to the lamb (Alexander 1960; Poindron and Le Neindre 1980). Injections of progesterone and oestrogen that induced maternal behaviour in non-pregnant multiparous ewes failed to do so in non-pregnant primiparous ewes, indicating that maternal experience plays an important role in the manifestation of adequate maternal behaviour at parturition (Poindron and Le Neindre 1980). However no study has been made of the effects of parity on maternal behaviour in the later post-lambing period. Theories on parental investment suggest that as parents become older they should invest more in their offspring, as their own potential for future reproduction falls (Trivers 1972). In red deer there is some evidence that duration of suckling and calf condition are correlated with age of hind (Clutton-Brock et al. 1982). In the present study however it appeared that primiparous mothers were the more attentive to their lambs past the immediate post-partum period, and that older animals often appeared inadequate in their maternal behaviour in that they were inattentive to their lambs calls and rejected suckling attempts in the lamb's first week of life. Although a quantitative study is required to substantiate this qualitative assessment, if correct, it illustrates the difficulty of ascribing strategies concerned with increasing overall lifetime reproductive success compatible with natural selection, to domestic animals existing under conditions of artificial selection imposed by the farmer.

The effects of nutrition on maternal behaviour have been studied mainly in the immediate post-partum period. Thomson and Thomson (1949) found that the plane of nutrition of the ewe had a large effect on her attentiveness to the lamb at birth. They observed that low-plane ewes frequently exhibited little or no sustained maternal behaviour even with a lively lamb. Arnold <u>et al.</u> (1979) found that ewes on a high plane of nutrition had a higher milk yield throughout lactation than ewes on a low-plane diet, and they continued nursing after the low-plane ewes had weaned their lambs. However the interaction of nutrition with other factors that affect maternal behaviour has yet to be studied from birth to weaning in sheep living under extensive conditions.

Individual differences in temperament have been shown to contribute to individual differences in maternal behaviour in cats (Lawrence 1980b) and non-human primates (Altmann 1980; Stevenson-Hinde <u>et al.</u> 1980). In cats the temperament of the mother appeared to interact with her nutritional state to produce individual variability in the quality of mothering in weeks 1 and 2, and in the timing of weaning (Lawrence 1980b). In sheep Thomson and Thomson (1949) found that although ewes with high milk yields tended to be the most attentive mothers, a few ewes on the low-plane diet, who had almost no milk, were also very attentive. Arnold and Morgan (1975) also found that behavioural differences between individual ewes at lambing were invariably larger than any differences due to breed, age of ewe, plane of nutrition, climate or location.

The study of individual differences in mothering should be useful in understanding the causal mechanisms that underlie maternal behaviour (Wood-Gush et al. 1984). However a great deal more information is required before the study of individual differences can usefully be applied to the improvement of maternal behaviour in sheep.

2 Control of lamb's movements by mothers

From the third week of life lambs in the present study were grazing actively at increasing distances from their mothers. This agrees with Hewson and Verkaik (1981) who found a significant increase in the distances between lambs and their mothers from lambing to 4 weeks of age.

One behaviour pattern of the ewes which affected the distances between themselves and their lamb, was for them to merely lift their heads from grazing. This frequently, but not invariably, had the effect of causing the lamb to run towards its mother and attempt to nurse. It seemed that the lamb had been conditioned to respond to the raised head of the ewe as a cue to nursing. On occasions however, the ewe would refuse to let the lamb nurse and would walk off with the lamb following at heel. Lambs also ran to their mothers when the latter lifted their heads in alarm indicating that this behaviour may, in the past and even now, have anti-predator value to sheep. Ewbank (1967) noted similar behaviour in Clun Forest ewes without attributing any special significance to the raising of the ewe's head.

3 Do ewes seek help from humans?

Some shepherds maintain that ewes with trapped or ill lambs will 'ask' for help from humans. In 4:3:1 two examples were given of ewes apparently indicating to humans the presence of their lambs trapped in ditches. In both situations the mothers involved were gimmers, suggesting that the response has a large innate component. A possible explanation is that the movement of the ewe towards her lamb is basically defensive, but it inadvertently alerts humans to the plight of the lamb. There are reports of ewes showing maternal defensive behaviour against coyotes (Berger 1978a), and foxes and ravens (Alexander et al. 1967). A knowledge of the existence of this behaviour amongst hill-walkers could save some lamb lives, at least in the less remote hill areas. Both walkers in these examples were unaware of the significance of the ewes' behaviour.

4 Weaning

Weaning in sheep may be triggered by the decreasing milk supply of the ewe. Arnold et al. (1979) found that when the milk supply fell below about 550 cc per day ewes began to reject nursing attempts by lambs. Following weaning, 2 alternatives exist; that the mother and her offspring remain close associates, as in cattle (Bos indicus) (Rheinhardt and Rheinhardt 1981) and red deer (Cervus elephus)

(Clutton-Brock et al. 1982), or the pair separate and cease to associate.

In this study nursing was a very rare event by the 25th week. Following the cessation of nursing the bond between ewe and lamb, as measured by the MAI, significantly weakened (Figure 4.1 and Table 4.1). In addition to this, the number of interactions between daughters and their mothers was extremely small from 9 months of age onwards. Such findings clearly contradict those of Hunter and Milner (1963) who wrote that "...sheep are social, not solitary animals and form groups, the family and the home range group being the 2 social groups formed...." They suggest that the mother-daughter bond is of a permanent nature, yet in their paper they present only qualitative evidence to show that ewes and daughters graze the same area of hill. No measurement is made of associations between mother and daughter, and whether they used the same areas synchronously or separately. Similarly, Hunter (1964) wrote that it was well known that 1 year old ewe-lambs continued to follow their mothers at that age, although no evidence was presented to support the statement.

The results in the present study showing that the ewe-daughter bond ceases to have any discernable social significance in the field, is supported by Australian work on domestic sheep (Arnold and Pahl 1974; Arnold et al. 1981), and also by the work of Geist (1971) and Berger (1979a) on bighorn. Geist found that both sexes of bighorn lambs were largely independent of their mothers by the rut, although he states that final separation did not occur until just prior to lambing in March of the following year. Berger (1979a) reports that the percentage of time lambs were found within 7m of their mothers had declined by 6 weeks of age, whilst associations with peers and other ewes had risen. In Soay sheep, Grubb (1974b) observed that by the middle of the rut ewe-lambs had generally left their dams, although some did maintain contact with their mothers for a number of years.

Evidence suggests that it is the ewe which is primarily responsible for the decline of the bond. Shillito Walser et al. (1983) tested the conflict between the ewe's maternal bond and her social bond with other members of the group in a T-maze experiment. Until the lamb was 40 days old, ewes of the 3 breeds being tested, Dalesbred, Jacob and Soay, almost invariably went to the lamb as their first choice. However with the increasing age of the lamb, ewes spent significantly less time near their offspring and made more movements towards the flock. In addition when weaned lambs were released into a field with their mothers, the attraction of the lambs to their mothers was not reciprocated and nursing attempts were aggressively rejected by ewes (Shillito-Walser et al. 1982a). Similarly in the present study it was the ewe-lamb who appeared to actively search for its mother. However since approaches to the dam were not rewarded presumably the lamb's attraction to its mother would also wane. Berger (1979a) reported that lambs reared in a desert environment received more milk in the earlier stages of lactation, and spent more time near their mothers, than lambs reared in a mountain environment who received less milk. It was certainly the case in the present study that ewe-lambs' vocalising and searching for their mothers ceased rapidly if they were unsuccessful in locating their dams. It was also occasionally observed that a ewe-lamb would seem to recognise its mother at a distance and vocalise to her. However on gaining no response the lamb would make no attempt to move closer and eventually would resume grazing. One point clearly demonstrated in the experiment described in 4:3:3 was that at a stage when they rarely associated with their mothers on the hill (at about 11 months of age), ewe-lambs still retained the ability to recognise their mothers. The decline of the ewe-daughter bond was not merely a result of ewe-lambs failing to recognize their mothers.

This section has supplied some proximal reasons for the separation of the ewe and her daughter. Functional arguments for separation will be discussed in 4:4:3.

4:4:2 <u>Ewe-Lamb Associations with Peers and other Group Members</u>

The trends for associations with peers (the PAI) and with members of the group excluding peers and mothers (the GAI) partly mirrored seasonal changes in sociability in these sheep. Hunter and Milner (1963) noted that hill sheep were more dispersed in summer than winter, a point that is confirmed and elaborated upon in Chapter 5. Thus the rise in the PAI and GAI in Autumn 1981 and the continuing rise of the PAI in Winter 1982, are partly an expression of the animals forming larger and more clumped sub-groups. Similarly, the fall of these 2 indices in Summer 1982 is an expression of the dispersion of the group in summer. Finally, both indices rise in Post-Weaning 1982 indicating a return to the large sub-groups of winter (Figures 4.1 and 4.2).

This explanation is however incomplete for it fails to take account of the significant rise in the PAI, above the GAI during

Autumn 1981 and Winter 1982. The rise in the PAI was caused by a significant preference, shown by the ewe-lambs, to associate with peers, commencing approximately at the time that ewe and daughter began to separate in Autumn 1981. Initially these peer associations formed within sub-groups containing a variety of age classes, but in Winter 1982 the ewe-lambs formed peer groups that became completely independent in their movements from those of the older ewes. (See Chapter 6 for a full description of the behaviour of the ewe-lambs in Winter 1982.)

The preference shown for peers by ewe-lambs after separation from the dam at approximately 7 months old, should not be confused with the formation of 'juvenile bands' of playing lambs formed from the age of 3 weeks in Blackface (Hewson and Verkaik 1981), Soay sheep (Grubb 1974b) and bighorn (Geist 1971; Berger 1979a; 1979b). Juvenile bands were observed in the present study but play declined after the 5th week and so also did the occurence of these groups. During separation from the dam, from October onwards, ewe-lambs chose each other as grazing associates, not as play partners.

Indirect evidence for peer group formation is found in the cluster analyses of the Autumn 1981 and Winter 1982 home range data. In the dendrogram for Autumn 1981 (Figure 3.11) ewe-lambs tended to be found in small clusters at the base of the dendrogram, within larger clusters containing a variety of age classes. In figure 3.13, the dendrogram for Winter 1982, 13 ewe-lambs are found within C5/Wnt 82. Of the other 4 ewe-lambs only one (Number 83) is found in a cluster containing animals over 3 years old (C3/Wnt82), the other 3 being found in C1/Wnt82, a cluster containing the majority of 2 and 3 year old sheep (see also 3:3:2 part 3). This can only be indirect evidence of peer group formation as it contains no information as to the synchrony of use of the same areas by different ewe-lambs. However the interaction data of ewe-lambs in Winter 1982 (see 4:3:4) illustrates that they interacted much more frequently amongst themselves than with other members of the group, further indicating the existence of social peer groups at this time. Further evidence of the social separation of ewe-lambs from other group members in Winter 1982 can be found in Chapters 5 and 6. A similar situation has been described in feral and wild sheep. Geist (1971) found that lambs formed peer groups that moved about independently of the older ewes, and that during the rut when oestrous females were being courted by rams, the lambs tended to remain with their peers, rarely following their mothers. In Soay sheep Grubb (1974b) observed comparable patterns of behaviour; by the middle of the rut it was common for ewe-lambs to graze and rest together. In domestic sheep Arnold et al. (1981) found associations in unshepherded groups to be mainly between individuals of the same age and sex. Furthermore, Hunter and Davies (1963) (see 4:1) appear to have confounded the treatment effect (alteration of home range behaviour by removal of ewe-lambs from their home range groups at different ages) with an incidental increase in sociability between ewe-lambs that were penned together over winter. They chose to represent the number of associations formed within the treatment groups by counting the total number of pairs that were within the same grid square. Hence 3 ewe-lambs formed 3 pairs; 8 ewe-lambs formed 28 pairs. This computation biases towards the larger groups formed by penning. It also underestimates peer group formation in the control group left on the hill which, judging by the results in the present study, may have been greater than indicated by Hunter and Davies's analysis.

The extent to which individual ewe-lambs chose to associate with peers was variable (Figure 4.2). Ewe-lambs such as Number 84, with low PAIs, tended to have high MAIs and GAIs, and the opposite was true for those ewe-lambs with high PAIs. It is not clear however whether ewe-lambs with high MAIs and GAIs were still attracted to their mothers and incidentally achieved high GAIs due to their mothers associating with other ewes, or whether the reverse was true. It would be interesting in future research to match other behavioural correlates (e.g. fearfulness or aggressiveness) to this tendency. Grubb (1974b) noted that during the rut, ewe-lambs varied in their preferences for grazing with dams or peers.

As mentioned in 4:3:1 ewe-lambs grazing in peer groups in Winter 1982 were observed on occasion to become separated from the other members of the group. Eventually they would look up from grazing and show some alarm, running back to the group vocalising. This behaviour was rarely observed in older animals as they tend not to become separated from the grazing sub-groups. It seemed that ewe-lambs at this stage were learning to maintain contact with grazing peer groups that, like adult sub-groups, show little response towards individuals that become separated.

The peer groups formed in Winter 1982 tended to disperse in Summer 1982 as indicated by the significant fall in the PAI (Figures 4.1, 4.2 and Table 4.2). In addition the interaction rates between ewe-lambs and between ewe-lambs and ewes are the same in Summer 1982 indicating a decrease in the age segregation found in winter. It was plain that, in the field, ewe-lambs at this stage were becoming more integrated into the group than previously (i.e. in Winter 1982), and were being found increasingly in sub-groups of mixed age, although often still with peers as close associates. This process of integration was to continue judging by the behaviour of gimmers in Autumn 1981 and Winter 1982.

The associations with other members of the group excluding mothers and peers (the GAI) was intended as a background measure against which the MAI and PAI could be compared. The PAI from Autumn 1981 onwards was significantly greater than the GAI, illustrating again the importance of peer associations in these seasons. In addition, from Winter 1982 onwards the GAI did not vary significantly from the MAI, indicating that ewe-lambs were not associate chosing to with their dams any more than with other ewes and gimmers in the group. The non-significant fall in the GAI, below the MAI in Summer 1982 (see Figure 4.1), was due to the inccreased variation in home range behaviour in summer (see Chapter 3). Ewe-lambs tend to use similar summer home ranges to those used by their mothers (see 4:4:3) . Therefore the chance of a ewe-lamb being found within 30m of its mother, in its 2nd summer, is greater than the chance of it being found within 30m of other group members that used different parts of the summer home range.

4:4:3 The Development of Home Range Behaviour in Ewe-Lambs

In this section the distinction will continue to be made between winter and summer home range behaviour as outlined in Chapter 3. In autumn and winter there is little variation within the group in the use of different parts of the hill, whereas in summer there is considerable individual variation in home range behaviour. Only 1 ewe-lamb (Number 52) left the group permanently during the study period (see 4:3:4). In Figure 3.17 and Table 3.13 it was illustrated that at the level of 2 clusters, the majority of ewe-lambs were found in the same cluster as their mothers, suggesting that ewe-lambs learn in their first summer the broad detail of the movements that they will use in their second summer, in particular whether they will use the south side of the reservoir or not.

At higher levels of similarity ewe-lambs are markedly less similar to their mothers, indicating that they do not adopt the exact home range patterns that they used with their mothers in their first summer (Figure 3.17 and Table 3.13). Perhaps the most likely explanation for this is that ewe-lambs are still socially attracted to their peers in their second summer, and that this may influence their movement patterns. Despite the process of integration of ewe-lambs back into the larger social group from the winter peer groups, there are some indications that peer associations were still of some importance in Summer 1982. Firstly in the dendrogram formed from the cluster analysis of the Summer 1982 home range data (Figure 3.13) clusters of ewe-lambs can be found together. Age was found to have a significant effect on clustering in Summer 1982 and this effect was found to be largely due to the ewe-lambs (see Table 3.10). Similarly there was a tendency for some ewe-lambs to be found together in the dendrogram for Summer 1981 (see Figure 3.9) (eg Numbers 50, 52, 101 and 113 in C2/Sum81), but this effect was not significant. The suggestion that peer associations affected ewe-lamb movements is supported by the findings of Chapter 5 that ewe-lambs in their second summer are more sociable, allelomimetic and synchronised in their movements with one another than are older ewes. In Chapter 7 an explanation for the observed development of summer home range behaviour from the ages of 1 to 6 years will be proposed based on the early experience gained by the ewe-lamb in its first summer.

The importance of early experience in the development of home range behaviour is apparently underlined by the experiment of Hunter and Davies (1963). Of their 2 treatment groups, Group 1 which was removed from the hill at 11 weeks of age showed by far the greatest change in home range behaviour, when compared to their mothers. Group 4 which was not removed from the hill until 6 months of age tended to return to their home range of origin. Key and MacIver (1980) have also shown the importance of maternal influences during the lamb's first summer in determining grazing preferences in later life, and Lynch <u>et al.</u> (1983) have shown a similar effect with the feeding of concentrate feeds.

Having separated from their dams, generally by October or November, ewe-lambs found on the summer range appear to be drawn back to the winter range by the movements of older animals (see Chapter 3; reasons for the return the winter range at this time are discussed in Chapter 6). However it is interesting to note that on 4 occasions ewe-lambs could not be found in the study area between October and November (see 4.3.5). Without the gathering-up of the groups in November for tupping, these ewe-lambs may have permanently left the group. Hunter (1964) recorded a larger number of ewe-lambs leaving their home range group of birth. The management at that time was not to put the sheep into fields but to tup them on the hill, with the result that ewe-lambs that had strayed into another home range may have been undisturbed and allowed to remain there.

Having demonstrated that ewe-lambs remain in the same group and adopt home range behaviour similar to that of their mothers it is logical to ask why they do not remain in association with mothers after weaning. It would seem that most features of the mother-lamb relationship and the subsequent associations formed by the ewe-lambs in the Howlet group, are in large part identical to those described in feral and wild sheep (see above). This behaviour has therefore been little changed, if at all, by artificial selection.

Reinhardt and Reinhardt (1981) have demonstrated in cattle that mother cows prefer their female and male progeny over non-related calves as grooming and grazing partners. They found these family relationships stable over as long a period as 5 years. In red deer the mother-daughter bond also appears more permanent than in sheep. Clutton-Brock et al. (1982) found that even daughters aged 3 years or over were found on average only 18m from their mothers. However red deer evolved as forest dwellers whilst sheep are a mountain grassland species living in a more open enviroment. Open habitats have been found to give rise to larger group sizes in ungulates, probably as an anti-predator response (Estes 1974: Jarman 1974; see Chapter 5). There must therefore have been selection for behaviours that brought about increases in group size. Separation of mother and young could bring about greater bonding between peers and other older members of the group (see below).

Pusey (1983) studying mother-offspring relationships in chimpanzees found that the separation that occurred several years after the birth of the young, was more a consequence of differing social requirements of mother and young than active rejection by the mother. It would appear that in sheep that a similar situation has developed but at a much earlier stage of development. After weaning which generally occurs gradually with little aggression shown by the mother, the ewe and lamb slowly separate. The following benefits may be conferred on the ewe-lamb by ceasing to associate with the ewe:

1) Peer groups like play groups may allow ewe-lambs to develop social and competitive skills with similar sized animals (Fagen 1981). They may also allow the ewe-lamb to develop social bonds that will help maintain the future cohesiveness of large social groups, in the same manner that the artificial penning of ewe-lambs by Hunter and Davies (1963) reinforced and created social bonds. Other workers (Arnold and Pahl 1974; Winfield et al. 1981) have shown in sheep the importance of bonds formed early in life. This assumes that larger groups infer increased fitness to the individual.

2) The independent movements of peer groups may be an advantage during the rut, if conceiving in the first winter of life is a disadvantage. Certainly many Soay ewe-lambs that gave birth generally failed to rear them succesfully (Grubb 1974b), and in the present study 2 ewe-lambs died giving birth in early Summer 1982. By moving independently of older oestrous females ewe-lambs may escape the attention of the ram.

It is suggested in some species that juveniles continue to learn from their dams how to find and process numerous seasonal and widely dispersed foods, and this may contribute to the length of time the bond is maintained (Wrangham 1977). It would seem that under natural conditions however, that there would be little benefit to ewe-lambs in maintaining a relationship with the dam after weaning in terms of learning. However in Chapter 6 a situation under the artificial conditions of this study is described where separation of the ewe and lamb appears maladaptive in terms of the benefits the lamb might have gained from imitative foraging with its mother.

This chapter has illustrated that earlier workers were mistaken in their assessment of the ewe-lamb bond in Scottish hill sheep. It is important to rectify this error as the work of Hunter and Milner (1963) and Hunter (1964) is frequently quoted as one of the very few accounts of the behaviour of hill sheep under extensive conditions. The data presented in this chapter have illustrated the similarity of the development of social behaviour in the domestic ewe-lamb to that of wild and feral sheep. Geist (1971) rejects the term matrilineal or family to describe bighorn home range groups due to the permanent separation of ewe and lamb, and it is suggested that this practice ought also be adopted for domestic sheep. There is clearly a great deal of difference between the family units formed in species such as the elephant (Douglas-Hamilton 1973) and the social organization of sheep as described in this chapter. These results also raise again questions over the forces that maintain these large social groups if family ties cannot be invoked; this topic will be returned to in Chapter 7.

CHAPTER 5 SEASONAL CHANGES IN SOCIAL BEHAVIOUR

INTRODUCTION

The social organization of a species can be categorised into 4 main areas: demography, dispersion and spacing behaviour, intra-group social behaviour and lastly changes through time in the above (Deag 1980). In this chapter we will examine the last of these. Separate patterns of social organization persisting for periods of time have been termed social phases (McBride 1979).

Certain species of ungulate exhibit a distinct social organization during the breeding season. In red deer the sexes live apart in the non-reproductive phase, whilst temporary harems form during the mating season (Mitchell et al. 1977). Similarly in wild and feral sheep and goats the sexes form separate groups during most of the year coming together only for the rut (Shackelton and Shanks 1984).

Seasonal availability of resources has been found to influence spacing behaviour in wild and domestic sheep. Dudzinski et al. (1969) found that Merino flocks that grazed as a single unit when sufficient forage was available, split into sub-groups during drought conditions. An increase in group size in Texan Barbary sheep (Ammotragus lervia) during the winter was thought to be due to the sheep congregating to use wheat fields in preference to naturally occuring forage (Gray and Simpson 1982). That desert bighorn sheep form smaller groups than Rocky Moutain bighorn living in a richer enviroment (Berger 1979b) further emphasizes the effect of resource availability on spacing behaviour. Resource availability can also affect social interactions. Frequency of threats was higher in red deer in winter at a time of food shortage, than in summer when food was more abundant (Clutton-Brock et al. 1982).

Different habitats or seasonal changes in foliage cover can also influence social behaviour. Red deer living on open ground are found in larger groups than those living in forests (Franklin et al. 1975). The large groups formed by roe deer (Capreolus capreolus) in winter in Europe are thought to be partly due to the loss of foliage cover (Bresinski 1982). These changes may be accounted for by an increased risk of predation associated with lack of cover. Nelson and Mech (1981) suggest that the yarding behaviour of white-tailed deer (Odocoileus virginianus) in winter, when they congregate in groups, is largely a response to wolf (Canis lupus) predation. Larger groups may form as one of several anti-predator strategies, for example reduced detectability of a compact herd (Treisman 1975), reduced risk to the individual (Hamilton 1971) and more effective predator detection (Pulliam 1973).

