Aspects of the ecology of feral goats (Capra (domestic)) in the Southern Uplands.

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Aspects of the ecology of feral goats (*Capra* (domestic)) in the Southern Uplands.

by

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ABSTRACT

Weights and growth rates, feeding ecology, population ecology and social and spatial organisation of feral goats in the Southern Uplands of Scotland were investigated between 1977 and 1980. Seven populations were described as to their origins, breed type and management.

In general, goats in the eastern populations were significantly larger than those in the western populations; those in the central populations were usually intermediate in size. This variation was probably related to variations in range quality.

Observations and faecal analyses showed that the feeding ecologies of goats and hill sheep, a potential competitor, were similar. In general, sheep used freely drained grasslands more and ate proportionately more grass than goats; the latter, possibly as a result of competition, ate more ferns, conifers, *Myrica* and rushes than the former. The very heavy use of ferns (bracken) by goats was discussed in relation to previous studies.

Population size varied between c. 500 and c. 15 depending partly on the degree of culling. Billies, in general, had lower survival rates than nannies and together with kids their numbers varied within populations more than those of nannies. Reasons for the sex differential in survival and the variability in kid production were discussed in relation to reproductive behaviour, climate and population regulation.

Group size varied in a predictable fashion with season, group type and population size. Complete sexual segregation did not occur but older billies tended to associate least with nannies, and especially so in the spring. Goats were spatially organised into hefts i.e. groups of individuals having highly overlapping home ranges; in general there was little overlap between heft home ranges and only billies moved between hefts and then predominantly at the rut.

The ecology of feral goats was compared with that of other species with particular reference to the questions of dispersal and territoriality. Recommendations for improved management and future research concluded the thesis.

I declare that this thesis .is original and entirely my own work except where otherwise stated.No part of it has been submitted previously for a degree at any other university.

DABullock

CONTENTS

APPENDIX 4: APPRAISAL OF THE USE OF FAECAL ANALYSIS TO ESTIMATE DIET

APPENDIX 5: DETAILED METHODOLOGY OF FAECAL ANALYSIS

APPENDIX 6: THE FREQUENCY OF OCCURRENCE OF PLANT SPECIES/ GROUPS IN THE FAECES OF FERAL GOATS AND HILL SHEEP

APPENDIX 7: POPULATION ESTIMATES OF FERAL GOATS IN THE SOUTHERN UPLANDS

APPENDIX 8: THE USE OF CLUSTER ANALYSIS TO IDENTIFY SOCIAL GROUPS OF FERAL GOATS

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INTRODUCTION

Feral goats (Capra (domestic)) are descendants of domestic stock now living wild. Goats are not native to Britain; they were first introduced by Neolithic peoples as domestic stock and are wholly or chiefly descended from the wild goat (C. aegragus) whose range extends from the Mediterranean basin eastwards to Central Asia (Harriss 1962; Reed 1959; Zeuner 1963). At the time of their introduction, goats were probably used for milk, meat and skins and as a clearer of scrub. These goats are believed to have been small, stocky and long haired (Greig 1969). The breed, the so called British, Old English or native goat, became extinct in domestication by 1930 (Greig 1969; Whitehead 1972).

The reasons for the decline of the British goat varied geographically but two primary factors were involved (Greig 1969). Firstly, from 1900 onwards, larger breeds with higher milk yields such as Saanen and Toggenburg began to be imported from continental Europe; these became increasingly popular. Secondly, at about the same time, the demand for mutton and wool increased. The effects of these changes was to make husbandry of British goats uneconomic but in the meantime, feral populations had become established in several parts of Britain (Buchanan-Smith 1932; Crook 1969; Greig 1969; Whitehead 1972).

At least in Scotland, many feral goats show characteristics of the British breed. They are small and light with billies less than 70 cm at the shoulder and weighing less than 70 kg whereas billies of modern breeds stand higher and weigh up to twice as much (personal observations). In addition feral goats are usually horned and lack neck tassles. Compared to most other forms, British feral goats are strikingly long haired, a feature that has frequently led to claims that they have reverted to the "wild type" (Darling 1937; Lever 1977; Tegner 1961; Thompson 1978; Whitehead 1972).