The presence of young may also affect spacing behaviour. In white-tailed deer, does with fawns avoid other adults (Nelson and Mech 1981) and in moose (Alces alces), cows are least gregarious during the summer when they have young calves at foot (Peek et al. 1974). Similarly in the hill kangaroo (Macropus robustus), a higher proportion of lactating females than other age-sex classes were found to be separated by more than 50m from conspecifics (Croft 1981).

Finally, population size and density place obvious constraints on group size. Peek et al. (1974) found group size in moose to be higher and more variable in dense populations and smaller and less variable in less dense populations.

Much of the above work relies heavily on information of group size, the measurement of which is a recurring problem in studies of social behaviour. In some instances where observational difficulties are great, any animals seen simultaneously in the same place are regarded as a group (Van Vuren 1983). Where possible, though, attempts have been made to establish criteria on which to base assumptions of group membership. A commonly used criterion is a specific distance based on observations of nearest neighbour distances (eg Clutton-Brock et al. 1982; see 2:4:1). Another possible method is based on relative distances, such as a multiple of the current nearest neighbour distance (Kummer 1968). Occasionally behavioural methods have been employed, for example approaching animals to observe which conspecifies they move to when disturbed (Lynch 1967). The problem with distance based criteria is the large variability found in nearest neighbour distances in most species. For example sheep grazing on heather have been found to have larger nearest neighbour distances than those grazing on grass (Dobie 1979). Thus although animals in certain situations can be shown for example to be spaced further apart and forming smaller groups, this does not indicate if features of social organization other than spacing have undergone quantifiable change. Information on aspects of social organization other than spacing is therefore important to understand fully the implications of different social phases to the animal.

The present chapter analyses seasonal changes in the social behaviour of the Howlet home range group. To date the only information available regarding social phases in hill sheep is the observation, made by Hunter and Milner (1963), that South-Country Cheviots formed larger groups in winter than summer. They suggested that the larger groups in winter were formed in response to the onset of oestrous. The dispersion in summer, they hypothesised, was caused by dominant sheep gaining access to the best vegetation, and causing subordinates to disperse to the poorer areas. This work seeks to examine these ideas in more detail.

5:2 MATERIAL AND METHODS

The data used in this chapter came from scans carried out in Summer 1981, Autumn 1981, Winter, 1982 and Summer 1982 (See 2:4:1), and from the Winter and Summer 1982 focal animal observations (see 2:4:2).

5:2:1 Analysis of Sub-Group Size

The evidence presented in Chapter 3 illustrated the existence of the Howlet home range group. This chapter will analyse seasonal changes in sub-group size, sub-groups being temporary sub-divisions of the total home range group. The term sub-group is used to remain consistent with previous sheep workers (eg Hunter and Milner 1963, Arnold and Pahl 1967, Dudzinski et al. 1969) and corresponds to the term party used by Clutton-Brock et al. (1982). As described in 2:4:1 sub-groups were determined by estimating firstly which animals were separated by less than 30m from each other (30m sub-groups), and secondly those animals that were separated by less than 10m from each other (10m sub-groups).

To examine seasonal changes in sub-group size 15 ewes and 10 ewe-lambs were selected at random. Sub-group sizes from 10 separate days were averaged for each of these animals in each season (except for ewe-lambs in Summer 1981). Each animal therefore had a seasonal estimate of sub-group size. Overall seasonal changes in sub-group size were analysed separately for the 2 age-classes, ewes and ewe-lambs, using Friedman 2-way ANOVA (Siegel 1956). As in Chapter 4 the Wilcoxon Matched-Pairs Test (Siegel 1956) was used as an a posteriori pair-wise test, α again being set at 0.01. Averaging of the individual mean sub-group sizes in each season, gave a seasonal estimate of typical sub-group size for the 2 age-classes. Jarman (1974) proposed typical group size as a more accurate representation than mean group size, of the size of group in which the average animal would find itself in a finite population. It involves summing the mean group sizes of individual animals and dividing by the total number of animals, rather than summing group sizes and dividing by the number of groups.

5:2:2 Analysis of Nearest Neighbour Distances

Nearest neighbour distances were recorded during the Winter and Summer 1982 focal animal observations. Each of these observations was 30 minutes. During Winter, 1982 11 ewes and 8 ewe-lambs were each watched for 5 samples. During Summer 1982, 7 ewes were watched for 6 samples and 6 ewe-lamb for 4 samples. The ewe data were a sub-set of a larger data set that traced the development of the mother-lamb relationship from birth to weaning (see 2:4:2). The data used in this chapter were taken from samples from the 5th week of the lamb´s life to the 14th week (180584 to 190884). A mean distance was computed for each sample by averaging the distance at the start and at the end of the observation. A seasonal estimate of nearest neighbour distance for each individual was then calculated by averaging these observation means.

5:2:3 Analysis of Effect of Lamb on Size of Ewe Sub-Groups

In order to assess what effect the presence of a lamb had on the size of ewe sub-groups, 10 ewes that were to be artificially weaned were compared to 10 ewes that were not to be weaned, before and after artificial weaning in 1982. Again for each of these 20 animals ten 30m sub-group sizes were randomly selected from 10 days pre- and post-weaning and averaged to give mean individual sub-group sizes for the 2 periods.

5:2:4 Analysis of Synchrony of Movement

To examine what effect season had on synchrony of movement 10 ewes and 10 ewe-lambs were selected randomly, and their movements over 10 separate days in the seasons Autumn 1981, Winter 1982 and Summer 1982 were analysed. The assumption was made that if animals were synchronized in their movements they would be observed in the same grid square during the same 2 hour period. For each of the 10 days a score was derived of the number of grid squares occupied by the sample animals at the same time of day (e.g. if all 10 sheep were occupying the same grid square the synchrony score = 1; if they were found in 10 different grid squares the synchrony score = 10). In each day depending on whether it was a morning or an afternoon session (see 2:4:1) only the time periods 1000-1200 hours and 1200-1400 hours were considered resulting in 1 synchrony score/day. Hill sheep are known to form larger sub-groups at night (Hewson and Verkaik 1981). The sampling regime in this study was not altered relative to sunrise or sunset and therefore to have considered the first (600-800 hours) and the last (1600-1800 hours) scans in winter with those in summer would have clearly been an unjustified comparison in terms of an analysis of synchrony of movement. By comparing only the middle of the day in each season it could be argued that the animals were at their maximal daily dispersion for that time of year and that any effect of daylight would be diminshed.

5:2:5 Analysis of Allelomimetic Walking

Scott (1945) defined allelomimetic behaviour patterns as those in which conspecifics performed the same act simultaneously. In this study allelomimetic waking was defined as where 2 or more animals walked, with their heads up, in line for a period longer than 15 seconds. The frequency of allelomimetic walking was derived by summing all instances in an observation separated by at least 4 minutes and dividing by the total observation time.

5:2:6 Analysis of Interactions

Appendix 1 contains the ethogram of interactions collected in the focal animal samples and subsequently analysed.

1) Cohesive interactions: In these an animal would approach

another to within 0.5m, most frequently from behind, and walk around the approached animal without any other act occurring. On occasion the head would be approached, again with the approaching animal walking around the approached sheep. These movements were similar to those found in mother-lamb pairs with the lamb often being left behind by the mother, and subsequently approaching her back, walking round her and grazing in front or at her head. In some instances, when for example a number of sheep were moving along the road towards the dam front (see Figure 2:1) a great number of these movements could occur in a very short time. As the only apparent result of these approaches was to cause sheep to move closer to one another, they have been regarded in this study as a cohesive behaviour pattern by which individual sheep avoid separation from moving sub-groups.

2 Agonistic Interactions: In these an animal would approach another to within 0.5m, and an agonistic act would follow. The agonistic acts observed in order of frequency of occurrence were: 1) Grazing Displacements. In these almost invariably the approaching animal displaced the head of the approached animal. The displacement could be achieved by butting the head or side of the approached animal or using a horn threat (Geist 1971), but often the approaching animal would start to graze at the same point as the approached animal, thus displacing it without overt aggression. Occasionally the approached animal would respond by using a horn threat or butting the head of the approacher. As described in 3:3:1 feeding displacements

occurred frequently at the feedblock in Winter 1982. Those focal animal samples involving feeding at the block are excluded from the present analysis. 2) Head Butting Contests. In these 2 sheep would become involved in a number of head butting exchanges. These were usually of a short duration but very occasionally they could last for an hour or more. Grubb and Jewell (1974) describe similar long duration contests between ewes. 3) Front Kicks. Very occasionally ewes would employ the display known as the front kick (Geist 1971). Ewes were observed using this display to cause lying sheep to stand, then lying down on the same spot. It was also used by sheep walking in line being stopped by the animal immediately in front.

3 Investigatory Interactions: In these an approach resulted in obvious investigation by one or both of the animals. Investigation was defined as when one of the animals placed its nose close to the head, side or back of the other animal. On occasions the investigating ewe would nibble the wool of the other. Occasionally agonistic behaviour could immediately follow an investigatory intraction. These mixed interaction types were defined as agonistic interactions.

To derive interaction scores for analysis, the occurrences per observation of the 3 different interaction types were averaged over the number of times individual sheep were sampled in a season. Thus each individual had a seasonal score for each interaction type.

5:3 RESULTS

5:3:1 Seasonal Changes in Sub-group Size

In Summer 1981 sheep tended to occur most commonly as single animals or in small sub-groups of 2, 3 and 4 (Figure 5.1). In Winter 1982 there was a greatly increased tendency for sheep to be found in larger sub-groups (Figure 5.1), the largest recorded sub-group consisting of 60 animals.

Season was found to have a strong effect on mean individual ewe sub-group sizes (Table 5.1). The sample animals were found in significantly larger 10m and 30m sub-groups in Winter 1982 than in the other seasons, whilst in Autumn 1981 they were found in significantly larger sub-groups than in Summers 1981 and 1982. There was no significant difference between 30m sub-group sizes in the 2 summer seasons.

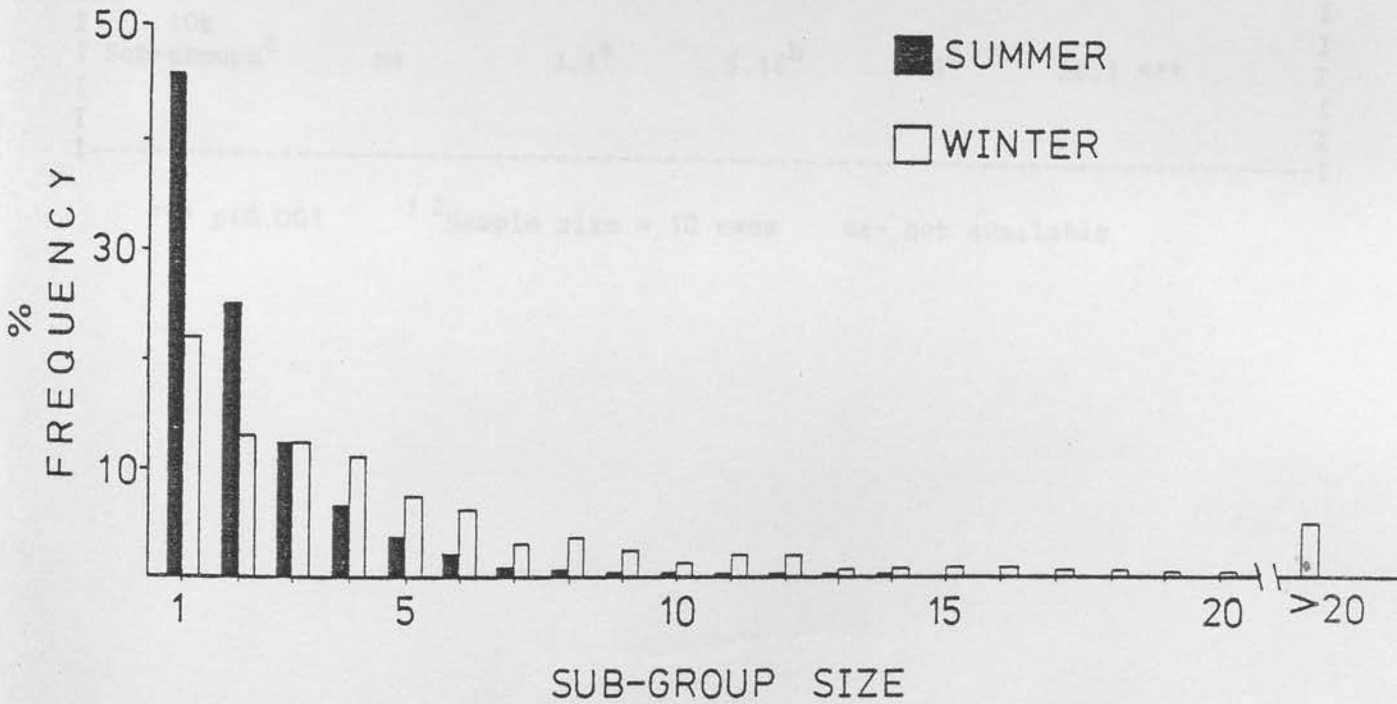
Season was also found to have an effect on the ewe-lambs´ 10m and 30m mean sub group sizes, although there were indications that the effect was less than in the case of the ewes (Table 5.2). Only Winter and Summer 10m and 30m sub-group sizes were found to differ at $P < 0.01$.

Direct comparison of ewe and ewe-lamb 10m and 30m sub-group sizes (Table 5.3) found that there was no difference in either data-set in Autumn 1981. In Winter 1982 ewe 30m sub-groups were significant larger than ewe-lamb 30m sub-groups, but there was no difference in the size of 10m sub-groups. In Summer 1982 ewe-lambs were found in significantly larger 10m and 30m sub-groups.

From observational notes it was clear that weather could have a strong effect on sub-group size. Strong winds and precipitation greatly increased the size of sub-groups in winter, and to a lesser

FIGURE 5.1

FREQUENCY (%) OF 30M SUB-GROUP SIZES IN SUMMER 1981 AND WINTER 1982


SUMMER
WINTER
% FREQUENCY
50
30
10
1
5
10
15
20
>20
SUB-GROUP SIZE

TABLES 5.1

ANOVA OF SEASONAL CHANGES IN EWE 10M AND 30M SUB-GROUP SIZES

Those values with the same suffix (eg a, b) are not significantly different at $p<0.01$ (Wilcoxon Matched Pairs Test). 10m and 30m data were analysed separately. See 5:2:1 for derivation of typical sub-group sizes

TYPICAL SUB-GROUP SIZE	SEASON				
	Summer 1981	Autumn 1981	Winter 1982	Summer 1982	Freidman χ_r^2
30m Sub-groups[1]	3.9^a	8.8^b	19.1^c	3.5^a	40.52 ***
10m Sub-groups[2]	na	3.4^a	5.16^b	1.6^c	28.1 ***

*** $p<0.001$ [1] [2] Sample size = 10 ewes na- not available

TABLES 5.2

ANOVA OF SEASONAL CHANGES IN EWE-LAMB 10M AND 30M SUB-GROUP SIZES

Those values with the same suffix are not significantly different at p<0.01 (Wilcoxon Matched Pairs Test).

	TYPICAL SUB-GROUP SIZE				
	SEASON				
	Summer 1981	Autumn 1981	Winter 1982	Summer 1982	Freidman χ_r^2
30m Sub-groups[1]	na	7.5^{ab}	9.5^{b}	5.6^{a}	9.95 **
10m Sub-groups[2]	na	3.0^{ab}	5.5^{b}	2.3^{a}	6.65 *

** p<0.01 * p<0.05 [1] [2] Sample size = 10 ewe-lambs na - not available

TABLE 5.3

COMPARISON OF EWE AND EWE-LAMB 10M AND 30M SUB-GROUP SIZES IN AUTUMN 1981, WINTER 1982 AND SUMMER 1982.

SEASON	TYPICAL SUB-GROUP SIZE			
	EWE 30m SUB-GROUPS	EWE-LAMB 30m SUB-GROUPS	Mann-Whitney U	
Autumn 1981	8.8	7.5	46.5	NS
Winter 1982	19.1	9.5	4.0	**
Summer 1982	3.5	5.6	9.5	**
	EWE 10m SUB-GROUPS	EWE-LAMB 10m SUB-GROUPS		
Autumn 1981	3.4	3.0	61.0	NS
Winter 1982	5.2	5.5	73.0	NS
Summer 1982	1.6	2.3	10.0	**

** $p<0.01$

TABLE 5.4

SEASONAL CHANGES IN EWE AND EWE-LAMB NEAREST NEIGHBOUR DISTANCES

Values shown are medians.

	NEAREST NEIGHBOUR DISTANCE			
	AGE-CLASS		Mann-Whitney	
SEASON	EWES	EWE-LAMBS	U	
Winter 1982	13.8[a]	14.1[c]	34.5	NS
Summer 1982	31.5[b]	12.24[d]	6.5	*

* $p<0.05$

Sample sizes - a= 11 ewes (28 hours)
- b= 7 ewes (21 hours)
- c= 8 ewe-lambs (20 hours)
- d= 6 ewe-lambs (12 hours)

extent in summer. In blizzard condition the entire group could be found sheltering together in the low part of the range. The group also coalesced into larger sub-groups towards nightfall as they moved uphill. In Autumn 1981, during the period 1600-1800 hours 30m sub-groups could contain 20 to 30 individuals. In Winter 1982 often all adult ewes could be found at dusk in one sub-group clustered about the feedblock (see Chapter 6). Other factors that affected sub-group size were vegetation and activity. Large sub-groups tended to form on Agrostis-Festuca, and recently burnt heather swards at certain times of the year. Conversely animals feeding on old heather or amongst bracken tended to do so in smaller groups. Lying sub-groups tended to be large and rapid movements, along the road for example, also tended to be performed by large sub-groups.

5:3:2 Analysis of Nearest Neighbour Distances

No difference was found between the nearest neighbour distances of ewes and ewe-lambs in Winter 1982 (Table 5.4). Ewe-lambs were however found to have significantly smaller nearest neighbour distances in Summer 1982 than ewes (Table 5.4), although attention should be drawn to the small number of ewe-lambs (6) sampled in Summer 1982.

TABLE 5.5

EFFECT OF LAMBS-AT-FOOT ON EWE 30M SUB-GROUP SIZES

Ewe Sample 1 are those ewes which were weaned artificially at the end of Summer 1982. Ewe Sample 2 are those ewes not weaned at the end of Summer 1982 and therefore had their lambs-at-foot in the post-weaning period.

TYPICAL SUB-GROUP SIZE			
PRE-WEANING			
Ewe Sample 1[a]	Ewe Sample 2[b]	Mann-Whitney U	
3.2	3.15	46.5	NS
POST-WEANING			
7.3	4.5	12.5	**

** p<0.005 (one-tailed test)   a b Sample sizes= 10 ewes

5:3:3 The Effect of Lamb on the Size of Ewes' Sub-groups

Following the removal of all lambs except replacement ewe-lambs at the end of Summer 1981 (see 2:3) it was observed that weaned ewes appeared to form larger sub-groups than unweaned ewes. In addition it was not uncommon to see ewes with lambs in summer moving along paths, perhaps 100m or more from other adult sheep. After ewes were weaned they were rarely seen walking along paths alone, and if doing so, they were observed to be vocalising in a distressed manner. On occasion in summer ewes were also observed grazing with their lambs completely out of sight of other sheep, a situation virtually unknown in ewes without lambs.

As described in 5:2:3 the mean sub-group sizes of 2 groups of ewes, 10 to be artificially weaned and 10 not to be artificially weaned, were compared pre- and post-weaning. As expected the 2 groups did not differ in the size of sub-groups that they were found in pre-weaning (Table 5.5). However in the post-weaning period those animals that had been weaned were found in significantly larger sub-groups than those that had not (Table 5.5).

5:3:4 Analysis of the Synchrony of Movement in Ewes and Ewe-lambs

Season had a strong effect on the probability of finding 10 randomly selected ewes in the same grid square (Table 5.6). Pair-wise tests found no difference between synchrony scores for Autumn 1981 and Winter 1982. There was however a significant difference between both of these seasons and Summer 1982, indicating that ewes by this measure were significantly less synchronized in

TABLE 5.6

ANOVA OF THE EFFECT OF SEASON ON THE SYNCHRONY OF EWE MOVEMENTS

See 5:2:4 for derivation of synchrony scores. Values shown are medians. Those values with the same suffix are not significantly different at p<0.01 (Mann-Whitney U Test).

SYNCHRONY SCORE			
SEASON			
Autumn 1981	Winter 1982	Summer 1982	Kruskal-Wallis H
5.5^{a}	4.5^{a}	9.0^{b}	15.47 ***

*** p<0.001, Sample size= 10 ewes

TABLE 5.7

ANOVA OF THE EFFECT OF SEASON ON EWE-LAMB SYNCHRONY OF MOVEMENT

Values shown are medians.

SYNCHRONY SCORE			
SEASON			
Autumn 1981	Winter 1982	Summer 1981	Kruskal-Wallis H
4.5^{a}	4.0^{a}	6.0^{a}	9.82 **

** p<0.01, Sample size 10 ewe-lambs

their movements in summer than in other seasons. Season also had an overall effect on the synchrony of ewe-lamb movements (Table 5.7). Synchrony tended to be less in Summer 1982 than in Winter 1982 ($p < 0.02$) but there were no significant differences between seasons at $p < 0.01$.

It was shown in Chapter 3 that in summer not only did the size of the group home range increase, but that there was also an increased variability in home range behaviour with sheep using areas of the group home range to differing extents. Therefore it is perhaps not surprising that there is a decrease in the synchrony of movements from winter to summer, due to these seasonal changes in home range usage. Direct comparison of ewe and ewe-lamb synchrony scores however allows the effect of a lamb-at-foot on ewes' synchrony of movements to be taken into account in the summer months, over and above any seasonal changes in the home range behaviour of the group. Ewes and ewe-lambs did not differ from one another in their synchrony scores in Autumn 1981 (Mann-Whitney U Test, $U = 41.5$, $n1, = 10$, $n2 = 10$, NS) or Winter 1982 ($U = 37$ $n1 = 10$, $n2 = 10$, NS). However they were found to differ significantly in Summer 1982 ($U = 10.5$, $n1 = 10.$ $n2 = 10$, $p < 0.01$) ewe-lambs expressing a greater synchrony of movement in summer than ewes.

5:3:5 <u>Seasonal Changes in Allelomimetic Walking</u>

Allelomimetic walking among ewes was observed at a frequency of 0.20/30 minutes in Winter 1982, with 11% (6/54) of samples containing at least one instance. The frequency of allelomimetic walking in

TABLE 5.8

EWE AND EWE-LAMB INTERACTIONS IN WINTER 1982

Values shown are median frequencies/30 minutes.

INTERACTION TYPE	AGE-CLASS EWE[a]	EWE-LAMB[b]	Mann-Whitney U
Cohesive	0.25	0.40	40 **NS**
Agonistic	0.17	0.35	37 **NS**

Sample size a= 11 ewes (27.5 hours)
b= 8 ewe-lambs (20 hours)

TABLE 5.9

EWE AND EWE-LAMB INTERACTIONS IN SUMMER 1982

Values shown are median frequencies/30 minutes.

INTERACTION TYPE	AGE-CLASS EWE[a]	EWE-LAMB[b]	Mann-Whitney U
Cohesive	0.00	1.62	1 **
Agonistic	0.09	0.88	6 *

* p<0.05 ** p<0.01 Sample size a= 7 ewes (21 hours)
b= 6 ewe-lambs (12 hours)

ewe-lambs was similar at 0.24/30 minutes, with 17% (7/41) of samples containing at least one instance. However in Summer 1982 although the frequency of allelomimetic walking in ewe-lambs was 0.28/30 minutes, with 25% (6/24) samples containing at least one instance, in 42 samples no observations were made of ewes allelomimetic walking.

5:3:6 <u>Seasonal Changes in Interaction Type and Frequency</u>

There was no significant difference in the frequency of cohesive and agonistic interactions in ewes and ewe-lambs in Winter 1982 (Table 5.8). Both ewes and ewe-lambs tended to perform more cohesive than agonistic interactions. The median frequency of investigatory interactions in both ewes and ewe-lambs was 0 /30 minutes.

In Summer 1982,however, · ewe-lambs were involved in significantly more cohesive and agonistic interactions than ewes (Table 5.9). In particular the difference in frequency of cohesive interactions was striking. This was a result of ewes performing less cohesive interactions in Summer than Winter 1982 (Mann-Whitney U Test; $U = 14$, $n1 = 11$, $n2 = 7$, $p < 0.05$) and ewe-lambs performing more cohesive interactions in Summer than Winter 1982 ($U = 6.5$, $n1 = 6$, $n2 = 8$, $p<0.05$). There were no significant differences in ewe agonistic interactions between Winter and Summer ($U = 35.5$, $n1 = 7$, $n2 = 11$, NS) or ewe-lamb agonistic interactions between Winter and Summer ($U = 11.5$, $n1 = 6$, $n2 = 8$, NS). Again the median frequency of investigatory interactions in ewes and ewe-lambs was 0 /30 minutes.

5.4 DISCUSSION

The results presented in this chapter show that the Howlet ewes exist in at least 2 separate social phases. The winter phase (October-March) contrasts with the summer phase (April-September); it is characterised by larger sub-groups, smaller nearest neighbour distances, a degree of synchrony between the movements of individual sheep, the occurrence of allelomimetic walking and the use of cohesive grazing movements (see Tables 5.1; 5.4; 5.6; 5.8 and 5.9). The relationship between these separate measures of social organization will be discussed below.

Following Gray and Simpson's (1982) assertion that larger winter group sizes in Texan Barbary sheep were due to them congregating at wheat fields, it is necessary to consider the possible effects that the feedblocks fed in Winter 1982 (see 2:3, Chapter 6) might have had on sub-group size. It is conceivable that the larger sub-group sizes were a response to the presence of this concentrated source of nutrients. In Chapter 6 it is illustrated that ewe-lambs made little or no attempt to feed off the feedblocks, moving independently of the ewes at this time of year, whilst ewes were highly attracted to the blocks. This could have resulted in the significantly larger ewe 30m sub-groups (see Table 5.3). However it should be noted that ewe 30m and 10m sub-groups sizes increased in size relative to summer in Autumn 1981, some time before feedblocks were present on the hill. In addition ewe winter 10m sub-groups sizes did not differ significantly from ewe-lamb winter 10m sub-group sizes, indicating that the difference in winter 30m sub-group sizes was more a reflection of the number of animals available to form sub-groups in these 2 age-classes than a real difference in the causal basis of grouping. Assuming simplistically that there was no mixing at all between the 2 age-classes in Winter 1982 (again see Chapter 6 for evidence of the separate movements of ewes and ewe-lambs at this time of year), the ratio of ewes (excluding gimmers) to ewe-lambs was 2.2:1. Although some small effect of feedblocks on sub-group size cannot be discounted, it would seem that it could not have been a major cause of the larger Winter sub-groups.

Season also affected to some extent the social behaviour of ewe-lambs. In Autumn 1981 and Winter 1982 they behaved in a similar manner to the ewes (see above). However although the size of ewe-lamb 10m and 30m sub-groups also decreased in Summer 1982, they remained larger than ewe sub-group sizes. Similarly although season had some effect on ewe-lamb synchrony of movement, by comparison ewe-lambs were found to be significantly more synchronized than ewes in Summer 1982. Ewe-lambs in summer also had smaller nearest neighbour distances and performed similar or greater amounts of allelomimetic walking and cohesive interactions than in winter. (See Tables 5.2; 5.3; 5.4; 5.7; 5.8 and 5.9). It would appear therefore that the difference between ewe-lamb winter and summer social phases was much less than in the case of ewes. In discussion of the social phases of the Howlet home range group an explanation is required both of the seasonal changes in social behaviour, and of the differences between ewe and ewe-lamb behaviour in summer.

5:4:1 The Winter Phase

The formation of larger sub-groups in winter has already been noted in hill sheep (Hunter and Milner 1963). Larger groups in Winter have also been found in a number of other northern latitude ungulates such as red deer (Knight 1970; Moen 1973), white-tailed deer (Moen 1973; Nelson and Mech 1981), moose (Geist 1963; Hauge and Keith 1981), roe deer (Bresinski 1982) and mouflon (Pfeffer 1967). An exception to the above trend is the red deer population on Rhum that forms smaller parties in winter than summer (Clutton-Brock et al. 1982).

It seems that these seasonal changes in grouping behaviour may be affected by food supply. Past reviews of social organization in ungulates have dealt with the relationship between ecology and social organization (Estes 1974; Jarman 1974; Geist 1974). Jarman (1974) has suggested that small bodied antelope are selective feeders of browse and that this limits their group size, browse being a dispersed food, whilst larger bodied antelope being unselective grazers have no such constraint on group size. Within this classification medium body-weight, mixed feeders are likely to experience the largest changes in diet over the seasons, as the quality and quantity of grass declines in the dry season. Underwood (1982) has shown that this class of antelope also experience the largest seasonal changes in group size, presumably in relation to their changing food supply. Sheep can be described as selective mixed feeders that show seasonal variation in diet in response to the decline and quality of grass (Hunter 1962; Martin 1964; see Chapter 6). There would therefore appear good reason to suspect seasonal variation in herbage supply as causing the changes in sub-group size described in this chapter. Indeed Geist (1974) writes that it is accepted knowledge that as forage resources for northern ungulates decline group size increases. Unfortunately he makes no reference as to why this should be so.

Hill swards generally consist of a patchwork of vegetation types and in summer the prefered Agrostis-Festuca swords can often be found in dispersed localities (see Figure 2.2). The quality of grass available to be selected by hill sheep declines sharply in Autumn and Winter (Eadie 1967) and the use of heather increases, (Milne 1974; see Chapter 6 for more detail). Hill swards in effect in winter become more uniform in quality and the distribution of preferred resources less patchy. It could be argued that a reduction in the variability of sward quality allows animals to form larger sub-groups; in other words with reduced dispersion of resources the benefits of larger sub-groups outweigh the costs.

Intuitively it would seem that a major cost of increased sub-group sizes at a time when feed resources are diminished would be increased intra-group competition. However athough in red deer the frequency of threats increased in winter (Clutton-Brock <u>et al.</u> 1982) there was little evidence that this was the case in the present study (see Tables 5.8 and 5.9). It is known that sheep and deer at this time of year have reduced growth rates and voluntary feed intakes (Forbes 1982). A reduction in feed requirements could result in less feeding competition, although this would not explain the differences in winter sub-group (party) size, between this study and that of Clutton-Brock <u>et al.</u> 1982. A more detailed analysis is indicated to estimate the costs, in terms of feeding competition, of larger winter sub-groups in sheep.

Larger winter sub-groups may have anti-predator value to sheep. It is generally accepted that predation was a major factor in the formation of ungulate groups (Ewer 1968, Leuthold 1977). Wolf predation has been argued as being responsible for the formation of large winter groups in white-tailed deer (Nelson and Mech 1981) and roe deer form larger groups in Winter due to the lack of cover; an indirect anti-predator response (Bresinski 1982). Domestic sheep have existed under relaxed predation pressure for many thousands of years, and increases in winter sub-group sizes cannot be related directly to predation pressure. Larger winter sub-groups maybe however an atavistic anti-predator behaviour. Lawrence and Wood-Gush (1982) found that store lambs feeding in a tall, dense brassica crop looked up more often and had smaller nearest neighbour distances than lambs feeding in an equally tall but less dense crop. This finding and the suggestion of Martin (1964) (discussed in Chapter 6) that the diurnal movement pattern of sheep is a form of anti-predator behaviour, indicate the importance that atavistic anti-predator behaviour may have as a causal factor underlying grouping in sheep.

There are however theoretical reasons for believing that anti-predator behaviour could not have been wholly responsible for the evolution of large winter sub-groups in sheep. Pulliam (1973) produced a model showing that the probability that an approaching predator would be detected increased rapidly with group size at small group sizes, but quickly levelled off as group sizes increased. Groups of bighorn larger than 5 members show little increased benefit in terms of smaller numbers of feeding interruptions to scan for predators and increased foraging efficiency (Berger 1978b). Further Crisler (1956) considered that caribou (<u>Rangifer arcticus</u>) were more easily caught by wolves when in large herds because they could not see the wolf's approach. Leuthold (1977) has suggested that predation sets the lower limit of gregariousness in ungulates and intra-group competition the upper limit. Functionally therefore it seems that large winter groups of northern ungulates are unlikely to be wholly an adaptation to predation.

Hunter and Milner (1963) proposed that the increase in sub-group size in winter was an adaptation to improve ewes' chance of being mated at the rut. More recently Jarman (1974) has suggested that in antelope, feeding style and group size dictate the probability of females being found in a given place at a given time, and that this probability of female location determines male mating strategy. It seems therefore that large winter sub-groups form in response to changes in ecological parameters and are then the focus of the mating behaviour of the male, rather than being formed in direct response to the rut.

One last aspect that must be considered is the effect of weather conditions and the requirements for shelter on sub-grouping in sheep. Blaxter <u>et al.</u> (1963) have shown in sheep that considerable heat losses result from winds as low as 16 km/hr. In the field hill sheep have been found to consistently seek shelter when wind speeds exceed 38 km/hr (Munro 1962). It was noticeable that the area occupied through autumn and winter by the Howlet home range group was in the lee of the prevailing SW winds (see Figures 3.7 to 3.10). Thus although winter forage (ie principally heather and <u>Agrostsis-Festuca</u> species poor swards (Hunter 1962; Martin 1964; Milne 1974) can be widely available (see for example Figure 2.2), if conserving heat is of importance to sheep, the localities where they can graze with a minimum of heat loss maybe limited. In addition it was noted that in bad weather sheep tended to form larger sub-groups, although Clutton-Brook et al. (1982) found the opposite effect in red deer. It may be that in addition to responding as a group to a vegetation x climate interaction, sheep also attempt to seek shelter from one another by forming larger sub-groups.

In conclusion it seems likely that the increase in sub-group sizes in winter is largely in response to reduction in the dispersion of preferred resources. The effect of prevailing weather conditions is most probably to limit the area over which the sheep can forage in winter without incurring excessive heat losses. There is not enough evidence at present to predict the cost of intra-group competition in these winter groups. Some increase in group size may have an atavistic anti-predator value to the sheep, but this cannot it seems account for the formation of winter sub-groups of 20 or 30 animals. The breeding season can probably be discounted as a causal factor underlying larger winter groups. Sheep may gain some shelter benefit from sub-group members.

The results in this Chapter illustrate the proximal behavioural mechanisms underlying larger winter sub-groups. Ewes in the winter phase are strongly influenced in their movements by other group members as seen for example in the synchrony of movement of group members, the occurrence of allelomimetic walking and the use of cohesive grazing movements (see Chapter 6 for a description of group movements to the feedblock).

Finally it is worth considering the possibility that artificial selection has increased the motivational basis of group behaviour in sheep. Estes (1974) has recognised that grouping in ungulates has a 'psychological' basis, as evinced by the uneasiness expressed by animals separated from the group. If artificial breeding has selected for a greater grouping tendency then under the conditions prevailing in winter, where resources are not dispersed, hill sheep may form larger sub-groups than would be the case if they were still only under natural selection. This enhanced grouping tendency may have adverse effects through high grazing pressures found within sub-groups which are larger than those that would be optimally selected in the wild animal.

5:4:2 <u>The Summer Phase</u>

The digestibility of hill grasses is high when they commence growth (Black 1967) and sheep in summer respond by grazing the Agrostis-Festuca swards in preference to others (Hunter 1962; Martin 1964; see Chapter 6). Grass swards are often widely distributed in small and large clumps on the hill, as in the present study site (see Figure 2.2). At this time of year Hunter and Milner (1962) described sheep as being more dispersed. In Chapter 3 it was suggested that there were 2 behavioural components involved in this summer dispersion. The first, described in Chapter 3, was the expansion of the area used by the home range group into a summer range. An expansion of the area used by the group could obviously lead to a greater dispersion of the group members, but not necessarily. The group could continue to use the larger area as large sub-groups as they have been shown to use the Winter range (see 5:4:1). In order to observe a greater dispersion of group members there must also be change in grouping behaviour. It was illustrated in Chapter 3 that movement to the additional area of the summer range was by certain individuals only. This implies some change in grouping behaviour. However the relationship between individuals using the same areas of the summer range, as identified using cluster analysis (see Figures 3.9 and 3.15) was not discussed. Again within an area, such as that used by C1/Sum81, ewes could continue to act as a single group. The smaller sub-groups found in summer in the present study (see Table 5.1) indicate that there may be underlying changes in the social behaviour of ewes at this time. This point will be returned to, but first it is necessary to ask what benefits there might be in forming smaller sub-groups in summer.

In summer ewes are lactating and their energy requirements are high (Spedding 1973). It is also at this time of year that ewes must recover body reserves depleted by gestation and lactation (Armstrong et al. 1979). The formation of smaller sub-groups in summer may be an adaptation to allow ewes to make better use of the dispersed patches of good quality forage, leading to a reduction in feeding competition. This argument would be in agreement with Jarman's (1974) thesis that dispersion of resources results in smaller group sizes. Hunter and Milner's (1963) suggestion of territorial behaviour where dominant sheep prevent subordinates from feeding on the best vegetation, forcing them to disperse and forage elsewhere, would only apply if the resource was worth defending (Brown 1964; Horn 1968). It is now accepted that most ungulates, except those feeding on dispersed and highly nutritious browse, compete by feeding as fast as possible, as the cost of defending a relatively diffuse, widespread forage is greater than any benefit in the form of increased forage intake (Geist 1974; Jarman 1974; Broom 1981). The present study actually found a decrease in the median frequency of ewe agonistic interactions in summer (Tables 5.8 and 5.9).

It should also be noted that in African ungulates, group sizes in most species increase following the rains and decrease through the dry season in response to a diminished and more dispersed food supply. (Leuthold 1977; Underwood 1982). A similar situation has been described in desert bighorn (Leslie and Douglas 1979).

The disperson of the group in summer was achieved by an expansion of the winter range (see Chapter 3), and also an underlying change in ewes grouping behaviour. Evidence for this is found in the larger nearest neighbour distances, the decrease in the synchrony of ewes´ movements, and the lack of allelomimetic waking and cohesive grazing movements. These results indicate not only a change in spacing behaviour, but also a change in the extent to which ewes are influenced in their behaviour by other sheep. There seems in fact some justification from these results for suggesting that ewes in summer behave individually, in comparison to the strong group behaviour found in winter. As described in 5:3:3 ewes were often observed walking along paths with their lambs, considerable distances from other sheep (see Appendix 3, Figure 6 for a more detailed description of summer movements). Grubb and Jewell (1966) describe Soay ewes in summer as being extremely regular in their movements, and in the present study certain ewes were found, with only their lambs as company, to occur regularly at the same location at the same time of day (see Chapter 6). This regularity of movement in summer, performed in the absence of other ewes, indicates that ewes are following individual motivations being relatively uninfluenced by decisions concerning other adult sheep.

If we assume that anti-predator behaviour was an important factor in the evolution of grouping in sheep (see above), then the dispersion of the group in summer would appear to increase the risk of predation, albeit hypothetical predation. Perhaps more relevant to domestic sheep, is the question of how the proximal motivation to group is satisfied under the dispersed conditions found in summer. Relaxed predation may have been influential in allowing hill sheep to disperse in summer. However in winter when relaxed predation must also be considered as a factor influencing group behaviour, ewes separated from a sub-group responded quickly by moving closer to other sheep, often vocalising as they did so (see Chapter 6).

From the results presented in this chapter it would appear in fact that the presence of a lamb is crucial to the individualistic behaviour of ewes in summer. The comparison between ewes with lambs and ewe-lambs without, consistently found ewe-lambs to behave in summer in a manner more reminiscent of the winter phase with smaller nearest neighbour distances, a greater synchrony of movement and more allelomimetic walking and cohesive grazing movements (see Tables 5.3 to 5.9). The presence of a lamb was not however the only difference between these 2 age-classes. Ewe-lambs could be regarded as being immature and that their behaviour was affected by their developmental stage. In winter however, at a time when they were less developed they showed no differences in social behaviour to ewes (see 5:4:1). Further, the finding that weaned ewes immediately formed larger sub-groups than unweaned ewes (see Table 5.5), illustrated the effect that the presence of a lamb had on ewes′ sub-grouping behaviour. Also the behaviour of those ewe-lambs that gave birth to lambs that subsequently survived (Numbers 68, 73 and 75) was subjectively similar to that of ewes with lambs. Finally the only mother-daughter relationship to remain strong into the second summer of the ewe-lamb´s life was that between No 49 and her mother No 34, a yeld ewe (see Chapter 4).

There is evidence from other species that the presence of young offspring affects the grouping behaviour of adult females. Hill kangaroo females with young were found to be the least gregarious of all age/sex classes (Croft 1981). In moose, cows with calves were found to have a consistently lower frequency of association with other adults than cows without calves, throughout the period from calving in early summer to weaning the following year (Hauge and Keith 1981). Peek et al. (1974) also found moose cows with calves to be the least gregarious age/sex class.

Mother-young pairs foraging separately might intuitively be thought of as at risk from predation. In white-tailed deer, does also adopt a solitary life in summer with their fawns, but these deer live under forested conditions where it is argued protection against predation with young-at-foot is best achieved by ´freezing´ behaviour and cryptic colouration (Nelson and Mech 1981). For open grassland species such as the sheep, grouping is an important component of anti-predator behaviour (Berger 1978; see 5:4:1). However as mentioned previously, small increases in group size at small group sizes can markedly improve predator recognition and consequently decrease individuals´ surveillance rates (Pulliam 1973; Berger 1978; Bertram 1978). Consequently if the lamb is thought of as a group member, as capable of spotting a predator as an adult, then a mother-lamb pair becomes a group of 2, with the chances of perceiving a predator attack being increased. In the case of domestic sheep where predation is relaxed but there still remains a strong motivation to group, the presence of a lamb may satisfy the ewe's need for a companion allowing her to act more independently of other ewes.

If the above is correct one might predict the effect to strengthen as the lamb matures, becoming more mobile and more responsive to visual and olfactory stimuli. The analysis of the sub-grouping behaviour of weaned and unweaned ewes found that even in September the removal of lambs had a marked effect on ewe sub-group size (Table 5.5). Qualitatively the contrast between unweaned and weaned ewes in September was marked, with unweaned ewes often moving independently of other group members, whilst weaned ewes not in close contact with other sheep were often evidently in distress (see 5:3:3).

It is clearly not the case that ewes in summer are completely solitary animals. The typical summer 30m sub-group size in this study was 3-4 animals (see Table 5.1). Therefore the tendency to sub-group still existed. By comparison with winter however the cohesiveness of these groups was much less and perhaps most significantly ewes were able to move between areas of their home range without requiring the presence of other adults. This flexibility of movement may be crucial in allowing the ewe to forage efficiently at this time of year.

In conclusion the dispersion of the large winter sub-groups into smaller summer sub-groups seems largely an adaptation to allow sheep to make better use of an environment where good quality feed resources are quite widely dispersed in space. Evidence suggests that ewes in summer become much less gregarious and more individualistic in their behaviour, being less influenced by the movements and behaviour of other sheep. It seems that the presence of a lamb, is crucial in allowing ewes to behave in this way. Functionally the lamb may act as any other group member increasing the probability of a mother-young pair recognising a predator. Proximally it may satisfy the ewe´s motivation to group. It is suggested therefore that with a lamb a ewe is better able to forage on the dispersed pastures found on the hill in summer.

<u>SUMMARY:</u>

1) The Howlet home range group were found to exist in 2 separate social phases. In winter the sheep were extremely gregarious and formed large sub-groups, as a result of cohesive grazing movements and allelomimetic walking movements. Of the causal factors influencing sub-group size in winter the decline in the variability of sward quality was thought most important. Prevailing weather conditions may have acted to localise the winter foraging area. Atavistic anti-predator behaviour was thought responsible for the proximal motivation to form groups, but could not be assumed to influence the formation of large sub-groups of between 10 and 30 animals. It was assumed that the mating strategy of the male would be influenced by the probability of location of ewes rather than the converse. There may also be a tendency for sheep to use one another as shelter in bad weather.

2) In summer ewes were found to be much less gregarious than in winter, forming small dispersed sub-groups. There seemed some justification in regarding ewes as behaving individualistically as there was evidence that they tended to be uninfluenced by the behaviour of other group members. The presence of a lamb was found crucial in the individualism of ewes in summer. It was argued that lambs could conceivably act as efficiently as adult sheep in locating predators, but that in the case of domestic sheep they may be more important in satisfying the ewe´s motivation to group. By behaving more individualistically ewes maybe able to respond more efficiently to the growth of nutritious but quite widely dispersed grass swards. In particular the ability of the ewe to move large distances only accompanied by its lamb, gives the ewe a flexibility in foraging behaviour that it cannot express in winter.

CHAPTER 6: HOME RANGE SIZE, SOCIAL ORGANIZATION AND THE USE OF FEEDBLOCKS

6:1 INTRODUCTION

The management of free-ranging domestic animals such as the hill ewe, presents a number of unique problems to those concerned with improving sheep farming systems. Unlike more intensive systems where behaviour is often not a limiting factor to production, under extensive conditions behaviour can be expected to have a greater significance. For example it was recognized in the 1960s that partly due to the selective grazing behaviour of hill sheep (Hunter 1962) and partly due to the limitations of stocking hills at winter carrying capacity, that the improvement of hill farming systems required separation of the grass and heath communities (Armstrong _et al._ 1979). From this realization stemmed The 2-Pasture System where improved pasture was set aside for the critical times of mating and lactation (Russel 1983)

As mentioned above the winter carrying capacity of the hill has traditionally been the upper limit to stocking rates. The number of sheep maintained on the hill over winter can of course be increased by the provision of supplemental feed. In the past hay was generally used (Hunter and Milner 1963) but more recently feedblocks have been developed to supplement the diet of hill sheep during winter (Kendall 1977). Ewes are in mid-gestation in January and the provision of feedblocks has been found to increase lamb birth weight significantly (Lippert 1983). Feedblocks contain varying proportions of cereal or molasses, minerals and extra nitrogen in the form of urea (Ducker _et al._ 1981). Attempts are made to limit the sheep's intake of feedblock, to 100-200 g/day by hardening the block, adding unpalatable ingredients and only replacing blocks once a week even if they have been consumed before this time (Lippert 1983; Ducker _et al._

1981). The main advantages of feedblocks are proposed to be that they reduce competition for concentrate feed in a group as they are constantly available, and that they allow animals to regulate intake according to their needs. However in a study of the use of feedblocks, 19% of 2931 ewes sampled, did not eat from the feedblock on offer and intake was found to be significantly affected by the age of ewes (Ducker et al. 1981).