This similarity of coat pattern and horn shape of some feral goats to that in the wild goat (Tomich 1969) is not evidence of reversion however; the appearance of feral goats is believed to be similar to that of their domestic ancestors (Greig 1969) whose long outer hair and thick underwool (Ryder 1970) had presumably been selected for as an adaptation to cold winter conditions.

Goats, because of their intractability, probably established feral populations soon after their first domestications. In the Scottish Highlands, the collapse of the shieling system, the clearances and (in Wales also) rural depopulation have been suggested as the main factors responsible for the origin of feral populations; in short, they arose through changes in the socio-economic status of rural people leading to neglect (Crook 1969; Greig 1969; Hughes, Dale, Williams & Rees 1973; Megaw 1963).

In the Southern Uplands, most populations are believed to have been established between one and two hundred years ago; their origins have been variously reported as stock owned by miners, railway workers and farmers (A. Finlay pers. comm.; Greig 1969). Some populations may have been deliberately established by farmers in the interests of their livestock. Goats are variously believed to kill adders, prevent contagious abortion in cattle and sheep, act as weather prophets, lead sheep to shelter during storms and graze luxuriant vegetation on cliffs where sheep, tempted by such herbage, would probably become trapped. The validity of these assertions has not been tested; however, their contribution to maintaining populations at the wishes of the local people has been important.

Considering their economic and ecological importance feral goats have received surprisingly little attention from the scientific community. Most published reports relate to their eradication or control (e.g. Clark 1976; Rudge 1982; Tomich 1969; Williams and Rudge 1969; Yocom 1967). Coblentz (1978) noted how ecologists have regarded feral goats as unfashionable objects of study and commented on the irony of this trend in view of their great effect on certain ecosystems.

Studies of feral goats in Britain (Boyd 1981; Buckland 1978; Crook 1969; Greig 1969; McDougall 1975; Munton 1975; Stevenson-Jones 1977) have indicated that their ecology and behaviour are similar to those of hill sheep and that the two species may compete. The aim of the present study was to investigate several aspects of the ecology of feral goats in the Southern Uplands. Given a lack of basic ecological information I surveyed several populations in order to ascertain the following: comparative growth rates, population ecology, habitat use and feeding ecology. Since feral goats in the Southern Uplands are usually sympatric with hill sheep, I also undertook a comparison between the ecologies of these two species.

The increasing demand on uplands for afforestation, recreation and industrial development necessitates the collection of baseline data on the organisms living there. Consequently, I felt justified in surveying several populations instead of monitoring one intensively. Advantages of the former approach were that firstly, comparisons between populations could be made; secondly, since the time available for fieldwork spanned only two and a half years, a comparative study was more likely to yield information useful to management and conservation.

The thesis is divided into five chapters. The first describes the study areas and, as far as has been ascertained, the history of the goat population in each; the second, third, fourth and fifth chapters describe studies of weight and growth rates, feeding ecology, population dynamics and social and spatial organisation. Then follows a general discussion.

I have followed Corbet and Southern (1977) in avoiding the use of formal binomial names for domestic animals since this may lead to confusing terminology. Throughout the text, scientific names have been used for all plants and for animal parasites. For other animals I have used their vernacular names; their scientific names are listed in Appendix 1.

Statistical analyses were conducted according to the methods of Sokal and Rolhf (1969) and the null hypothesis was rejected at a probability (p) of 0.05 or less. For sample sizes of less than 30, confidence limits were calculated using the 't' distribution. In the presentation of data, n.d. indicates that no data were available. Analyses were performed on desk calculators and the computing facilities (NUMAC) at the University of Durham.

The terminology for age classes used throughout the figures is age classes 0 yr, 1 yr, 2 yr corresponding to the first, second and third years of life respectively and so on. Greenwich Mean Time was adopted throughout.

CHAPTER 1. THE STUDY AREAS AND THE HISTORIES OF THEIR FERAL GOAT POPULATIONS.

All the study areas were in the Southern Uplands of Scotland and the Cheviot Hills (Figures 1.1). The bedrock consists of sedimentary rocks of the Ordovician and Silurian ages together with series of granite intrusions in the south-west and north-east. Four of the seven study areas are Sites of Special Scientific Interest and have been described by Ratcliffe (1977).

The accounts of the histories of the various goat populations are speculative. The brief notes presented with the description of each study area are the result of conversations with shepherds, foresters and landowners and also include references to the surveys of Greig (1969), North (in litt.) and Whitehead (1972).

1. Craigdews Wild Goat Park

The Forestry Commission's Wild Goat Park at Craigdews (NX5072, Figure 1.1) occupies approximately 100 ha of upland, unafforested ground with a granite bedrock which reaches approximately 260 m at the highest point (Craigdews). The park was formed in order to provide an area where goats could be readily observed by the public and also to preserve a stock of Galloway feral goats. The fence was completed in 1969 and 27 goats captured in several areas of central Galloway were introduced in 1970 (Jeffries 1971).

The vegetation consists of a mixture of wet heaths, soligenous mires and freely drained grasslands the latter heavily overgrown with *Pteridium*. A thorough vegetation survey has not, however, been conducted. Several granite outcrops in the centre of the park are used by goats.

Figure 1.1

The locations of the study areas (circles) and meteorological stations (squares) in the Southern Uplands. 1, Craigdews Wild Goat Park; 2, Cairnsmore of Fleet; 3, Moffat Hills; 4, Langholm-Newcastleton Hills; 5, Kielderhead Moors; 6, Nether Hindhope and 7, College Valley. Meteorological stations are 1, Clatteringshaws; 2, Eskdalemuir and 3, Redesdale. Thin lines indicate the 300m contours.


N
Glasgow
Edinburgh
SCOTLAND
EIRE
WALES
ENGLAND
WOOLER
CARLISLE
1
2
3
4
5
6
7
1
2
3
0
km
50

This study area was unique in being used solely by goats; sheep have been absent for at least 12 years. The population is regularly and heavily culled with the aim of retaining about 40 goats (R.W. Baird *in litt.*) and given supplementary food in late winter. These goats have relatively large parasitic burdens (A. Russel pers. comm.).

2. Cairnsmore of Fleet

This massif of granite, the highest point on its whaleback ridge reaching 710 m, is situated in Kirkcudbrightshire (NX5067, Figure 1.1). It is the only area in south-west Scotland that remains unafforested throughout the range of altitudes from low lying moorland (90 m) up to submontane levels.

The eastern slopes which include most of the Cairnsmore of Fleet National Nature Reserve (Cairnsmore of Fleet N.N.R.) are gently contoured moorland with a prevalance of peaty gleys and blanket peat of varying thickness. These support large areas of *Molinia caerulea* grassland which grades into soligenous mire and abundant *Myrica gale*, *Juncus acutiflorus* and *Sphagnum*. At slightly higher levels and on extensively burnt ground there are large areas of wet heath dominated by *Calluna vulgaris* and *Trichophorum caespitosum* communities with *Sphagnum* rich facies and, in places, *Trichophorum*-*Eriophorum* blanket mire with *Molinia*. Areas of dry heath are limited and found mainly on rocky ground.

The eastern corrie of Cairnsmore of Fleet has a covering of submontane *Vaccinium myrtillus* heath but the moderately steep western slopes are dominated by *Calluna* and *Vaccinium* communities with, in areas where there has been extensive burning, *Nardus stricta* and *J. squarrosus*. The summit vegetation consists of *Festuca ovina*-*Vaccinium* and *Festuca*-

Rhacomitrium heaths.

The area is managed as sheep walk with, exclusively, the Blackface breed. In the northern area some rough shooting and stalking occurs although the numbers of red deer and red grouse are low. With the exception of its south-western slopes, Cairnsmore of Fleet is surrounded by coniferous plantation, extensions of which continue to encroach on the hill pasture.