Other workers have found indirect evidence that provision of supplemental feed to free-ranging ruminants affects their home range behaviour. Lippert et al. (1982) found that hill ewes spent more time grazing the vegetation type on which the feedblock was placed. Similarly Martin and Ward (1973) found that placement of a 3:1 meal-salt mixture increased utilization of perennial grasses in range-land cattle. As home range size has been found to be related to the dispersion of resources (Jarman 1974; Clutton-Brock and Harvey 1978) some effect of supplemental feed on home range behaviour might be predicted. However natural seasonal variation in the dispersion of resources might also lead to seasonal variation in home range size. Georgii (1980) found that roe deer occupied larger home ranges in summer than winter, as do red deer (Clutton-Brock et al. 1982). In feral goats seasonal changes in home range behaviour were at least partly in response to changes in habitat utilization (O´Brien 1984). Singer et al. (1982) found that a beech mast failure during winter brought about increases in home size in wild boar. Seasonal changes in home range size have not been studied in domestic hill sheep.

Observations of the daily movements of hill sheep that go to make up the composite measure of home range size have revealed that they possess a basic diurnal movement pattern in which they move up hill at night, and down in the morning (Hunter 1954). Seasonal variation has been reported in this diurnal pattern in Blackface sheep (Hewson and Wilson 1979; Hewson and Verkaik 1981). In both studies uphill movement was less pronounced between June and August than in March, and on one study site some sheep ceased the diurnal pattern during this latter period. Soay sheep also exhibited some seasonal variation in their diurnal movements (Grubb and Jewell 1974). The causal factors underlying sheep movements are at present poorly understood.

This chapter will analyse seasonal variation in home range size and diurnal movements. Special attention will be paid to the interaction in Winter 1982 between daily movements, home range size, social organization and the effects of feedblocks. The behaviour of ewe-lambs in Winter 1982 will also be examined in detail.

6:2 MATERIAL AND METHODS.

The scan sampling technique described in 2:4 provided the data for this chapter.

6:2:1 Analysis of Home Range Size

Many methods have been devised to estimate the size of home ranges. Conceptually the simplest of these is the convex polygon method (CPM) (Southwood 1966), which involves drawing the smallest convex polygon which contains all of the location points of an animal, and taking the area of this convex polygon as an index of the size of the animal´s home range. This method has been widely used to measure home range size (Odum and Kueunzler 1955; Dards 1978, MacDonald et al. 1980) and is a well recognised statistical technique for ordering bivariate data (Green and Silverman 1979). The main disadvantages of the CPM are that it is sensitive to sample size; it is readily affected by occasional movements on the periphery of the range and it can include large areas of land never visited by the animal (Jennrich and Turner 1969; MacDonald et al. 1980). In its favour it should with sufficient observations grow close to the true home range size (Schoener 1981).

Jennrich and Turner (1969) and Koepl et al. (1975) have derived bivariate normal models to estimate home range size (see 3:2:2). The main advantage of the bivariate normal method is that the estimate of home range size it produces is independent of sample size. However the underlying assumption of bivariate normality seems unrealistic given that the resources which govern the movements of animals are not usually evenly distributed in space. In addition the F distribution, upon which the model is based theoretically extends to infinity, another unrealistic assumption given that an animal's activity may quite suddenly truncate at the edge of its home range. Finally estimates from this method are often large in comparison to those achieved by other methods (MacDonald et al. 1980; Schoener 1981).

In this chapter the CPM was used to estimate home range size in order to make the results comparable to those obtained in other studies of home range size in sheep (Grubb and Jewell 1974; Hewson and Wilson 1979; Hewson and Verkaik 1981). In addition relativley large amounts of location data were available for analysis increasing the likelihood of a close fit between the real home range size and the CPM's estimate (Schoener 1981).

It was of interest to calculate seasonal estimates of home range size, therefore 10 multiparous ewes and 10 ewe-lambs were selected at random for each of the 4 seasons Summer 1981, Autumn 1981, Winter 1982 and Summer 1982. All data points were included in the analysis except those values that were separated from the main body of points by more than 3 empty grid squares, this criterion of exclusion resulted in very few points not being used in the analysis. The area of the convex polygon was calculated using the map-makers formula (Jennrich and Turner 1969):

$$A \text{ (Area of Polygon)} = \frac{1}{2} \sum_{i=1}^{n} (x_i y_{i+1} - x_{i+1} y_i)$$

Here (x_i, y_i) is the ith ordered location point from a total of n points. Therefore from the location points:

x_i	y_i	$x_i y_{i+1}$	$- x_{i+1} y_i$	
69	88	6072	- 5544 =	528
63	88	5292	- 5720 =	-428
65	84	5460	- 6636 =	-1176
79	84	6794	- 6300 =	494
75	86	6600	- 5934 =	666

				84

$$A = \frac{1}{2} \times 84$$

$$= 42 \text{ (grid units).}$$

Observation-area curves were used to estimate the number of observations necessary to produce a true seasonal estimate of home range size (see Appendix 2).

6:2:2 Analysis of Diurnal Movements

In order to analyse seasonal changes in diurnal movement patterns 10 ewes and 10 ewe-lambs were chosen at random and their movement patterns collated for 5 mornings and 5 afternoons in each of the 3 seasons Autumn 1981, Winter 1982 and Summer 1982. The data were taken from between the following dates:

1) Autumn 1981 : 131081 to 311081

2) Winter 1982 : 020282 to 250282

3) Summer 1982 : 170582 to 210682

Sheep were scored as having moved between one or more grid squares in an upwards direction (score = +1) or a downwards direction (score = -1). Animals could also remain in the same grid square or move along contours (score = 0). Each animal received scores (either +1, -1 or 0) for 5 mornings and 5 afternoons in the 3 seasons. These scores were summed to give each sheep a seasonal average movement score for morning and afternoon (eg +1, +1, -1, 0, 0 = +1). Wilcoxon Matched Pairs Tests were used to compare each individual's average movement scores in the morning and in the afternoon. Each average movement score for an animal is the equivalent of 20 hours of observation (eg 5 mornings x 2 scans x 2 hours). In a Matched Pairs Test therefore with 10 animals, 400 hours of observation were required.

6:2:3 <u>Analysis of Utilisation of Feed Blocks</u>

Animals were recorded during the Winter 1982 scores as eating or standing within 3m of the feedblock. For analysis of this data the group was divided into ewe-lambs (n = 17), gimmers (n = 11), 3 year old ewes (n = 9) and those ewes older than 3 years (n = 26).

6:3 RESULTS

6:3:1 Seasonal Estimates of Home Range Size

Season was found to have a strong effect on the size of ewes' home range (Figure 6.1). Ewe home ranges in Winter 1982 were significantly smaller than those in Autumn 1981 and Summers 1981 and 1982 (Table 6.1). The cumulative observation-area curves (Appendix 2, Figure 3) illustrate further the difference between summer and winter home range sizes. Ewe-lamb home range sizes were also significantly affected by season (Figure 6.1; Table 6.2) their home ranges in Autumn 1981 being significantly smaller than those in the other seasons (Table 6.2).

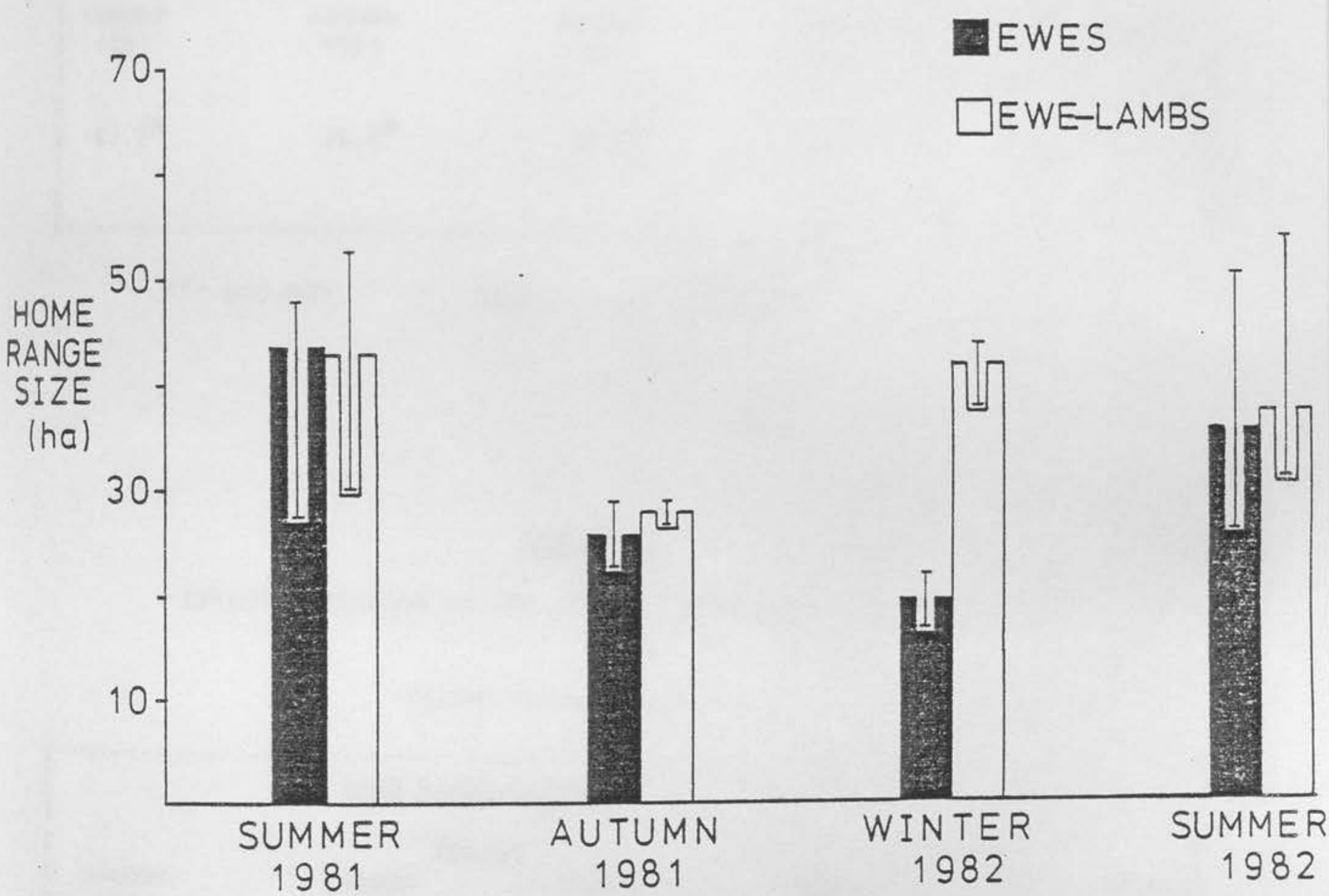
Variability in the size of home ranges was greatest in Summers 1981 and 1982 in both ewes and ewe-lambs (Figure 6.1). Ewe home range sizes in Summer 1981 ranged between 18 ha and 61.75 ha and between 20.5 ha and 63.5 ha in Summer 1982. Variation in ewe home range size was least in Winter 1982 (range 10.5 ha to 33 ha), whilst variation in ewe-lamb home range size was least in Autumn 1981 (range 25 ha to 35 ha). Despite median ewe-lamb home range size being similar in winter and summer the variation in size in winter was much less. The observation-area curves (Appendix 2, Figures 1 and 2) again illustrate the greater variability in ewe home range size in summer compared to winter.

Ewe-lamb home range sizes were significantly greater than ewe home range sizes in Winter 1982 (Mann Whitney U Test; $U = 0$, $n1 = 10$, $n2 = 10$, $p < 0.002$). There were no statistical differences between ewe and ewe-lamb home range sizes in the other seasons.

FIGURE 6.1

SEASONAL VARIATION IN EWE AND EWE-LAMB HOME RANGE SIZES

Home range estimates were derived by the convex polygon method. The values shown are medians and inter-quartiles.



EWES
EWE–LAMBS
70
50
30
10
HOME RANGE SIZE (ha)
SUMMER 1981
AUTUMN 1981
WINTER 1982
SUMMER 1982

TABLE 6.1

EFFECT OF SEASON ON THE SIZE OF EWES HOME RANGE

Those values with the same suffix are not significantly different at p< 0.01 (Mann-Whitney U Test). Values shown are medians.

HOME RANGE SIZE(ha)				
SEASON				
Summer 1981	Autumn 1981	Winter 1982	Summer 1982	Kruskal-Wallis H
43.5[a]	25.0[a]	19.5[b]	35.4[a]	16.38 ***

*** p<0.001 Sample size= 10 ewes

TABLE 6.2

EFFECT OF SEASON ON THE SIZE OF EWE-LAMBS HOME RANGES

Values shown are medians

HOME RANGE SIZE(ha)				
SEASON				
Summer 1981	Autumn 1981	Winter 1982	Summer 1982	Kruskal-Wallis H
42.8[a]	26.8[b]	42.0[a]	37.0[a]	13.75 ***

*** p<0.001 Sample size= 10 ewe-lambs

TABLE 6.3

ANALYSIS OF EWE AND EWE-LAMB DIURNAL MOVEMENTS IN AUTUMN 1981

This table shows the average movement scores for individual ewes and ewe-lambs in Autumn 1981, the values in parenthesis being the 5 movements that go to make up these scores (-= down, L= level, += up). The Wilcoxon Matched Pairs Test was used as a test of significance. Ewes and ewe-lambs were analysed separately.

AGE-CLASS	TIME OF DAY 600 to 1000	TIME OF DAY 1400 to 1800	d	Sig^{n}
Ewes	-4(----L)	3(+++LL)	-7	
	-3(---LL)	3(+++LL)	-6	
	-5(-----)	4(++++L)	-9	
	-5(-----)	-1(-LLLL)	-4	T= 0
	-4(----L)	4(++++L)	-8	
	-4(----L)	3(+++LL)	-7	n= 10
	-4(----L)	3(+++LL)	-7	
	-4(----L)	2(++LLL)	-6	**
	-3(---LL)	3(+++LL)	-6	
	-4(----L)	3(+++LL)	-7	
Ewe-lambs	-4(----L)	2(++LLL)	-6	
	-4(----L)	2(++LLL)	-6	
	-5(-----)	2(++LLL)	-7	T= 0
	-3(---LL)	3(+++LL)	-6	
	-2(--LLL)	3(+++LL)	-5	n= 10
	-2(--LLL)	1(+LLLL)	-3	
	-2(--LLL)	1(+LLLL)	-3	**
	-5(-----)	3(+++LL)	-8	
	-4(----L)	3(+++LL)	-7	
	-5(-----)	3(+++LL)	-8	

** $p<0.01$

6:3:2 Analysis of Diurnal Movements

1 Autumn 1981

Both ewes and ewe-lambs showed highly significant tendencies to differ in the direction of their movements between morning and afternoon (Table 6.3). The average movement scores for individuals show the movement to have been generally down in the morning and up in the afternoon (Table 6.3). Comparison of the average movement scores of ewes and ewe-lambs found that there was no significant difference in the strength of their diurnal movements (morning: Mann-Whitney U Test; $U = 43$, $n1 = 10$, $n2 = 10$, NS; afternoon: $U = 31.5$, $n1 = 10$, $n2 = 10$, NS).

For a visual representation of the diurnal movements of ewes and ewe-lambs in Autumn 1981 see Appendix 3, Figures 1 and 2.

2 Winter 1982

Ewes and ewe-lambs in Winter 1982 again both differed in the direction of their movements in the morning and afternoon (Table 6.4). Ewes, compared to Autumn 1981, however showed no consistent pattern of movement in the morning resulting in the majority of average movements scores being 0 or -1. Ewes generally moved upwards between 1000-1400 hours. In addition in the afternoon they showed a very strong tendency to move downhill (Table 6.4). Ewe-lambs continued to move generally downhill in the morning and to a lesser extent than in Autumn 1981 uphill at night. Comparison of the

TABLE 6.4

ANALYSIS OF EWE AND EWE-LAMB DIURNAL MOVEMENTS IN WINTER 1982.

See Table 6.3 for a description of this table.

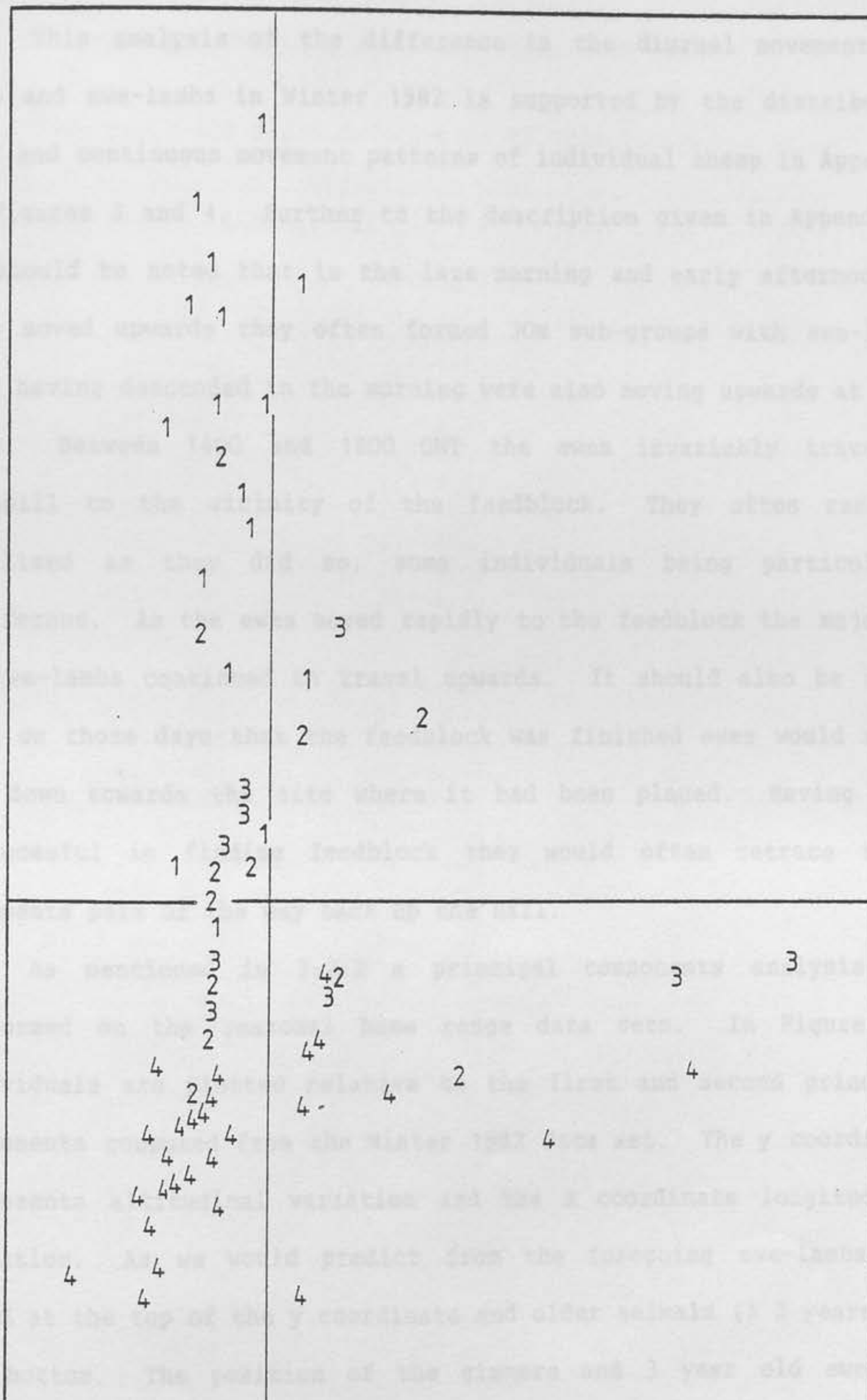
AGE-CLASS	TIME OF DAY 600 to 1000	TIME OF DAY 1400 to 1800	d	Sig^n
Ewes	-1(--+LL)	-3(---LL)	2	
	0(-+LLL)	-3(---LL)	3	
	-1(--+LL)	-3(---LL)	2	T= 0
	-1(-LLLL)	-3(---LL)	2	
	0(--++L)	-4(----L)	4	n= 10
	0(--++L)	-3(---LL)	3	
	-1(--+LL)	-2(+---L)	1	**
	-2(--LLL)	-3(---LL)	1	
	-1(--+LL)	-4(----L)	3	
	-1(--+LL)	-4(----L)	3	
Ewe-lambs	-2(--LLL)	0(+-LLL)	-2	
	-4(----L)	1(+++--)	-5	
	-4(----L)	1(++-LL)	-5	T= 10
	-2(--LLL)	-2(+---L)	0	
	-4(----L)	-2(+---L)	-2	n= 9
	-3(---LL)	1(+++--)	-4	
	-2(---+L)	1(++-LL)	-3	**
	-3(---LL)	-2(+---L)	-1	
	-5(-----)	2(+++-L)	-7	
	-4(----L)	1(++-LL)	-5	

** p<0.01

FIGURE 6.2

PRINCIPAL COMPONENTS PLOT FOR WINTER 1982

The x coordinate represents longitudinal variation in home range behaviour and the y coordinate altitudinal variation. The values correspond to the different age-classes (ie 1 = ewe-lambs, 2 = gimmers, 3 = 3 year old ewes and 4 = ewes aged 4 years and over).



average movement scores of ewes and ewe-lambs in Winter 1982 found them to differ significantly in their diurnal movement in both morning (Mann-Whitney U Test, $U = 1.5$, $n1 = 10$, $n2 = 10$, $p < 0.002$) and afternoon ($U = 1.5$, $n1 = 10$, $p < 0.002$).

This analysis of the difference in the diurnal movements of ewes and ewe-lambs in Winter 1982 is supported by the distribution maps and continuous movement patterns of individual sheep in Appendix 3, Figures 3 and 4. Further to the description given in Appendix 3 it should be noted that in the late morning and early afternoon as ewes moved upwards they often formed 30m sub-groups with ewe-lambs that having descended in the morning were also moving upwards at that time. Between 1400 and 1800 GMT the ewes invariably travelled downhill to the vicinity of the feedblock. They often ran and vocalised as they did so, some individuals being particularly vociferous. As the ewes moved rapidly to the feedblock the majority of ewe-lambs continued to travel upwards. It should also be noted that on those days that the feedblock was finished ewes would still run down towards the site where it had been placed. Having been unsuccesful in finding feedblock they would often retrace their movements part of the way back up the hill.

As mentioned in 3:2:2 a principal components analysis was performed on the seasonal home range data sets. In Figure 6.2 individuals are plotted relative to the first and second principal components computed from the Winter 1982 data set. The y coordinate represents altitudinal variation and the x coordinate longitudinal variation. As we would predict from the foregoing ewe-lambs are found at the top of the y coordinate and older animals (> 3 years) at the bottom. The position of the gimmers and 3 year old ewes is

TABLE 6.5

ANALYSIS OF EWE AND EWE-LAMB DIURNAL MOVEMENTS IN SUMMER 1982.

See Table 6.3 for a description of this table.