Cairnsmore of Fleet supports the largest population of feral goats in the Southern Uplands and possibly the British Isles (Chapter 4). Goats have been feral in the area certainly since the late nineteenth century and probably from as early as 1840 (Drakeford in prep.).

During the establishment of the population, additions from domestic flocks could have been frequent. Mackenzie (1980) suggested that this recruitment was from flocks of itinerant Irish goatherds who frequented Western Scotland up until the 1914-1918 war. The shape of the horns in the current population supports this view, the billies having scimitar (i.e. symmetrically curving) horns characteristic of Irish stock; dorcas (i.e. flared and twisted) horned billies, characteristic of Scandinavian and British stock (Mackenzie 1980), are found in the populations further east in the Southern Uplands.

During the last 50 years the Cairnsmore of Fleet population in common with others in south-west Scotland has been culled and harvested by the Forestry Commission (F.C.) and landowners respectively. Greig (1969) reported the cull of 122 goats by the F.C. on Round Fell, north-west of Cairnsmore of Fleet in 1969 and several large culls have occurred since then (Chapter 4).

3. Moffat Hills

The Moffat Hills in Dumfriesshire (NT1614, Figure 1.1) form a second rugged area in the Southern Uplands. The bedrock of the upper reaches of Moffatdale and its subsidiary glens consists of Silurian greywackes and shales showing evidence of past glaciation such as 'U' shaped corries and hanging valleys. There are several plateau summits above 760 m, the highest of which is White Coomb at 821 m (Figure 5.10).

Grasslands dominate the lower slopes; large areas of Festuca-Agrostis and Agrostis-Anthoxanthum grasslands occur with proportions of Nardus and Juncus squarrosus increasing on the wetter, peatier soils. Molinia dominated grasslands are infrequent and restricted to flushed situations. Blanket-mire (Calluna-Eriophorum) is extensive below some of the summits and examples of snowbed Vaccinium-Empetrum hermaphroditum heath with Nardus occur. Between approximately 300 m and 600 m is a zone of dry or moist heath communities dominated by Calluna and Vaccinium sometimes dissected by lines of scree. The summit vegetation is predominantly Festuca-Rhacomitrium heath.

The Moffat Hills are managed as sheep walk with predominantly, the South Country Cheviot and Blackface breeds and a smaller number of Swaledales. Approximately 330 ha of fenced coniferous plantation occurs on the western slopes of Moffatdale, from which goats were shot or driven out prior to planting in 1968 (Greig 1969); a smaller area (150 ha) has recently been fenced and planted on the eastern slopes. An extensive area of plantation occurs south of the study area at Craigieburn which is used to some extent by sheep and goats.

Goats have been feral in the Moffat Hills since at least 1910 (J. Dalgleish pers. comm.). Domestic stock of what appears to have been the British breed was in Moffatdale and the neighbouring Yarrow valley during the 19th century; at that time they were used for meat, milk and allegedly to prevent contagious abortion in cattle (Greig 1969). Several residents and past residents of the area interviewed by myself and Greig have remarked on goats being able to anticipate changes in the weather, in particular, the onset of storms.

4. Langholm-Newcastleton Hills

This area, representative of large tracts of relatively low lying and unspectacular hill country in the Scottish borders, forms part of the march between Dumfriesshire and Roxburghshire (NY4290, Figure 1.1). The southern part has a Carboniferous bedrock mainly of sandstones, and the northern part is composed of Silurian grits and shales with occasional exposures of Old Red Sandstones and igneous intrusions. The terrain varies from gently undulating moorland to steep, smooth sided hills deeply dissected by numerous water worn sikes and cleughs. The highest point is Roan Fell (568 m) but Arkleton Hill (521 m) forms a more distinctive peak (Figure 5.13).

There is an extensive area of blanket mire with *Rubus chamaemorus* which is deeply dissected and haggy on the plateau summits, and a smaller area of dry heath. Below the summits, *Festuca-Agrostis*, *Nardus* and *Molinia* grasslands occur. Mixed woodlands of *Alnus*, *Betula*, *Corylus* and *Sorbus* are found on the steeper sides of water courses. The area is noted for its rich bryophyte flora.

These moorlands were once famous for their grouse but presumably as a consequence of sheep grazing and muirburn, grouse stocks have declined. The area is now managed jointly as sheepwalk with the South

Country Cheviot and Blackface breeds and as grouse moor; a substantial amount of muirburn is practised annually.

The feral goats on the Langholm-Newcastleton Hills are believed to be primarily descended from those that escaped or were liberated during railway construction in the area around the turn of the century (A. Finlay pers. comm.); their range until 1963 included the western side of the Ewes valley (G. Laing pers. comm.). Goats are occasionally culled and harvested from this population but during the study period removals were limited to two billies shot each summer for trophy heads (B. Mitchell pers. comm. and pers. observ.).

5. Kielderhead Moors

These moors straddle the Scottish-English border between Northumberland and Roxburghshire (NT6501, Figure 1.1). Over much of the area a thick layer of peat overlies Carboniferous fell sandstone which in turn overlies cement stone. The moors form a high plateau. The maximum elevation of 602 m (on Peel Fell) is not much higher than that of the surrounding ground.

The predominant vegetation is blanket mire (Calluna-Eriophorum), deeply dissected to form extensive areas of hags, with Rubus and Trichophorum. Dry heath is also extensive and Vaccinium heath is well represented. Areas of grassland and basic flush occur which are associated with thin bands of limestone and calcareous shale.

The plateau is surrounded, except to the north-west, by the extensive coniferous forests of Kielder, Wauchope and Redesdale. The only natural woodland is patchy Salix scrub and isolated trees of Betula and Sorbus along burnsides.

The Kielderhead Moors are managed as sheepwalk during the summer; in the autumn, the hirsels of Blackface and Blackface/Swaledale crosses are removed to lower ground for the winter. Some rough shooting occurs but the numbers of grouse are low and muirburn is infrequent (B. Auld pers. comm.).

The origin of the feral goat population is unknown. The population was possibly contiguous with the one that until 1978 or 1979 occurred on the Bewcastle Fells. The latter were descended from goats tended by pastoralists operating a shieling system under the Barony of Brough; there are records of goats running wild on the Bewcastle Fells from as early as the 15th century (J. Johnston pers. comm.).

6. Nether Hindhope

Nether Hindhope is a hill farm on the Scottish border in Roxburghshire (NT7810, Figure 1.1), reaching a maximum elevation of approximately 507 m on Brownhart Law. It is entirely fenced and both the livestock and the feral goats are self contained. The bedrock consists of andesitic lavas and tuffs of Lower Old Red Sandstone age which give rise to soils of higher fertility than those of upland pastures further west. The scenery, typical of the Cheviot Hills, is of rounded predominantly grassy hills (knowes). In common with most hill farms in the area, hill sheep of the South Country Cheviot breed are the predominant livestock the year round.

There are large areas of Festuca-Agrostis grasslands extensively overgrown with Pteridium, which grade into Nardus grasslands on wetter slopes. *Molinia* grasslands occur on the flatter summits; this grades into wet heath (*Calluna*-*Molinia*) and the latter into blanket mire (*Calluna*-*Eriophorum*). None of the heath communities is extensive and they are occasionally burnt. A conifer plantation of approximately 2 ha with 15 year old trees is situated on the hill ground to which goats, but not sheep, have access.

Whitehead (1972) makes no mention of the goat population at Nether Hindhope. The past history of the population is uncertain. On occasion billies have been imported from the other feral populations in the Langholm-Newcastleton Hills and College Valley in an attempt to reduce inbreeding. There was also a period of about 30 years in this century when the population was regularly culled to less than 10 individuals (A. Crozier pers. comm.).

7. College Valley

College Valley runs north from the Cheviots in Northumberland (NT9130, Figure 1.1). In common with Nether Hindhope, the bedrock is mainly of andesitic lavas and tuffs of Lower Old Red Sandstone age but there are also some granitic intrusions. The soils are of relatively high fertility and *Festuca*-*Agrostis* grasslands, grading into *Nardus* grasslands on the more poorly drained slopes, predominate. Most of the lower level *Festuca*-*Agrostis* grasslands are overgrown with *Pteridium* and many of the south facing slopes and burnsides have a covering of *Ulex europaeus*. There are areas of mixed deciduous woodland, to which livestock and feral goats have access. Regeneration is insignificant within the study area. The flatter summits and the plateaux beneath tors (rock outcrops) are dominated by wet heaths and blanket mires. They reach an elevation of approximately 540 m on Newton Tors.