AGE-CLASS	TIME OF DAY: 600 to 1000	TIME OF DAY: 1400 to 1800	d	Sig^n
Ewes	-5(-----)	4(++++L)	-9	
	-4(----L)	4(++++L)	-8	
	-2(--+L)	4(++++L)	-6	T= 0
	-3(---LL)	0(+-LLL)	-3	
	-2(--LLL)	3(+++LL)	-5	n= 10
	-3(---LL)	3(+++LL)	-6	
	-3(----+)	3(+++LL)	-6	**
	-4(----L)	2(++LLL)	-6	
	-3(----+)	4(++++L)	-7	
	-5(-----)	5(+++++)	-10	
Ewe-lambs	-1(--+LL)	3(+++LL)	-4	
	-3(---LL)	5(+++++)	-8	
	-4(----L)	2(++LLL)	-6	T= 0
	-4(----L)	5(+++++)	-8	
	-1(--+LL)	3(+++LL)	-4	n= 10
	-3(---LL)	0(+-LLL)	-3	
	-3(---LL)	3(+++LL)	-6	**
	-3(---LL)	5(+++++)	-8	
	-1(--+LL)	5(+++++)	-6	
	-3(---LL)	3(+++LL)	-6	

** $p<0.01$

intermediary between these 2 extremes. Observational notes further illustrate the similarity between the movements of some of the gimmers and 3 year old ewes and the ewe-lambs. One gimmer (Number 50) was found consistently in the company of the ewe-lambs and others, principally Numbers 54, 55, 101, 113 and 114 also spent time in association with ewe-lamb peer groups. The movements of three 3 year old ewes, Numbers 1, 17 and 116, were also similar to the ewe-lambs, but these animals were only rarely found in association with the younger animals. The extent of altitudinal variation in movements in Winter 1982 therefore appears to be a direct function of age, although the causal factors underlying the distribution of the different age-classes may not be the same.

3 Summer 1982

As in Autumn 1981 both ewes and ewe-lambs showed a significant tendency to move downhill in the morning and uphill at night (Table 6.5). Comparison of ewes and ewe-lambs found no difference in the strength of their movements in the morning ($U = 35$, $n1 = 10$, $n2 = 10$, NS) or the afternoon ($U = 46$, $n1 = 10$, $n2 = 10$, NS).

Appendix 3, Figures 5 and 6 illustrates visually the locations of group members at different times of day and the continuous movements of individual sheep in Summer 1982. The movements of individual sheep could be extremely regular during the summer. Individuals such as Numbers 20, 28 and 45 were found to occur repeatedly with only their lambs, at the same location at the same time of day over a considerable number of days. Other individuals, such as Numbers 39 and 55 would adopt a repetitive movement pattern for a period of days and then suddenly alter the pattern to encompass another area. In the case of the above animals this occurred when they moved periodically from the south side of the reservoir to the winter range and then back again.

6:3:3 Analysis of Age Differences in Feed Block Utilization

1 Feeding at the block

Age was found to have a large overall effect on the frequency of eating feedblock (Figure 6.3; Table 6.6). Ewe-lambs, gimmers and 3 year old ewes were all observed eating less feedblock than ewes aged 4 years or more (Table 6.6). The age effect on feedblock utilization was further underlined by the percentage of the separate age-groups observed eating feedblock; 11% (2/17) of ewe-lambs, 36% (4/11) of gimmers, 33% (3/9) of 3 year olds and 74% (20/27) of ewes aged 4 years and over were observed feeding off the feedblock on at least one occasion.

As the mean rate per scan indicates, observation of animals feeding at the block was rare (Figure 6.3). This was due to the short duration of feeding bouts. Again it should be noted that the blocks appeared extremely attractive to the older ewes as evinced by the rapid large scale movements described in 6:3:2. On 2 occasions (010382 and 170382) the farmer replaced feedblocks in the middle of afternoon scans without disturbing the sheep, placing the blocks at the bottom of the range. On both occasions the sheep found the blocks the following morning and after only a short period many of the group had fed at the blocks.

FIGURE 6.3

FREQUENCY WITH WHICH DIFFERENT AGE-CLASSES ATE AND STOOD NEAR THE FEEDBLOCK.

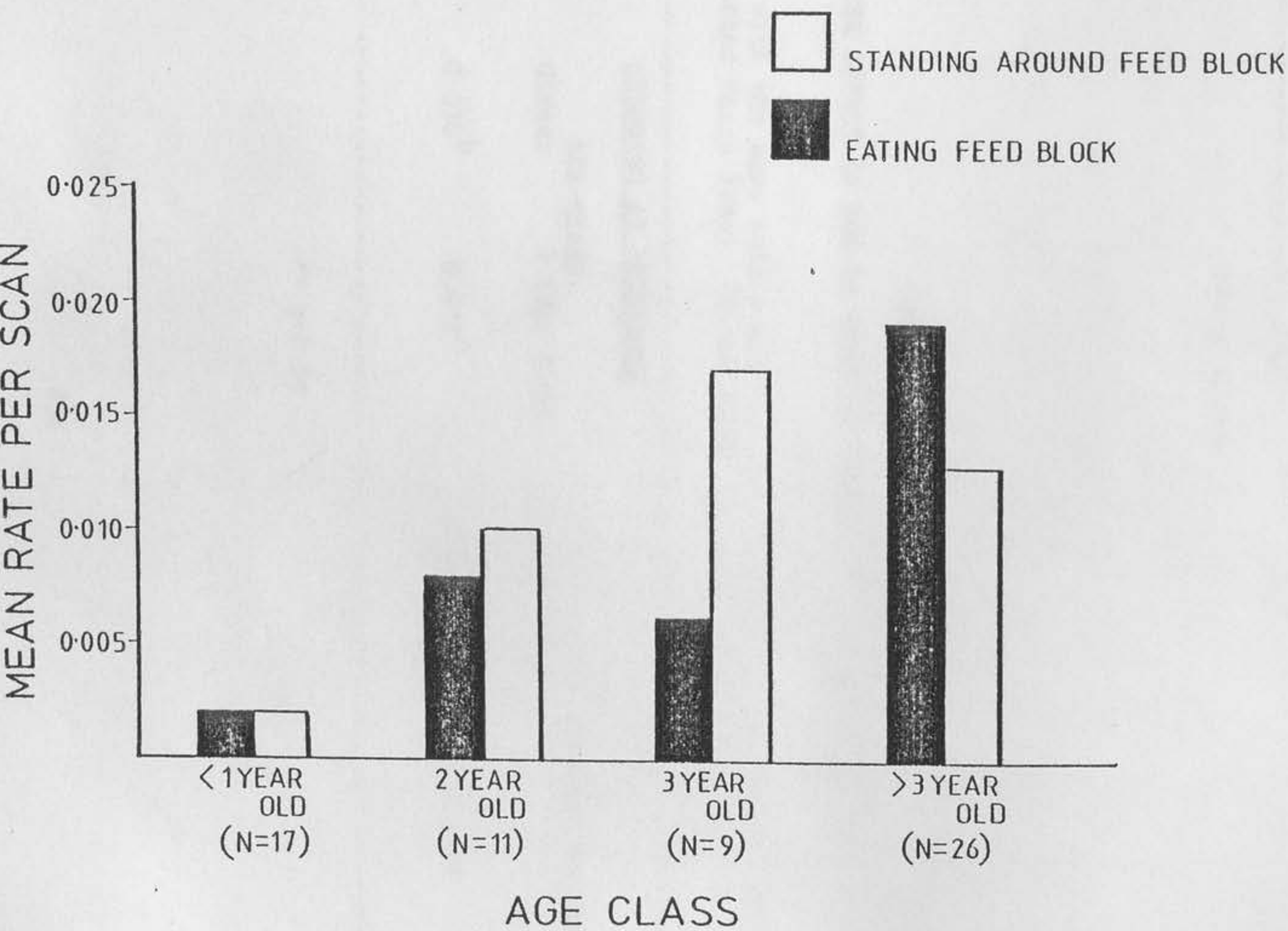

STANDING AROUND FEED BLOCK
EATING FEED BLOCK
MEAN RATE PER SCAN
0·025
0·020
0·015
0·010
0·005
<1YEAR OLD (N=17)
2YEAR OLD (N=11)
3YEAR OLD (N=9)
>3YEAR OLD (N=26)
AGE CLASS

TABLE 6.6

ANOVA OF THE EFFECT OF AGE ON EATING FEEDBLOCK

Those values with the same suffix are not significantly different at p <0.01 (Wilcoxon Matched Pairs Test). Values shown are mean rates/scan.

EATING FEEDBLOCK

AGE-CLASS				
Ewe-lambs	Gimmers	3 Year Olds	>3 Year Olds	Kruskal-Wallis H
0.002[a]	0.008[a]	0.006[a]	0.019[b]	16.833 ***

*** p <0.001

TABLE 6.7

ANOVA OF THE EFFECT OF AGE ON STANDING WITHIN 3M OF THE FEEDBLOCK.

Those values with the same suffix are not significantly different at p <0.01 (Wilcoxon Matched Pairs Test). Values shown are mean rates/scan.

STANDING AT FEEDBLOCK

AGE-CLASS				
Ewe-lamb	Gimmer	3 Year Olds	4 Year Olds	Kruskal-Wallis H
0.002[a]	0.010[b]	0.017[b]	0.013[b]	10.423 **

** p<0.01

2 Standing at the block

Age was found also to have an overall effect on the frequency with which animals stood near the feedblock (Figure 6.3; Table 6.7). Ewe-lambs stood near the block significantly less than other age-classes (Table 6.7)

Standing near a feedblock could occur for different reasons. An animal could be about to feed or have just fed, or an animal could be being prevented from feeding. Observations showed that competition at the feedblock was considerable. Certain animals could be seen to repeatedly displace others from the feedblock (eg Numbers 18, 26 and 48). These individuals subjectively appeared to spend more time in the vicinity of the block than other sheep and in addition they were were judged as being amongst the largest animals in the group. Some quantitative support for the hypothesis that the extent to which certain individuals were found standing near the feedblock may have been a result of feeding competition, comes from a significant negative rank correlation between standing at and feeding off the block, for animals that were seen to do either at least once (Spearman Rank Correlation Coefficient: $r_s = -0.3179$, $t = 2.065$, $df = 38$, $p < 0.05$).

6:4 DISCUSSION

6:4:1 Seasonal Variations in Home Range Size and Daily Movements

1 Summer

In Chapter 5 it was argued that the dispersion of preferred Agrostis-Festuca swards was influential in the formation of smaller summer sub-groups as dispersion would lead to reduced feeding competition and to increased forage intake. Clutton-Brock and Harvey (1978) have argued that where feed resources are aggregated in large irregularly distributed clumps, animals will occupy larger home ranges. Thus the larger summer home ranges of the red deer population on Rhum are associated with a reduction in the extent to which the high altitudes were used and an increase in the amount of time spent grazing on Juncus marsh and Molinia grasslands on the glen bottoms (Clutton-Brock et al. 1982). Similarly in the present study median home range size was largest in summer for both ewes and ewe-lambs (Figure 6.1; Table 6.1 and 6.2). Sheep in late spring and summer have been shown to have an overall preference for grass over other hill swards (Hunter 1962; Martin 1964; see Table 3.4). In the present study site Agrostis-Festuca species-poor and species-rich swards formed the bulk of the hill pasture, and much of these were found at either end of the reservoir and on the south side of the reservoir (see Figure 2.2). Therefore the increased sizes of home ranges in summer in the Howlet group would seem at least partly a response to the location of the hill pastures.

However the distribution of resources alone cannot explain the large increase in the variability of home range size found in Summers 1981 and 1982. Individuals were found to have home ranges varying by as much as 40 ha. This variability in home range size is consistent with the findings of Chapter 3 that only certain individuals expanded their range in summer. In general those individuals that moved regularly between the winter range and the south side of the reservoir, Area 4, (C2/Sum 81; C4/Sum 82) possessed the largest summer home ranges (eg Number 37: 61.75ha in Summer 1981; Number 30: 56.25 ha in Summer 1982). The type of large scale movement used by such animals is illustrated in Appendix 3, Figure 6. In contrast animals who confined themselves to either the winter range or to Area 4 had smaller home ranges. Of these, those that used Area 4 had the larger ranges as they always periodically revisited the winter range (eg Number 16: 32.25 ha in Summer 1981; Number 18: 27.5 ha in Summer 1982). Those animals that remained exclusively within the winter range tended to have the smallest summer ranges (eg Number 35: 18 ha in Summer 1981; Number 11: 27 ha in Summer 1982). Similar variability in summer home range size in Blackface has been recorded by Hewson and Wilson (1979) who measured ranges varying in size from 3.1 to 50 ha.

Factors other than the distribution of resources must therefore be responsible for the increased variability in range size. The importance of behavioural factors such as early experience and decreased gregariousness in summer in causing this variability will be discussed in relation to ecology in Chapter 7.

2 <u>Autumn</u>

In Autumn 1981 there was a decline in ewe and ewe-lamb home range size (Figure 6.1; Tables 6.1 and 6.2). There was also a decline in the variability associated with range size.

It has been shown previously that in autumn the attractiveness of heather increases relative to grass (Hunter 1962; Martin 1964; Welch 1984; see Tables 3.4 and 3.5). This seems due more to the declining quality of the hill pastures (Black 1967) than to any increase in the quality of heather, which also shows a decrease in digestibility from July to September (Milne 1974). In the study site large tracts of young and old heather are found in the winter range and in Area 4 (see Figure 2.2). If as suggested by the work of Blaxter et al. (1963) energy losses in sheep due to wind velocity are significant then small home ranges may result from sheep confining their grazing to relatively unexposed heather swards such as those found in the winter range (see Figure 2.1 and 2.2). In addition sheep show reduced growth rate and voluntary feed intake in autumn and winter (Forbes 1982). These physiological changes, themselves seemingly an adaptation to ecological change (Clutton Brock et al. 1982), could proximally result in smaller home ranges through the reduction in feed requirements.

These arguments in explanation of the reduction in autumn range size are essentially those suggested for the increase in sub-group size in autumn (see Chapter 5). Seemingly the return to the winter range by all members of the group, reported in Chapter 3 is prompted by ecological change, resulting in smaller home ranges and larger sub-groups. The return to the winter range could have been a proximal response, such as sheltering, or an innate reponse to an environmental cue; a migration. Geist (1971) has suggested that bighorn sheep are internally motivated to migrate but are synchronised by external environmental factors. It was felt in the present study that the movements from the winter range in spring and back to it in autumn were better explained in terms of an endogenous rhythm than a proximal response. Both movements occurred suddenly without any noticeable change in weather or herbage quality. Moreover the distribution of animals once established continued for a number of months as one would predict from a seasonal migration.

3 Winter

The significantly small home ranges of ewes in Winter 1982 appear attributable to the presence of feedblocks. As will be discussed in 6:4:3 and 6:4:4 the majority of ewe-lambs neither ate, stood near nor moved towards the feedblock (See Appendix 3, Figures 3 and 4). It seems that as a result of this their winter home ranges were significantly larger than ewe ranges (see 6:3:2). The downhill movements of ewes in the afternoon resulted in them spending the night in close proximity to the block (Appendix 3, Figures 3 and 4; Table 6.4). Observational notes taken at the time recorded the apparent attraction of ewes to the feedblock, with movements to it often being at the run and accompanied by vocalisations.

That the feedblocks significantly reduced home range size suggests that the block was supplying at least the equivalent in nutrients to the size of the area no longer grazed by the ewes. However as sheep at this time of year have been shown to be highly gregarious (Chapter 5), the group movements to the block could have been elicited by specific sheep which expressed a high 'attraction' to the block. It was noted that certain individuals were particularly vociferous when moving to the block. These sudden and rapid movements of the group to the block could, it seems, result in the disruption of grazing behaviour for some members of the group. Thus the small home range size of the ewes in Winter 1982 need not necessarily imply that all individuals had a range large enough to supply the optimal amount of nutrients under the prevailing conditions. This effect could be compounded for younger ewes by them being prevented from eating at the block by older animals (see 6:4:4).

An effect of the reduction in ewe home range size was to cause overexploitation of the herbage in the vicinity of the feedblock. The feedblocks tended to be placed on old heather, which is particularly susceptible to overgrazing and trampling (Milne 1984), and in the following summer heather plants in the locations where the feedblocks had been sited could be seen to have died. In addition to causing damage to heather swards, feedblocks in this study clearly did not allow ewes to make a fuller use of the available forage; a supposed point in favour of their use (Ducker <u>et al.</u> 1981). Finally a disproportionate quantity of faeces could be seen to have collected at the sites where the feedblocks were placed. In addition to obvious effects on the return of nutrients to other areas of the hill, this also resulted in these heavily dunged areas being avoided by sheep for many months.

6:4:2 <u>The Diurnal Movement Pattern</u>

Welch (1981) suggests that the diurnal up-and-down movement pattern is an innate response modifiable by strong needs. This study supports this conclusion although the term 'need' might be more accurately replaced by 'motivation', as the term motivation invokes a learning response (Adler 1979). That the behaviour is innate is suggested by its occurrence in 2 such geographically separated populations as St Kilda (Grubb and Jewell 1974) and the mainland of Scotland (Hewson and Verkaik 1981; the present study). The reversal of the pattern in Winter 1982 and the modifications to it in the other seasons in reponse to changes in the distribution of resources (see Appendix 3, Figures 1 to 6), indicates elements of learning and responsiveness to changes in causal factors such as feed supply. Other studies (Hewson and Wilson 1979; Hewson and Verkaik 1981) have also found seasonal changes in the basic pattern.

Welch (1981) found it hard to imagine any adaptive value to the diurnal pattern as it involved considerable effort for little, if any, apparent reward. Martin's (1963) suggestion that it is a form of atavistic anti-predator behaviour remains the most acceptable explanation of this behaviour. Other possibilities, for example that there may be advantages to the indivdual in the synchronization of its movements with other members of the group, or that the sheep may gain shelter from one another do not serve as explanations of why the animals should move uphill towards night.

In an agricultural context the greatest significance can be attached to the effect that placement of preferred resources can have on the basic diurnal movement pattern of hill sheep.

6:4:3 The Behaviour of Ewe-Lambs in Winter 1982

In Chapter 4 the belief that domestic ewe-lambs form permanent social bonds with their dams was challenged, on the basis of results from the present study and a critical examination of the literature.

It was suggested that natural weaning occurred at about 7 months of age and that from that point ewe-lambs ceased to associate with their dams, spending increasing proportions of time with peers during their first autumn and winter.

The difference between the behaviour of ewes and ewe-lambs in Winter 1982 (see 6:4:1) is not explainable in terms of preference for different hill swards, as Martin (1964) has shown that ewes and ewe-lambs in the absence of feedblocks had similar preferences throughout the year. Also it cannot be said that feedblocks directly caused the separation of ewe and daughters, as this occurred 2 to 3 months before blocks were first used. The difference would appear due the particular stage of social development of the ewe-lambs (ie formation of peer groups), reinforced by the strong effect of the feedblock on the movements of the ewes.

The ewe-lamb peer groups in Winter 1982 were generally unaffected by the movements of the older ewes. Geist (1971) similarly noted that in bighorn, lambs (male and female) from the beginning of the rut banded together into peer groups that often moved quite independently of adult ewes. He writes: "on a number of occasions a band of tamed bighorn ewes came running to me in anticipation of salt, while the lambs remained behind as a group on the rocky slope". Hansen (1965) made similar observations on captive Nelson´s bighorns. That a similar situation arose in the present study was plain from observation. In the middle to late afternoon, as the ewes customarily moved rapidly downhill to the feedblock, the ewe-lambs would continue to move uphill. This was remarkable given that the ewes vocalised loudly and ran downhill, often in full view of the ewe-lambs. The result of these separate movement patterns was that ewes spent the night in the vicinity of the feedblock, whilst the ewe-lambs camped at a considerable height away from the ewes (see Appendix 3, Figure 3).

These results are revealing to the understanding of leadership in sheep. Scott´s (1945) suggestion that older sheep tend to lead younger sheep appears a simplistic view. A point ignored in previous studies of leadership in sheep (Syme and Syme 1975; Arnold 1977) is that the decision to follow or not to follow, is as important as the decision of the first sheep to make the initial movement. Arnold´s (1977) finding that sheep tended to follow the most independent member of a flock, makes no allowance for internal motivational processes affecting the following response. The results previously obtained on leadership are, it seems, a result of only examining artificially forced leadership (ie herding) and not the naturally occurring leadership that occurs under hill conditions.

6:4:4 <u>The Utilization of Feedblocks</u>

The finding that age had a strong effect on eating feedblock (Table 6.8) is in strong agreement with direct studies of the intake of feedblock using chromic oxide as a marker (Ducker <u>et al.</u> 1981). The significantly low number of sightings of ewe-lambs eating or standing within 3m of the feedblock in the present study was clearly affected by the ewe-lambs in Winter 1982 being uninfluenced in their movements by the behaviour of the older animals (6:4:3). It should be noted however that 2 ewe-lambs (Numbers 83 and 84) almost invariably moved with the ewes to the feedblock and both were observed feeding off the block on occasion.

Gimmers and 3 year olds, although not differing from the ewe-lambs in the low number of times they were observed eating off the block, were found significantly more often within 3m of the block. This suggests that they were influenced by the presence of the block but were unable to eat as successfully of it as older ewes. However it seems that the gimmers can be separated into 2 types. Firstly there were those that behaved similarly to ewe-lambs. Number 50, for example was found a great deal of the time with the ewe-lambs whilst other gimmers (Number's 54, 55, 101, 113 and 114) all spent varying amounts of time following ewes or being found with ewe-lambs (see Figure 6.2). A lack of early experience of feedblocks may have been responsible for the behaviour of those gimmers most similar to the ewe-lambs. Pre-weaning familiarization of feedblocks and supplemental wheat has been found to have marked beneficial effect on intake when these concentrate feeds were offered in subsequent periods (Lobato and Pearce 1980; Lynch et al. 1983).

Other gimmers and 3 year olds tended to move with the older ewes to the feedblock. These animals were apparently prevented from feeding at the block, as evinced by the number of times animals in these age-classes were seen standing near the block as opposed to feeding, and the negative correlation between standing near the block and eating the feedblock. Lobato and Beilharz (1979) found that intake of feedblock was dependent on individual preference and that it was not a limiting resource. However the strong attraction of the ewes to the feedblock in the present study, indicate that the generally poor quality of the available forage enhanced the attractiveness of the blocks to the ewes and consequently increased competition. Variation in eating feedblock in this study could therefore be partly ascribed to the competitive ability of different age-classes of animal. Arnold and Maller (1974) similarly found that younger sheep were less competitive when feeding at troughs than older ones. It is not clear however, given that the majority of ewe-lambs did not feed off the block in their first winter, why a greater proportion of gimmers did not behave similarly to Number 50 and continue to remain unaffected by the presence of the feedblocks in their second winter of life. It seems that a fuller understanding of individual responses to feedblock requires a more long term study.

The older ewes also showed some variability in competitivesness. Some of the larger animals such as Numbers 18 and 48 subjectively appeared more successful at feeding off the block. This is in agreement with the findings of Dove et al. (1974) who found that social rank in wethers was related to body weight, wither height and height at the hocks. Lobato and Beilharz (1979) also found dominance in wethers to be related to liveweight and chest girth but not to wither height.

6:4:5 Practical Implications

As a result of the above behavioural factors it seems that the ewe-lambs must have suffered a reduction in growth rate, compared to the rate possible if they were receiving feedblock every day. Furthermore the lamb birthweights of gimmers and 3 year olds must have been affected by their inability to feed successfully at the feedblock.

In terms of wider implications it should be noted that it is common practice now for many hill farms to over-winter ewe-lambs on low ground. Therefore the same sequence of events observed in the Howlet group could not occur. However as the off-wintered ewe-lambs may still receive no early experience of feedblock, lack of early experience could still affect either their acceptance of feedblock or their ability to compete at the block in later years. In any event even with experience of competing for feedblock younger animals may still fare less well than older animals.

General solutions to these problems might be to train ewe-lambs to eat feedblock by holding them in a small paddock for a number of days (Speedy, 1980). The placement of more than one block, separated by at least 100m might reduce competition. Locating feedblocks in relatively unsheltered locations might prevent the large scale alteration of movement pattern described in this chapter, by preventing the sheep camping near the block. However bad weather has the effect of reducing block intake (Ducker et al. 1981), therefore care would be required to ensure that the benefit of the use of feedblocks was not lost. Finally a greater rotation of the location of feedblocks than was practised in the present study, including placing blocks on the upper part of the range, might ensure a better utilization of available forage and perhaps avoid the wasteful mass movements to the block on those days when the block was finished.

It does seem that if the use of feedblocks is to be continued further ecological, behavioural and nutritional data is required to ensure the optimal method for their use in a variety of farm conditions.

SUMMARY:

1) The seasonal variation in home range size, with the exception of winter, was ascribed to ecological changes. In summer the growth of dispersed Agrostis-Festuca swards was influential in the increase in range size. However other behavioural factors, namely early experience and decreased gregariousness, are necessary to explain the increased variability in home range size at this time. It was argued that the movement by the group back to the winter range constituted a migration, as an adaptation to reductions in hill pasture quality and worsening weather. Concurrent physiological changes such as reduced growth rate and voluntary feed intake, themselves responses to these ecological changes would contribute to smaller range sizes. The small ewe home range sizes in winter seem attributable to feedblocks that altered the basic diurnal movement pattern of the ewes.

2) The diurnal movement pattern can be regarded as an innate response but modifiable in relation to seasonal changes in the

distribution of resources. Its most likely function is as an atavistic anti-predator strategy as suggested by Martin (1963).

3) The behaviour of the ewe-lambs in Winter 1982 emphasised the breakdown of the bond with their dams, a result consistent with observations on wild sheep. They were generally uninfluenced by the large scale movements of ewes to the feedblock, maintaining the basic diurnal movement pattern and occupying larger home ranges.

4) Age was found to have a significant effect on utilisation of feedblock. Ewe-lambs for the reasons given above, rarely ate, stood near or moved towards the feedblock. Most gimmers and 3 year old ewes moved with the older ewes to the block, but were not as successful at feeding off it, presumably due to competition from the older aimals. Gimmers were however variable in their response to the block. One was never observed to move with the ewes to the block and some others moved alternatively with the ewes or with the ewe-lambs. It is concluded that a longitudinal study is required to interpret individual responses to the feedblock. The practical implications of this work are discussed.

CHAPTER 7 FINAL DISCUSSION

This thesis has revealed that hill sheep have a complex social organisation, related to their ecology and with management implications. This present chapter seeks to demonstrate the broader implications of this work. It will be reviewed in relation to past misconceptions about the social behaviour of hill sheep and to the possibilities for future research.

7:1 The Nature of Home Range Behaviour

Why do hill sheep limit their activity within definite boundaries? It was argued in Chapters 5 and 6 that spacing behaviour is influenced by the nature of the resource on which the animal depends. Several studies (Odendaal and Bigalles 1979; Georgii 1980; Singer et al. 1981; Clutton-Brock et al. 1982; O'Brien 1984; Chapter 6 of this thesis) have shown seasonal variation in ungulate home range size to be related to the distribution and availability of nutrients. Further it has been suggested that territories will form only when the energy cost of defending an area is more than repayed by the benefit of having sole access to the resources of that area (Brown 1964; Horn 1968; Davies 1978). Waser and Wiley (1979) have related the spacing behaviour of several species of primates to their diverse diets, ranging from figs to insects. The diets have resulted in each species having different spacial relationships between groups, movement patterns, group sizes and intergroup encounters. Wild, feral and domestic sheep generally feed on stable, regenerating climax-plant communities (Hunter 1962; Geist 1971; Hoefs 1974; Milner and Gwynne 1974). The regenerating nature of sheep habitat would it seems provide a basis for permanent home ranges. Geist (1971; 1974) has indeed argued that the initiation of wild sheep offspring into the home range is related to the stable nature of sheep habitat, whilst the explusion of moose calves from the dams home range is due to the unpredictability of the sub-climax plant communities that form moose habitat. Thus tradition (or early experience) plays an important role in the development of home range behaviour of the ewe-lamb (see 7:1). Further Clutton-Brock et al. (1982) have argued that hinds tolerate the presence of their daughters in the group as the chances of their survival outside of the matrilineal group would be low. Although sheep groups are not matrilineal (see Chapter 4) the same argument could apply as daughters only rarely leave their home range group of origin.

Other factors however may also influence the restriction of sheeps´ movements to a home range. Workers studying sheep and cattle in flat or gently undulating terrain have apparently failed to observe home range behaviour (Lynch 1967; Dudzinski et al. 1969; Hodder and Low 1978). This effect may be due to differences in the distribution and availability of resources between hilly and flat habitats, but it may also reflect the importance of topographical features in delimiting home range areas (Roath and Krueger 1982). It is also possible that sheep have evolved a psychological need to be within the boundaries of a home range. Ruff (1969) found that heart rate in ground squirrels increased as a function of the squirrels´ distance from their burrows. Similar responses could prevent sheep from straying far beyond a boundary they are familiar with.

7:2 The Home Range Behaviour of the Individual in Relation to that of the Group

Chapter 3 examined a question raised by both the work of Hunter (1964) and Grubb and Jewell (1966); namely do individual sheep use different areas of the group home range to the same extent? The area occupied by the Howlet home range group was found to be at a minimum in winter and at a maximum in summer. These seasonal variations in the distribution of the group were called the winter and summer ranges respectively following the precedence of workers on wild sheep (Woolf et al. 1970; Geist 1971). It was demonstrated using cluster analysis that individual variability in home range behaviour within the group was similarly at a minimum in winter and increased markedly in summer. It should be noted that cluster analysis has not previously been applied to ungulate location data. Previous workers have used it to cluster association data and then presented distribution maps of associated individuals (Arnold et al. 1981; Clutton-Brock et al. 1982). Although location data does not contain information on the synchrony of range use, it does give indirect evidence of associations as animals in order to associate, must at least have similar home range behaviour. In addition there are a far wider range of options available for its analysis with Clustan (Wishart 1978), the most widely accepted cluster analysis package (Everitt 1974). Ward's method of cluster analysis, not applicable to the analysis of association data, has derived classifications from location data in this study with a high biological relevance.

The results in the present study indicate that hill sheep have evolved 2 distinct social phases. Hunter (1964, p160) wrote: 'It is difficult to decide if the members of a home range group have identical grazing patterns. The indication is that this is not so, but each sheep establishes a proprietorship over certain patches with different sheep.´ This subjective assessment of the relationship between individuals´ home ranges ignores the existence of the winter phase (see above and 7:5). As a description of the summer phase it can be expanded upon. The analysis of inter-cluster variability in Summer 1981 and1982 (Figures 3.10 and 3.16) found similarity in the locations of the 5 clusters irrespective of the membership of the clusters (Table 3.11). This suggests that the locations of the dispersed Argostis-Festuca swards provides the group with a number of grazing ´niches´ not necessarily limited to the 5 identified by cluster analysis in Chapter 3. Sheep, partly influenced by early experience (see below), occupy different niches. The rather individualistic behaviour of sheep in summer (Chapter 5) allows them the flexibility to make large scale movements between discrete parts of the niche (Appendix 3, Figure 6) accompanied only by their lambs. In effect ewes appear to adopt a number of different foraging strategies, ranging from those that remain in the winter range using small home ranges, to those that extend their range size in summer to include areas not used in winter, with the large scale movements that this entails.

Early experience can only be partly implicated in affecting the niches eventually occupied by an adult ewe of 4 years or more, as consistency of summer home range behaviour increased with age (Figure 3.17). As stated earlier in Chapter 3, in general ewe-lambs used the south side of the reservoir if their mothers had done so, there were however 4 exceptions (see Table 3.13). The lack of consistency in the summer home range behaviour of gimmers and 3 year old ewes

(Figure 3.17) may have been related to the obvious disruption to home range behaviour that ewes lambing for the first time suffered. In one extreme example Number 1 after lambing remained within the fenced area of the dam front, an area of approximately 1 ha, for a period of a month, before resuming a more normal movement pattern. Within the cohort of ewes aged 4 years and over there was evidence that consistency continued to increase with age. The effects of early experience on summer ranging patterns were therefore not immutable, and this can be seen as advantageous given that resources are bound to vary in location through time.

This description of summer home range behaviour within a home range group bears a strong resemblance to the inter-group variability described by Hunter (1964). That is that certain individuals, largely due to their early experience, limit their ranging to specific areas. Hunter (1964) illustrated that some home range groups had lower production levels than others due to them existing on poorer habitats. One result of the increased variability in summer movement patterns in the present study was that the size of individuals' home ranges could vary considerably (Chapter 6). Future work could undertake to examine to what extent the behaviour of hill sheep in summer allows individual members of a home range group to maximise forage intake. The possibility exists that behavioural factors result in certain individuals within a group foraging less successfully and consequently having poor production levels. Early experience, already dealt with, is obviously one such factor. Alternatively there may exist other behavioural correlates with the tendency to expand home range in summer. Geist (1981) has suggested that 'dispersal' individuals that gain access to better habitats through their dispersion, may be more inquisitive and roaming than individuals that do not so disperse. Variability in exploratory behaviour and fearfulness, as has been found in cattle (Dennison 1984), could be a partial explanation underlying the movements to the south side of the reservoir in this study.

Furthermore it would be of interest to examine the foraging behaviour of more closely confined sheep of different breeds, to assess to what extent intensive husbandry of sheep, with its subsequent effects on ecology, affects the expression of seasonal social phases in sheep.

7:3 The Nature of the Ewe-Lamb Bond

Chapter 4 disputed the assertion of Hunter and Milner (1963) and Hunter (1964) that the bond between the ewe and its daughter was permanent, by showing that in terms of associations the bond ceased to have apparent significance in the field beyond the 7th to 8th month of the ewe-lamb´s life. Further it was shown by experimentation that the separation was not due merely to ewe-lambs failing to recognise their dams.

This finding raises fundamental questions as to the social basis of home range groups. It has generally been assumed, following Hunter, that the supposedly permanent ewe-daughter bond was probably the single most important cohesive bond within a home range group:

´The ewe-daughter bond appears to be critical in determining social structure´ (Darling and Boyd 1977, p137).

'Hunter's work ... confirms that hill sheep form small family groups ... (Owen 1976).

'The first social bond a sheep develops is with its dam ... Once established it will usually remain intact in females until broken by separation (Arnold and Dudzinski 1978).'

There is sufficient evidence now to suggest that bonds with specific other individuals are relatively unimportant to the social cohesion of home range groups in sheep. Firstly ewes and daughters despite remaining in the same group do not form permanent relationships. Further the seasonal changes in home range and social behaviour (Chapters 3 and 5) indicate that of greater significance to the maintenance of group structure is the preference shown for an area (facilitated by early experience) and the general motivation to form sub-groups. The evidence for this is the lack of a significant relationship between the membership of clusters in summer and autumn (Chapter 3). As typical sub-group size in summer was 3-4 animals (Table 5.1), we can assume that animals found within clusters were more likely to associate than animals found in different clusters, and that some form of social bonding existed between animals using similar areas in summer. Yet on return to the winter range in autumn, the animals, on the basis of their home range behaviour, mixed at random relative to summer (Tables 3.8 and 3.12). Geist (1971) has suggested that bighorn ewes can belong to more than one home range group, again indicating that movement patterns and general grouping behaviour are stronger elements in the formation of home range groups than specific individual bonds. The finding of Arnold *et al.* 1981 that associations between individual Dorset Horns and Merinos did not extend for periods longer than 3 months further emphasizes the transient nature of individual relationships in sheep.

It was argued in Chapter 4 that predation may have selected for behaviour patterns that facilitated the formation of larger groups in sheep. Separation of the ewe and daughter and formation by the ewe-lamb of a number of relatively weak bonds, principally with peers but also with other older sheep in the group, may have been 2 such behavioural processes. This rather fluid social structure in turn, it seems, must have been an important factor in the domestication of sheep.

7:4 Social Phases

´Domestic sheep vary considerably in their flocking behaviour, from the close-packed ´mobs´ of grazing Merinos, to the almost solitary roving of ... the Scottish Blackface. Scottish Blackface lambs are too dispersed to play very much and the adults do not form flocks´ (Ryder 1983, p7).

It is a commonly stated view that one of the important features of hill breeds is that they split up into small sub-groups and that this favours the better utilization of the irregularly distributed hill swards (Owen 1976). As has been found in Chapters 3 and 5 and discussed in 7:2 this is broadly true for the summer phase only. In autumn and winter, it seems largely as a response to the decline in the variability of sward quality and worsening weather, sheep show an increased gregariousness. This increased sociability results in a greater synchrony of movement patterns (Chapter 5) and consequently it seems in a decrease in the individual variability in home range behaviour (Chapter 3). There seems little justification in regarding either one or other of these seasonal phases as 'normal' Blackface behaviour. Both are the animal's response (adaptation) to current ecological circumstances.

Some of the possible causes and effects of the increased variability in social and home range behaviour in summer have been dealt with previously (7:2). One possibility not discussed is that the spacing behaviour of the ewe in summer is a response to a change in hormonal titres. Emlen (1952) suggested that flocking responses in birds have a neural basis, and are influenced by hormonal factors only as these stimulate disruptive responses associated with sexual or parental activity. In the same way increased levels of prolactin in the ewe as a result of suckling (Mepham 1976), may be a proximal cause of the decrease in sociability in summer. However, although prolactin has been implicated previously in some physiological aspects of maternal behaviour in birds (Hinde 1970) there is no available evidence that it affects spacing behaviour. Furthermore a recent attempt to implicate gonadotropin in changes in spacing behaviour in the squirrel monkey (Saimir sciureus), did not met with success (Burke et al. 1981).

7:5 The Use of Feedblocks

The provision of winter feed is a crucial aspect in the improvement of traditional hill farming systems. It allows a greater number of animals to be kept on the hill during the winter period which in turn means that there is a greater number of animals available to graze the abundant summer growth. The poor quality of summer herbage on hills is partly a result of under-use (due to the limits set by winter stocking rates) and the accumulation of dead herbage (Owen 1976). It would seem from the results of Chapter 6 that feedblocks were developed rather more for the convenience they afford shepherds in the difficult task of feeding hill sheep in winter, rather than for their ethological and ecological aptness. The main advantages, other than ease of handling, that they are claimed to have are negated by the social organization of hill sheep.

Feedblocks are claimed to reduce competition for food in groups as they are freely available at all times (Ducker *et al.* 1981). This is not the case as gimmers and 3 year olds were apparently prevented from feeding off the block by the older ewes (Chapter 6). It should be stressed again that behavioural observations of feeding rate (Chapter 6) closely match the direct measurement of intake using chromic oxide (Ducker *et al.* 1981). The gregarious nature of hill sheep in winter ensures that the feedblock is not freely available to individual sheep when they wish to feed off it, as single animals moving towards the block cause other animals to follow (Chapter 6). It is also claimed that animals are able to regulate their intake of block according to their needs. However Ducker *et al.* 1981 found those animals in good condition ate more than those in poor condition. As they point out this could have been due to ewes being thin because they ate less block, or the converse. It seems that further work is required to ascertain the nature of dominance during the winter phase, and its effect upon ewe condition and the ability to compete for supplemental feed. Finally feedblocks are also said to allow sheep to make better use of the available winter forage (Ducker et al. 1981). It was however found in this study that the effect of the block was to significantly reduce ewe home-ranges. The significant increase in ewe-lambs home range size compared to that in autumn may indicate that, in the absence of feedblock, the continuing reduction in forage quality in winter forces a compensatory increase in ranging as suggested by Grubb and Jewell (1966). This further emphasizes that feedblocks do not encourage wider use of winter herbage.

Finally the results of Chapter 6 have significance for the management of ewe-lambs on the hill during their first winter. During this time ewe-lambs will be uninfluenced by the behaviour of their dams and other older ewes. As mentioned previously ewe-lambs are commonly off-wintered on low ground where their feeding management can be controlled (Cunningham 1982). However on return to the hill the work of Hunter and Davies (1963) suggests that ewe-lambs may form home ranges on the periphery of existing ranges and probably on poorer habitat. It seems that if ewe-lambs are to be off-wintered the formation of home range groups must be prevented by fencing, giving control over movements and feeding management. If this added expense is to be avoided then greater attention must be given to methods of supplying supplemental feed to hill sheep in ways that do not prejudice diiferent age-classes of animal. This must involve a greater awareness of those aspects of social organization most likely to be affected by feeding management.

7:6 Concluding Remarks

It is important to determine how typical are these results of other populations of sheep. The previous anomalous position of hill sheep, with regard to the permanency of the ewe-daughter bond, can now be discounted. Evidence from Australian work on domestic sheep (Arnold et al. 1981), from feral sheep on St Kilda (Grubb and Jewell 1974) and bighorn sheep in America (Geist 1971; Berger 1979a) supports the results in this thesis that the ewe-daughter bond is short lived.

Of the complex interaction between social organization and ecology described in Chapters 3 and 5, the position is perhaps less clear. In general terms it seems reasonable to assume that provided certain conditions are met populations of sheep should behave similarly to the situation described in the present study. These conditions are:

1) Northern temperature climate with seasonal growth of herbage in late spring and summer.

2) Montane topography; valleys with running water.

3) Distribution of vegetation types similar to the present study with heaths and the less digestible grass swards at medium to high altitudes. The better grass swards being found at medium to low altitude and following both main and minor tracts of water.

These conditions do not seem uncommon in Scotland (see for example Hunter 1962; Hunter 1964) or in Northern America (see Roath and Krueger 1982). As discussed in Chapter 3 there is evidence of similarity in home range behaviour between Hunters´ (1964) study and the present work. Further Chapter 5 also confirmed the seasonal social phases described by Hunter and Milner (1963). However, there may even be similarity between the Howlet group and sheep living under rather different ecological conditions. In Chapter 3 it was shown that there was a great deal of concordance between this study and the findings of previous workers on bighorn (Mills 1937; Davis 1938; Woolf _et al._ 1970). Yet in these populations the direction of the summer expansion is upwards towards the high lying alpine pastures found in the Rocky Mountains between 3000-4000m (Buechner 1960; Shannon _et al._ 1975).

There are bound to be differences between populations of Blackface in the extent of the summer expansion, as the expansion will be controlled in part by the distribution of resources which will vary considerably, and sheep movements are learnt and passed traditionally from generation to generation. However the decrease in gregarious and the greater individuality of movements in summer appears to be an adaptation and ought to be present in all populations although its expression may be diminished by the current resource distribution.

One point made in Chapter 1 was that at present the effects of domestication and artificial selection on the behaviour of farm animals are little understood. Although this may not seem important from a practical point of view, it has been recognized that there is relatively little effort being made in creating a theoretical framework for the study of domestic animals (McBride 1984). It has been apparent in this thesis for example the difficulties of discussing sheep grouping behaviour in terms of predation, when that pressure is no longer present. To illustrate the difficulty; although sheep still group and according to theory first formed groups as an anti-predator response (Ewer 1968), I have observed the only real predator of sheep today, a fox, run through the Howlet group within metres of grazing sheep without disturbing them. Again, it is plain that no matter how many times a domestic sheep scans for predators, in or out of groups, it will have no effect on the sheep's ultimate destiny at the abattoir. These and other points, such as for example the nature of parental investment in extensively husbanded farm animals, can be examined by determining the 'goodness-of-fit' between modern ethological concepts derived from theoretical studies of natural selection and observations of the domesticated species. This approach is likely to be of more relevance to the extensively rather than the intensively husbanded animal, and would give more structure to what at present is a rather poorly defined subject in theoretical terms.

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APPENDIX 1

BEHAVIOURAL CATEGORIES

This appendix contains a description of behavioural categories recorded during focal animal samples and subsequently used in this thesis. In order for behaviour to be classed as an interaction the approacher had to come within 0.5m of the approached animal.

Cohesive Grazing Patterns:

Back Circled- Individual approached. No reaction from either individual. Approacher normally moves around approached individual and starts grazing in front or

Head Circled- As above but approach occurs in front of the approached animal.

Walk Side By Side- Occasionally the approached animal would walk beside the approacher for a number of steps.

Run Side By Side- As above but the animals would run.

Agonistic Interactions:

Butted- Animal approached and butted on head side or back.

Horn Threatened (Geist 1971)- Horns lowered and raised in an aggresive movement without touching the approached sheep.

Shoulder Shoved- Approached animal is shoved by the shoulder of an approacher.

Displaced- Approached animal is displaced from grazing by one of the above acts.

Head Displaced- Approached animal is displaced from grazing by the approacher staring to graze at the same place.

Run Head Down- After ´losing´ an interaction animal runs away from opponent with head close to the ground.

Stand Head Down- As above but ´loser´ stands with head down with back to opponent.

Front Kick (Geist 1971)- The approached animal is hit by one of the front legs of the approacher usually on underside of the chest. If the approached animal is lying down the approacher may paw at its back in order to get it stand up.

Investigatory Interactions:

Sniffed- Approached animal is investigated by an approacher which extends its nose and brings it close to the head, side, or back of the approached animal.

Nibbled- Approached animal has some of its wool nibbled or chewed by the approacher.

APPENDIX 2

OBSERVATION-AREA CURVES FOR SUMMER 1981 AND WINTER 1982.

Observation-area curves (Odum and Kuenzler 1955) were calculated for the following reasons: a) As a true seasonal estimate of home range was required and because the sample seasons were contiguous (see 2:4:1), it was felt that observations should be taken from as breif a period within a season as possible; b) It would seem advantageous from the point of view of future work to have some estimate of how many observations were necessary to achieve an accurate seasonal estimate. 6 multiparous ewes were selected at random and observation-area curves were calculated in Summer 1981 (Figure 1) and Winter 1982 (Figure 2). When the curves for the 6 ewes in the 2 seasons were averaged (Figure 3) 40 observations were found in both seasons to estimate over 90% of the area estimated by 60 observations (close to the maximum collected in all seasons). In addition by 40 observations the differential between the 2 seasons had stabilized. Forty observations were therefore used to give the estimates of seasonal home range sizes in Chapter 6.