College Valley is managed as sheepwalk for the Blackface breed in the study area although hirsels of South Country Cheviot sheep predominate further upstream in areas once frequented by goats.

The goats, in common with those that frequented other areas of the Cheviot, are reputed to be descended from individuals liberated by Lindisfarne Monks when their priory was dissolved in the 16th century. Alternatively, the goats may be descended from those used during the 18th and early 19th centuries for making whey, when drinking of the latter was a minor health cult at Wooler (Brewster 1976).

The most likely explanation for the continued existence of feral goats in areas of intensive sheep farming, such as College Valley, is because shepherds believe that the goats are beneficial to their stock. Nevertheless, the College Valley goats are regularly culled to less than 20 in order to reduce alleged competition for forage with sheep and damage to walls, plantations and hayfields (Brewster 1976; McDougall 1975; Tegner 1961).

Climate

In terms of the relative conditions used by Birse and Dry (1970), the study areas are cool, cold or very cold; rather wet or wet; foothill, upland or mountain depending on altitude.

Climate was more precisely described by meteorological data from three stations in the Southern Uplands. From west to east there were: Clatteringshaws (NX554780), altitude 178 m; Eskdalemuir (NT235026), altitude 242 m; Redesdale (NT834955), altitude 238 m, (Figure 1.1). Mean monthly fluctuations in total rainfall, the number of days with snow lying and mean temperature for four consecutive years at Eskdalemuir

Figure 1.2

Monthly fluctuations in mean temperature (± extremes), total rainfall (●) and the number of days with snow lying at 0900h (o) at Eskdalemuir Observatory, between January 1977 and October 1980.


+30
+20
+10
0
-10
Temp. (°C) →
200
100
Rainfall (mm) →
20
10
Snowlie (dy) →
J
D J
D J
D J
1977
1978
1979
1980

(Figure 1.2) showed the strongly seasonal nature of the climate. Most plant growth occurs at temperatures at or above 4^{o}C (Birse and Robertson 1970), so that the main growing season was between March and November.