The observation-area curves in Summer 1981 (Figure 1) again illustrate the individual variation in home range behaviour that exists in summer. There is large variation in size of home range (contrast Numbers 35 and 42). In contrast in Winter 1982 the variation in home range size is much reduced

FIGURE 1

OBSERVATION-AREA CURVES FOR 6 EWES IN SUMMER 1981

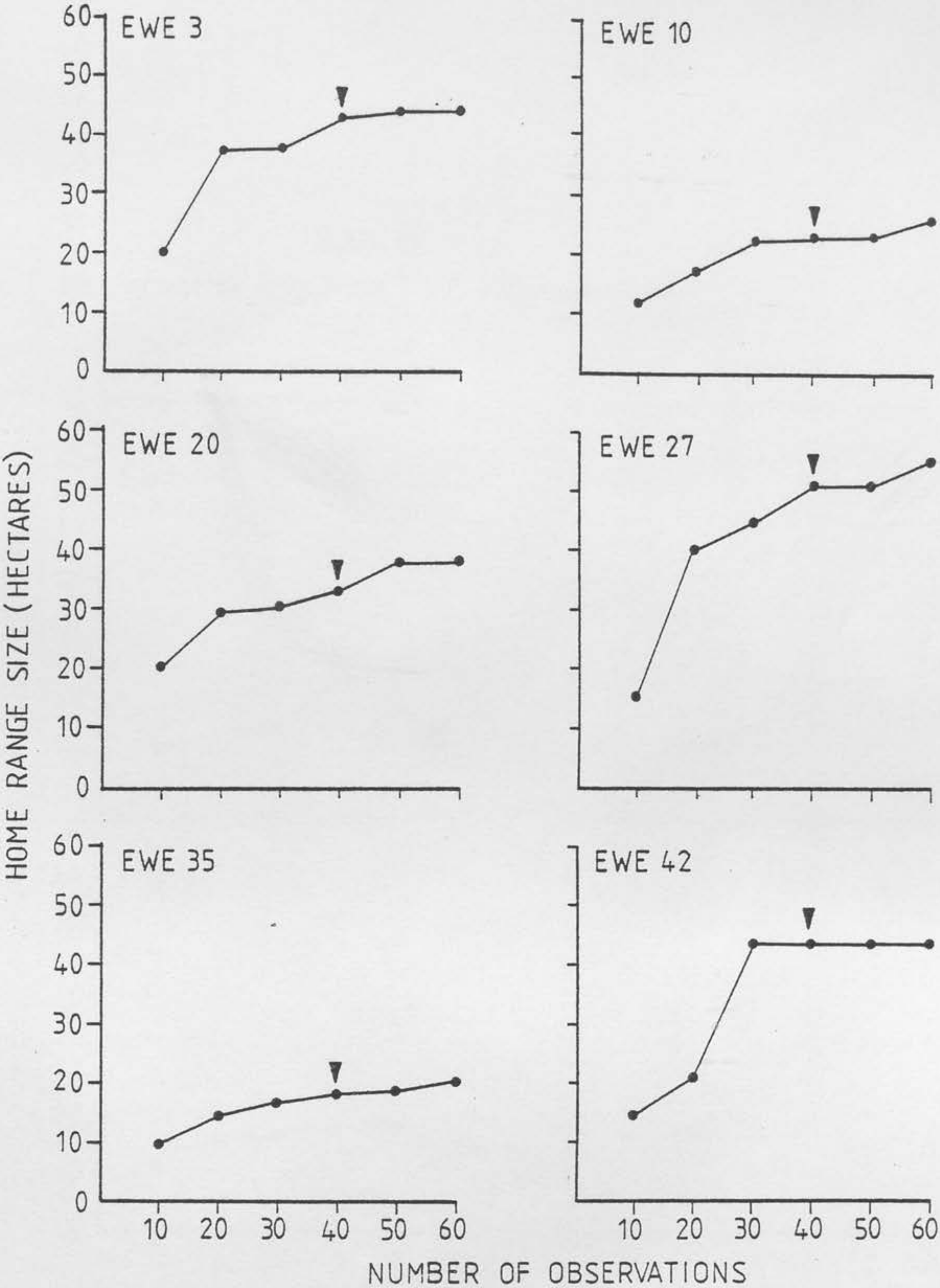

EWE 3
EWE 10
EWE 20
EWE 27
EWE 35
EWE 42
HOME RANGE SIZE (HECTARES)
NUMBER OF OBSERVATIONS
0
10
20
30
40
50
60

FIGURE 2

OBSERVATION-AREA CURVE FOR 6 EWES IN WINTER 1982.

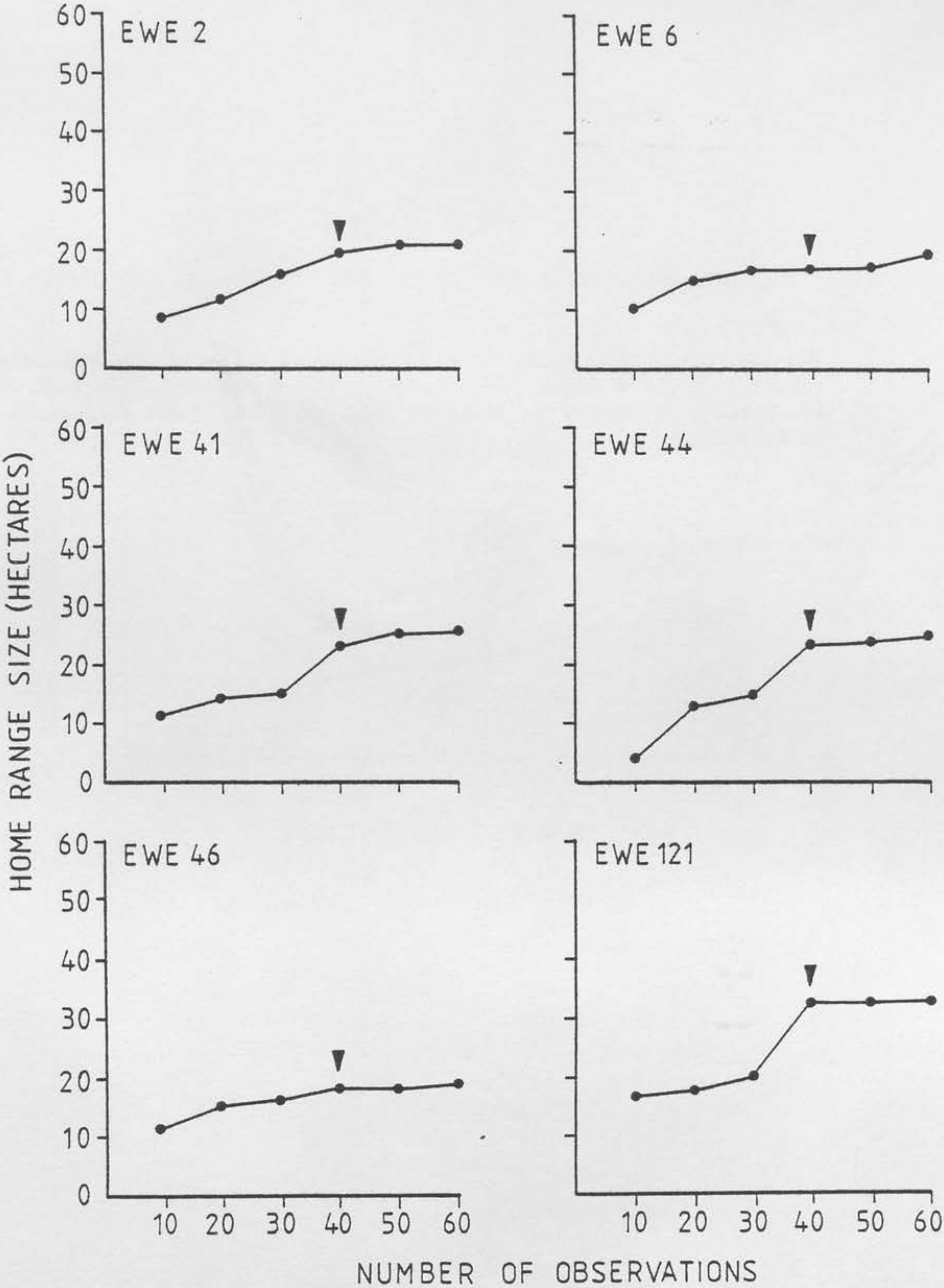
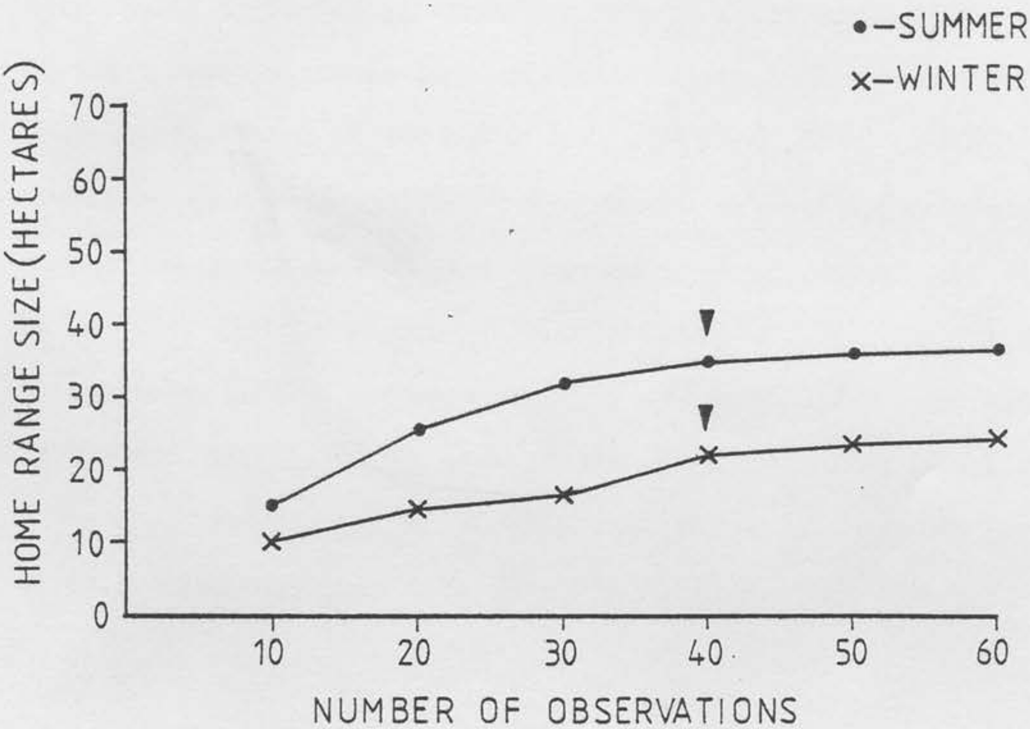

EWE 2
EWE 6
EWE 41
EWE 44
EWE 46
EWE 121
HOME RANGE SIZE (HECTARES)
NUMBER OF OBSERVATIONS
0
10
20
30
40
50
60

FIGURE 3

AVERAGE OBSERVATION-AREA CURVES FOR SUMMER 1981 AND WINTER 1982

The average observation-area curves were derived by averaging the curves for the 6 individual sheep in the 2 seasons. In both seasons 40 observations estimated over 90% of the area estimated by 60 observations.


•–SUMMER
×–WINTER
HOME RANGE SIZE (HECTARES)
70
60
50
40
30
20
10
0
10
20
30
40
50
60
NUMBER OF OBSERVATIONS

APPENDIX 3

DAILY MOVEMENTS IN AUTUMN 1981, WINTER 1982 AND SUMMER 1982.

In order to illustrate daily movements in different seasons distribution maps of sheep locations at different times of day were prepared. The different times of day were morning (600-800 GMT), mid-morning (1000-1200 GMT) and afternoon (1600-1800 GMT). Two scans were chosen at random to represent each of these times of day in each of the 3 seasons Autumn 1981, Winter 1982 and Summer 1982. From each scan the locations of 20 randomly chosen ewes and 10 randomly chosen ewe-lambs were taken. (Different numbers of ewes and ewe-lambs were chosen to approximate to the demography of the group (see 2:2:3)). In addition the continuous movement patterns of individual sheep were illustrated during selected morning (600-1200 GMT) and afternoon (1200-1800 GMT) scans in each of the 3 seasons. The above figures have been placed in an appendix to allow the reader a better visualization of points made in all 4 of the results chapters.

1 Autumn 1981

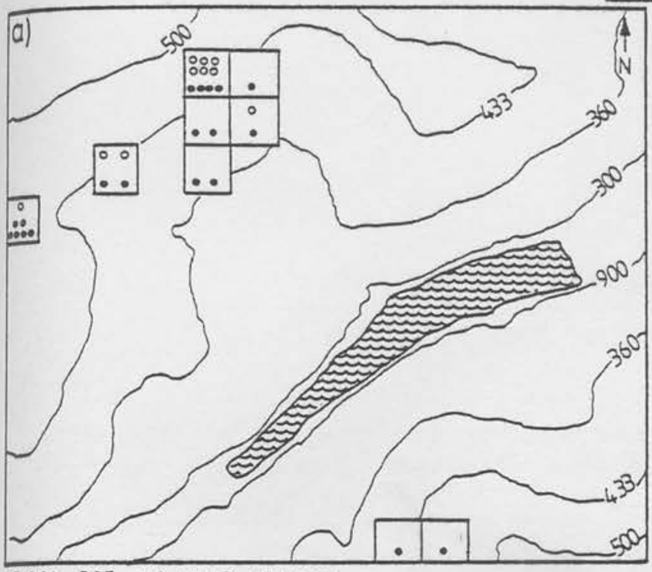
At first light the sheep were almost invariably found on high ground (Figure 1, a and b). By mid-morning they had descended but as Figure 1, c and d shows the extent of the downward movement and the degree of dispersion of the group was variable between days. In the afternoon they were again found on higher ground, although in the 2 examples given, not as high as between 600-800 GMT (Figure 1, e and f). This suggests that they continued to move upwards beyond 1800 GMT. Other points to note are the continuing occupation of the south side of the reservoir by some of the group, and the overlapping

FIGURE 1

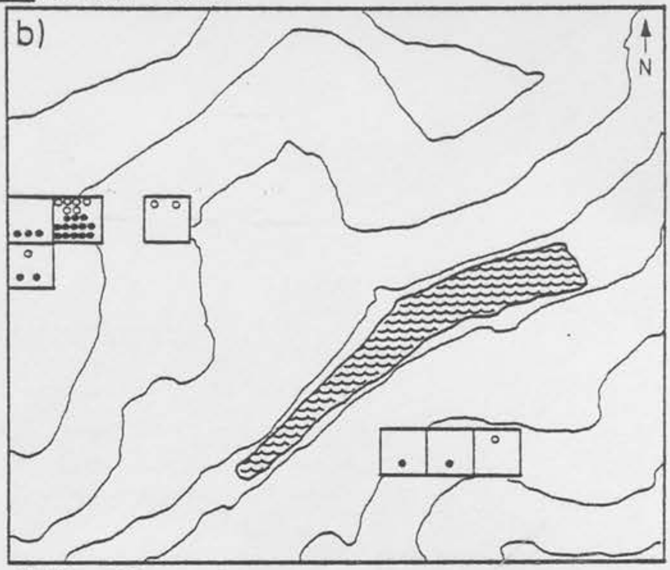
DAILY MOVEMENTS OF THE HOWLET GROUP IN AUTUMN 1981

The closed circles represent the ewes and the open circles the ewe-lambs. Only those grids which are occupied are illustrated.

MORNING (600 - 800)

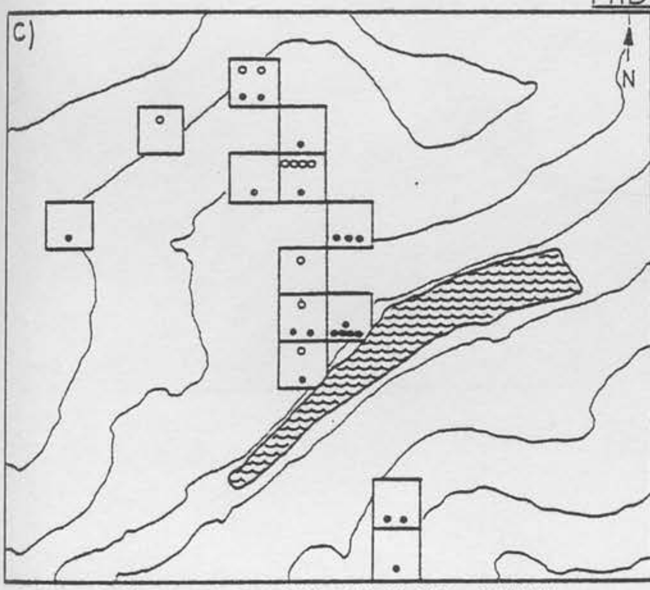


171081; 3°C; NO WIND; SUNNY

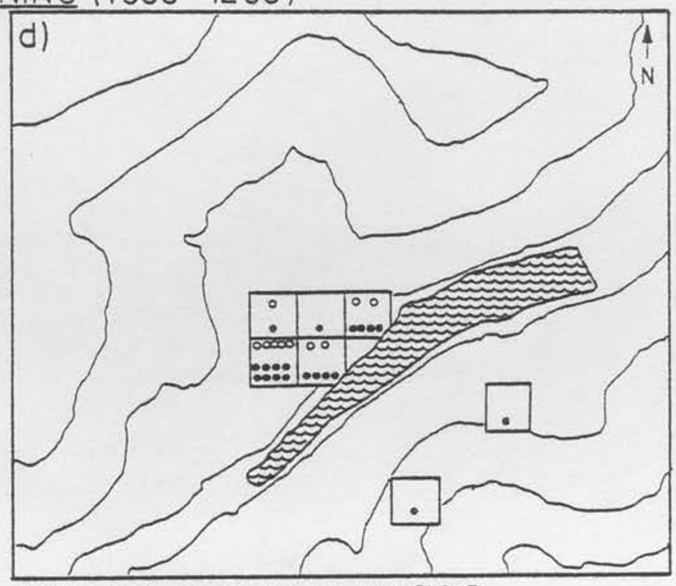


031181; 10°C; WIND FORCE 6, SOUTH; RAIN

MID MORNING (1000 - 1200)

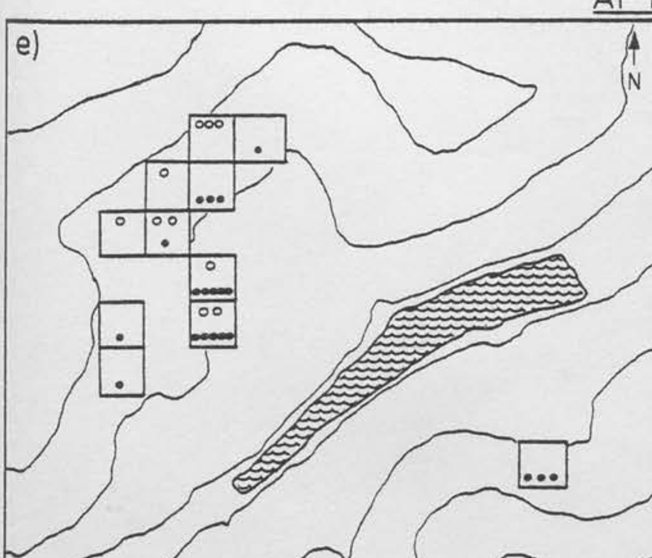


151081; 12°C; WIND FORCE 1, VARIABLE; SUNNY

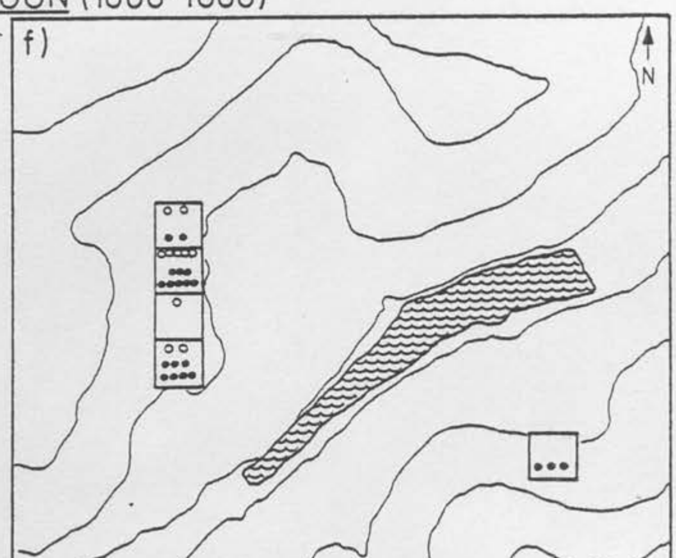


241081; 8°C; WIND FORCE 3, SW; CLOUD

AFTERNOON (1600-1800)



191081; 8°C; WIND FORCE 5, SW; SUN + CLOUD



261081; 4°C; WIND FORCE 5, SE; RAIN

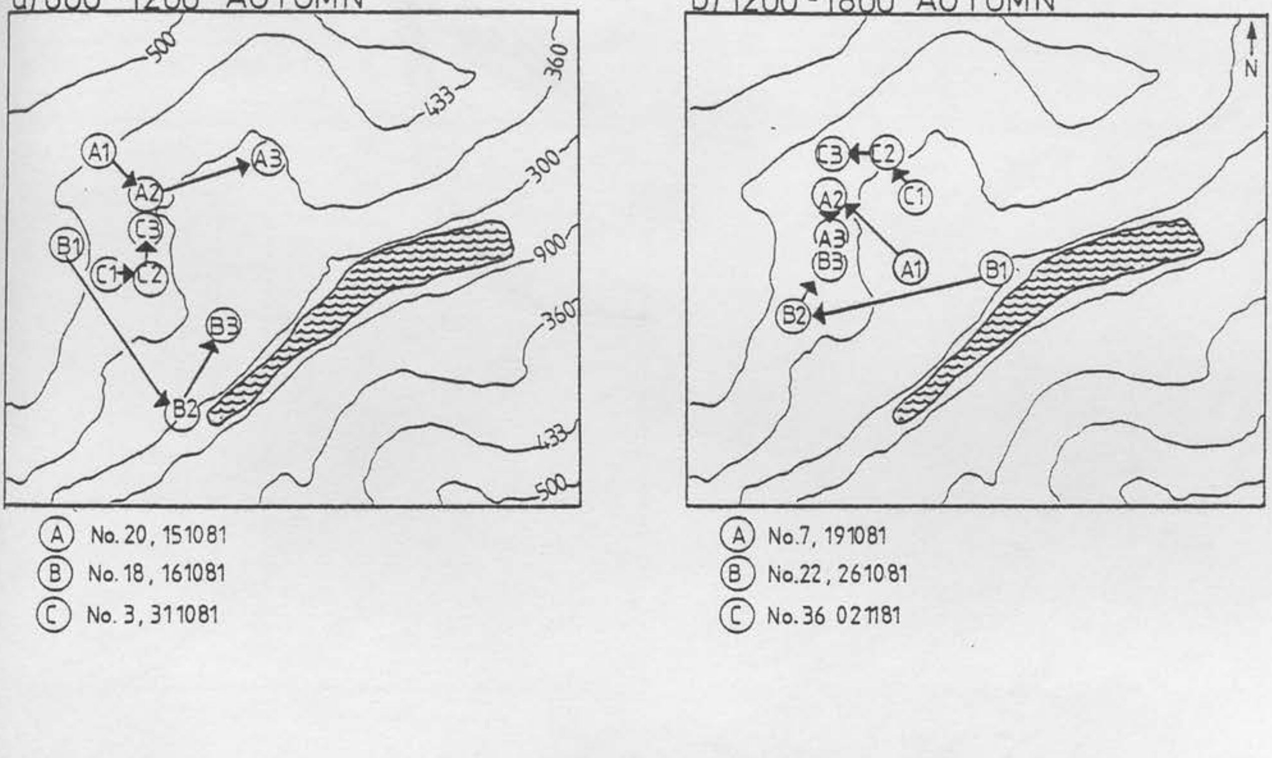
FIGURE 2

CONTINUOUS MOVEMENTS OF EWES IN AUTUMN 1981

The positions of each ewe correspond to the centres of the grid squares that they were occupying when observed. The arrows indicate the order of movement.

a) 600-1200 AUTUMN

b) 1200-1800 AUTUMN



a)
Ⓐ No. 20, 151081
Ⓑ No. 18, 161081
Ⓒ No. 3, 311081

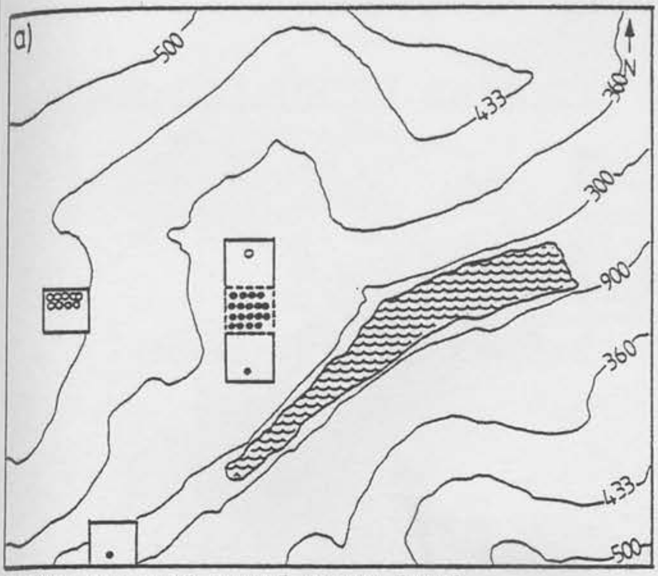
b)
Ⓐ No.7, 191081
Ⓑ No.22, 261081
Ⓒ No.36 021181

FIGURE 3

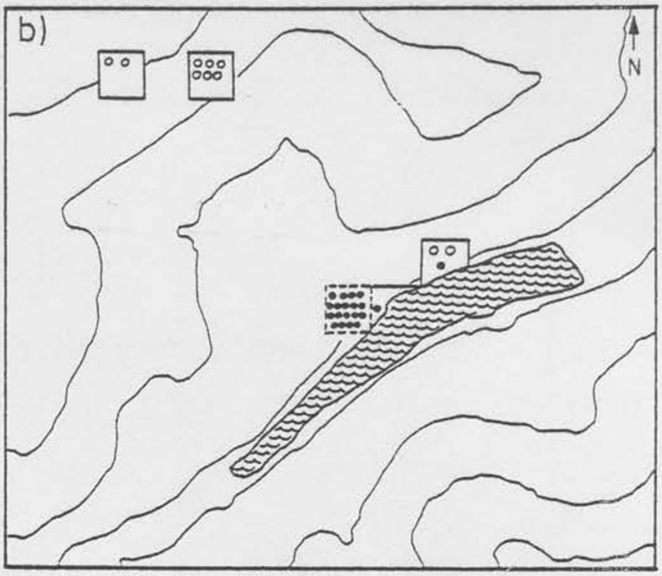
DAILY MOVEMENTS OF THE HOWLET GROUP IN WINTER 1982.