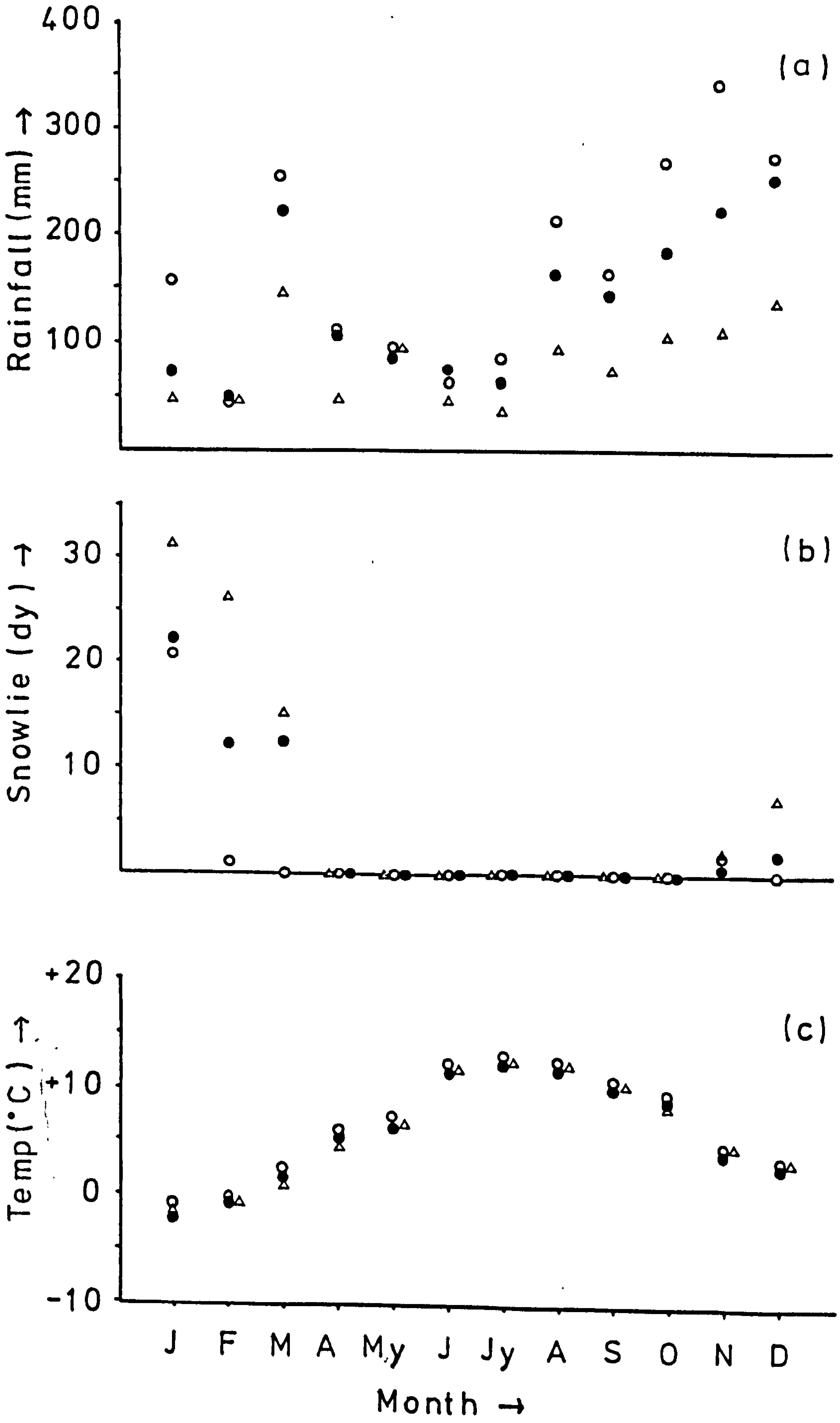
Using the climatological data described above, seasons were delimited as follows: spring, from the onset of conditions suitable for primary production to the major flush of plant growth; March, April and May; summer, the period of highest mean temperatures, June, July and August; autumn, declining mean temperatures and declining primary production, September, October and November; winter, lowest mean temperatures and negligible primary production, December, January and February. These seasons were useful in describing the life cycle of hill sheep and feral goats, both of which have birth seasons in spring and rutting seasons in autumn.

Comparison of the individual years revealed little variation in the seasonal trends with the exception of the winter of 1978-1979 during which minimum and mean temperatures were lower and the number of days with snow lying higher than in other winters; the spring of 1979 was similarly cold and snowy compared with other springs (Figure 1.2).

Comparing climatological data from the three stations in 1979, Clatteringshaws received more total rainfall, had fewer days with snow lying and higher mean temperatures than either Eskdalemuir or Redesdale. The last two stations were climatologically similar although Redesdale received appreciably less total rainfall than the others and more days with snow lying (Figure 1.3). The data indicated a general trend of warm, wet weather in the south-western through to cold, dry weather in the north-eastern Southern Uplands respectively.

<u>Figure 1.3</u>

Comparison of the monthly fluctuations in total rainfall (a), number of days with snow lying at 0900h (b) and mean temperature (c) for 1979 at Clatteringshaws (o), Eskdalemuir (•) and Redesdale (Δ) meteorological stations.


400
300
200
100
Rainfall (mm) ↑
(a)
30
20
10
Snowlie (dy) ↑
(b)
+20
+10
0
-10
Temp (°C) ↑
(c)
J
F
M
A
My
J
Jy
A
S
O
N
D
Month →

CHAPTER 2. WEIGHTS AND GROWTH RATES.