The grid square represented with incomplete sides indicates the position of the feedblock on that day

MORNING (600-800)

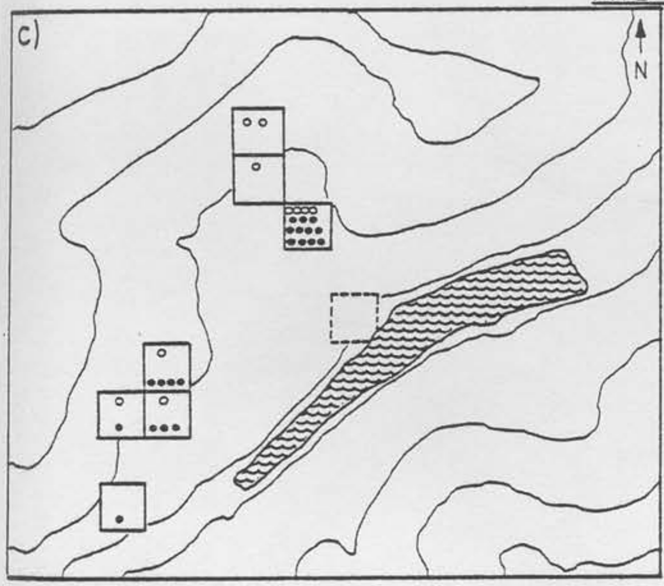


120282; 5°C; WIND FORCE 7, SOUTH; CLOUD

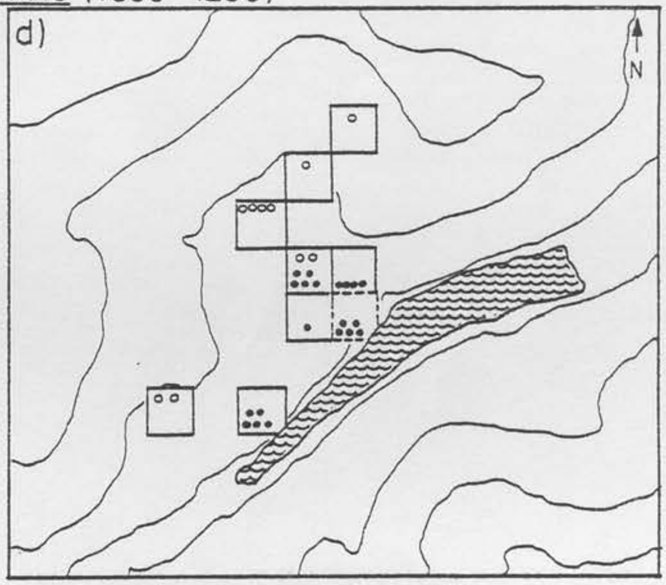


160282; −1°C; NO WIND; SUN

MID MORNING (1000-1200)

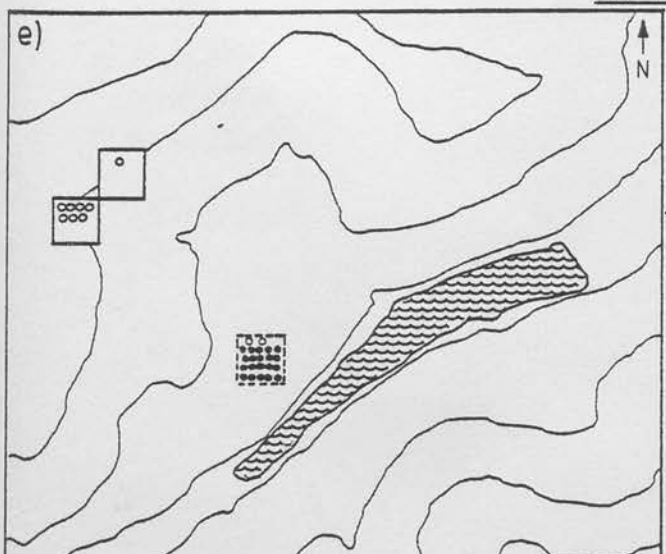


090282; 4°C; WIND FORCE 4, SE; RAIN

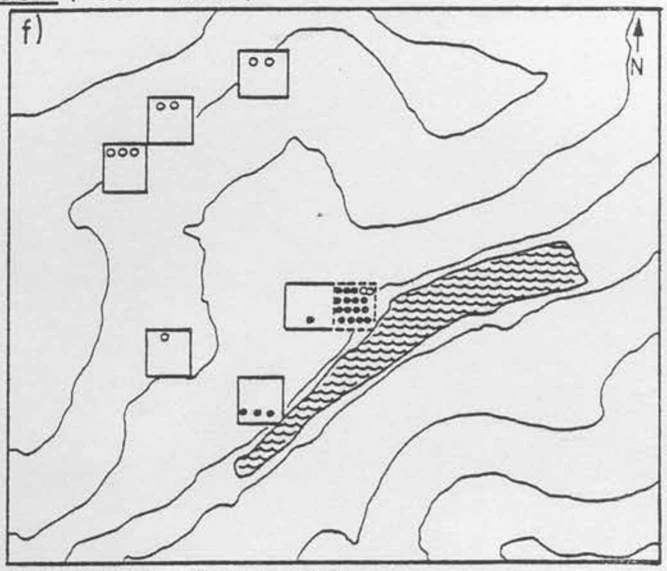


170282; 3°C; WIND FORCE 4, SE; CLOUD

AFTERNOON (1600-1800)



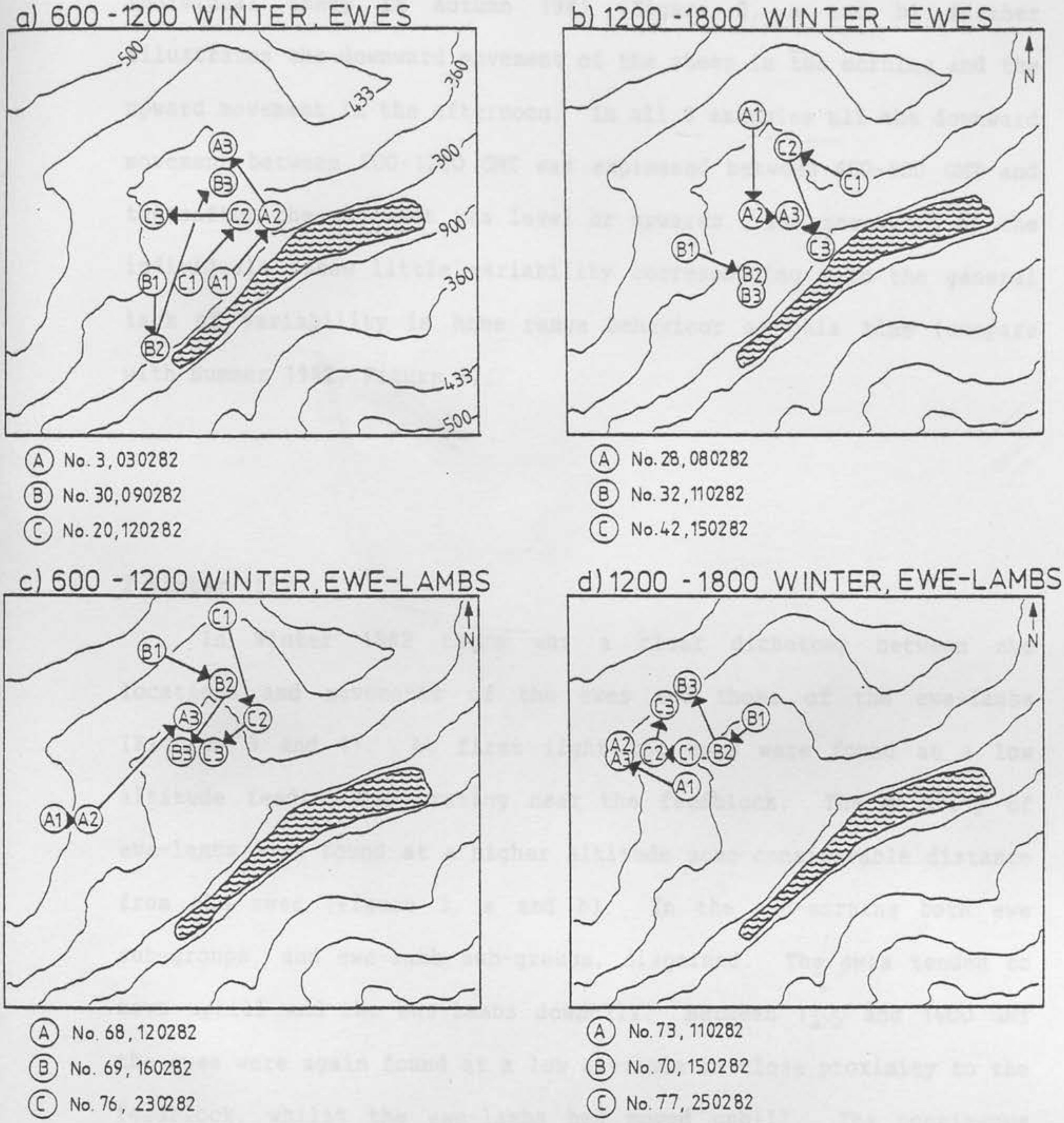
110282; 5°C; WIND FORCE 5, SW; SUN



150282; 5°C; NO WIND; SUN

FIGURE 4

CONTINUOUS MOVEMENTS OF EWES AND EWE-LAMBS IN WINTER 1982



a) 600 - 1200 WINTER, EWES
500
433
360
300
900
360
433
500
A1 A2 A3
B1 B2 B3
C1 C2 C3
A No. 3, 030282
B No. 30, 090282
C No. 20, 120282
b) 1200 - 1800 WINTER, EWES
N
A1 A2 A3
B1 B2 B3
C1 C2 C3
A No. 28, 080282
B No. 32, 110282
C No. 42, 150282
c) 600 - 1200 WINTER, EWE-LAMBS
N
A1 A2 A3
B1 B2 B3
C1 C2 C3
A No. 68, 120282
B No. 69, 160282
C No. 76, 230282
d) 1200 - 1800 WINTER, EWE-LAMBS
N
A1 A2 A3
B1 B2 B3
C1 C2 C3
A No. 73, 110282
B No. 70, 150282
C No. 77, 250282

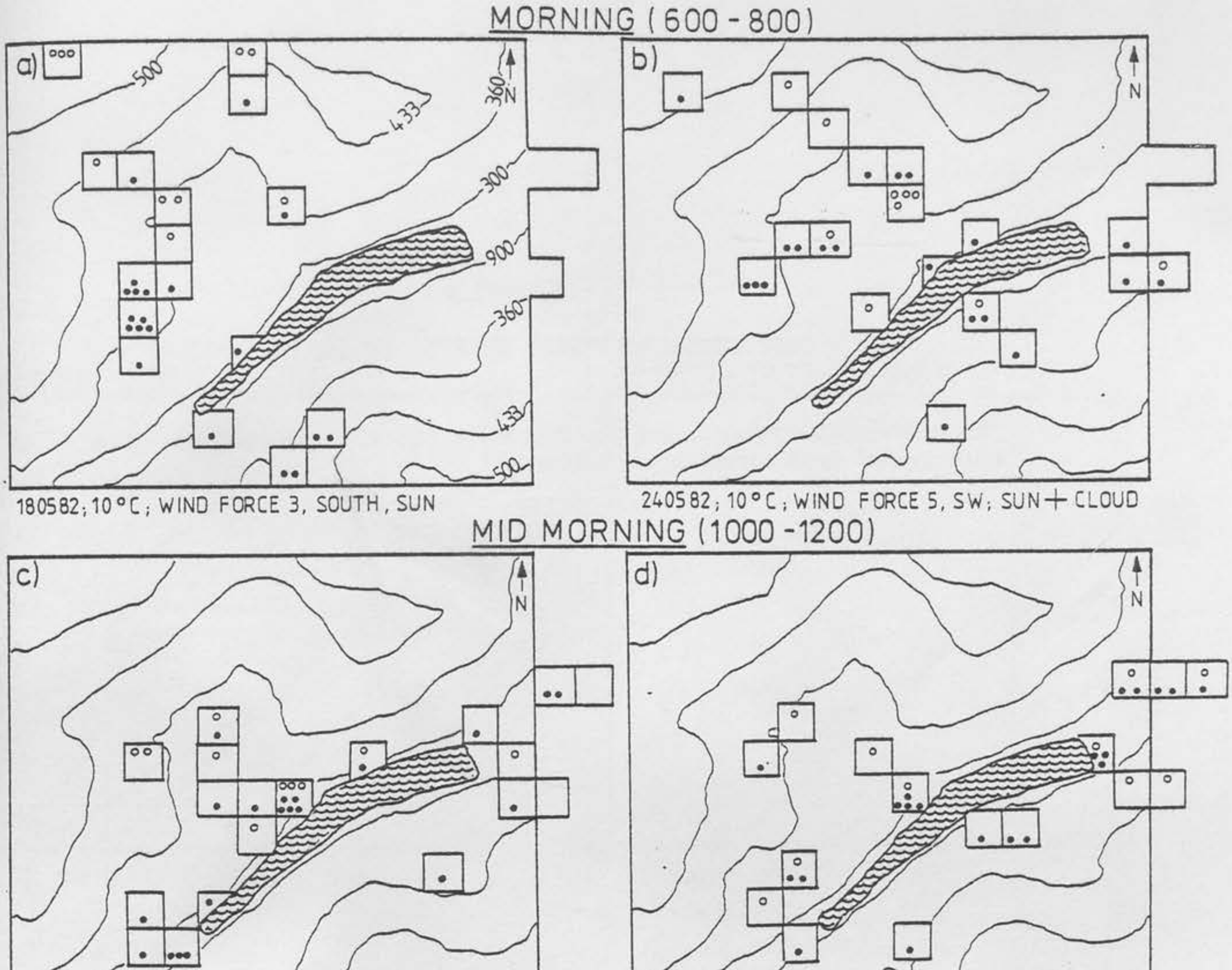
distributions of ewes and ewe-lambs. The continuous movements of individual sheep in Autumn 1981 (Figure 2, a and b) further illustrates the downward movement of the sheep in the morning and the upward movement in the afternoon. In all 3 examples all the downward movement between 600-1200 GMT was expressed between 600-800 GMT and thereafter the movement was level or upwards. The movements of the individuals' show little variability corresponding with the general lack of variability in home range behaviour at this time (compare with Summer 1982, Figure 6).

2 Winter 1982

In Winter 1982 there was a clear dichotomy between the locations and movements of the ewes and those of the ewe-lambs (Figures 3 and 4). At first light the ewes were found at a low altitude feeding on, grazing near the feedblock. The majority of ewe-lambs were found at a higher altitude some considerable distance from the ewes (Figure 3, a and b). In the mid-morning both ewe sub-groups, and ewe-lamb sub-groups, dispersed. The ewes tended to move uphill and the ewe-lambs downhill. Between 1400 and 1600 GMT the ewes were again found at a low altitude in close proximity to the feedblock, whilst the ewe-lambs had moved uphill. The continuous movements of individual ewes and ewe-lambs underline the age segregation found in the group at this time (Figure 4). The ewes between 600 and 1200 GMT were found at a low altitude and through the morning either moved along contours or uphill. In the afternoon they started moving downhill from 1400 hours and by 1600 hours the

FIGURE 5

DAILY MOVEMENTS OF THE HOWLET GROUP IN SUMMER 1982



180582; 10 °C; WIND FORCE 3, SOUTH, SUN

240582; 10 °C; WIND FORCE 5, SW; SUN + CLOUD

170582; 17 °C; WIND FORCE 4, SOUTH; SUN + CLOUD

140682; 15 °C; WIND FORCE 1, NW; SUN + CLOUD

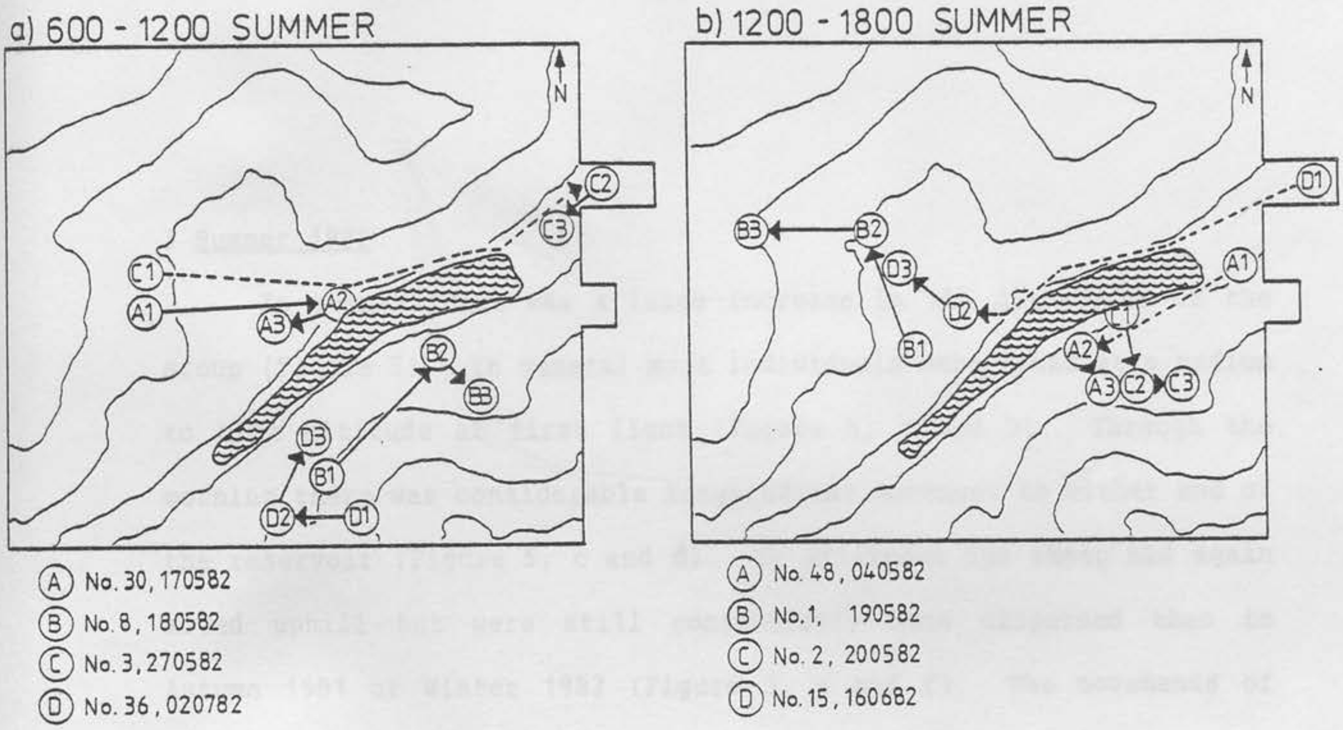
190582; 20 °C; WIND FORCE 1, SOUTH; SUN + CLOUD

160682; 10 °C; WIND FORCE 2, EAST; CLOUD

FIGURE 6

CONTINUOUS MOVEMENTS OF EWES IN SUMMER 1982

The movements represented by dotted lines are assumed to have taken that route from other observations.



a) 600 - 1200 SUMMER
b) 1200 - 1800 SUMMER
N
A No. 30, 170582
B No. 8, 180582
C No. 3, 270582
D No. 36, 020782
A No. 48, 040582
B No.1, 190582
C No. 2, 200582
D No. 15, 160682

majority of ewes were again found at a low altitude. The ewe-lambs were found at a high altitude at first light moving downhill or horizontally through the morning and then uphill in the afternoon (Figure 4, c and d). Again note the lack of variability in the movements in winter and the large proportion of the sampled animals that are found in the same grid squares.

3 Summer 1982

In summer there was a large increase in the dispersion of the group (Figure 5). In general most individuals were found at a medium to high altitude at first light (Figure 5, a and b). Through the morning there was considerable longitudinal movement to either end of the reservoir (Figure 5, c and d). By afternoon the sheep had again moved uphill but were still considerably more dispersed than in Autumn 1981 or Winter 1982 (Figure 5, e and f). The movements of individual sheep in Summer 1982 illustrate increased variability in movement patterns (Figure 6). Of particular interest are the large scale movements expressed by Animal C (Figure 6a) and Animals A and D (Figure 6b), in contrast to the smaller scale movements of Animals A and D (Figure 6a) and Animals B and C (Figure 6b). Note the overlapping distributions of ewes and ewe-lambs and the occupation of the south side of the reservoir by a number of members of the group.

APPENDIX 4

FURTHER DETAILS OF SAMPLING METHODS

1 Scan Samples

During each 2 hour scan, or circuit, of the study site the following sequence was followed. Firstly weather data were recorded before the scan commenced. When marked sheep were located the time of day was noted and the membership of 30 m and 10 m sub-groups were estimated by eye. The central point of a 30 m sub-group was used to estimate the location of all individuals within that 30 m sub-group. In addition the activity of all individuals was recorded.

2 Focal Animal Samples

When sampling focal animals the following sequence was followed. At the start of each sample time of day, location of focal animal and weather conditions were noted. The behaviour of focal animals was recorded continuously as pre-determined behavioural categories (see Appendix 1). Each sample lasted for 30 minutes. Samples were recorded at random between the hours of 0600 and 1800 GMT.