Introduction

Knowledge of weights and growth rates are necessary for studies of biomass, energetics, sexual dimorphism and taxonomy. Further, because size accounts for some of the variation in life history parameters between taxa (Krebs and Davies 1981) it should be a central theme in studies of ecology and behaviour (Western 1979). Growth rates and adult body size are determined both by environmental and genetic factors. We may expect, for instance, variation in body size between populations if these vary in their nutritional backgrounds. Also, in a polygynous society such as that of feral goats (Shank 1972), we should expect differences in size between males and females since the sexes may have dissimilar life history strategies (Jewell 1976). It is necessary to quantify sexual differences in body size before examining their possible causes and effects.

Despite the large number culled, there are few data on weights and growth rates of feral goats. Brown (1977) and Crook (1969) presented series of age and sex-specific measures of body and horn size for Welsh feral goats and Bareham (unpub.) has done the same for the population on Holy Island, off Arran. Some data are also available from islands off New Zealand such as Macauley Island (Williams and Rudge 1969) and Raoul Island (Rudge and Clark 1978).

These studies have shown that feral billies are larger and grow faster than nannies. This appears to be so for other caprinids such as wild American sheep (Aldous, Craighead & Devon 1958; Blood, Flook & Wishart 1970; Bunnell & Olsen 1976) and feral sheep (Doney, Ryder, Gunn & Grubb 1974). It is the purpose of this chapter firstly, to document age and sex related variation in size of feral goats and secondly, to compare size in several populations from the Southern Uplands. The data are from two sources; the first is from measurements of live or freshly dead goats and the second from skeletal measurements.

Methods

All goats were aged by counting the number of annual rings on their horn sheaths (Chapter 4). Greig (1969) demonstrated that this was an accurate ageing technique for Scottish feral goats. Among recaptures, discrepancies in age using this method were all attributed to difficulties in counting whilst restraining goats in poor weather and poor light or wear on the horns. Most individuals were only caught once and for consistency, no attempt was made to alter ages as a result of better estimates in later captures. The majority of goats were caught between late September and December.

For measurements of live individuals, goats were mustered with trained dogs and a shepherd or teams of people. Since sheep folds and dry stone walls are inadequate for restraining goats it was necessary to drive them into fenced corrals or steadings. The number and type of measurements taken are listed below; where possible they follow those described by Langvatn (1977) for use on deer. All body and horn measurements were taken using a flexible fabric tape measure that was repeatedly checked for accuracy against a metre rule.

1. Total weight measured to 0.5 kg was taken using a 120 kg spring balance. Goats were restrained in a tightly wrapped net or sling of negligible weight which was hooked onto the balance suspended on a beam.

2. <u>Heart girth</u> was the distance around the chest measured just behind the forelegs.

3. <u>Body length</u> was taken from the nose along the frontal plane of the head between the base of the horns and along the spine to the junction between the last sacral and first caudal vertebrae.

4. <u>Shoulder height</u> was the distance between the left forehoof and the highest point on the left shoulder.

5. <u>Tail length</u> was taken from the junction between the last sacral and first caudal vertebrae to the tail's fleshy tip.

6. <u>Ear length</u> was the distance between the notch of the external opening and the tip.

7. <u>Horn length</u> and the length of the increment between successive annual rings (increment length) were measured in millimetres along the anterior horn keel. Successive increments were referred to as 0-1, 1-2, 2-3 and so on from the horn tip to its base. Where only one horn was measured, this was the left one.

Heart girth, body length and shoulder height were measured to the nearest centimetre. Tail and ear lengths were measured to 0.5 cm and horns to the nearest millimetre.

Since there appeared to be differences between some populations the data were handled on a population basis. Two comparisons were made; the first was between the sexes and the second between individuals of the same age-sex class within different populations. Growth of all indices of body size was approximately linear between the first autumn or early winter of life and the third; this time period was therefore used to calculate growth rates expressed as mean growth increment/mean animal/year.

The magnitude of size differences between populations for each age-sex class was estimated statistically using one way analyses of variance for unequal sample sizes or 't' tests where unknown variances were not assumed to be equal. If analyses of variance revealed overall significant differences, multiple comparison tests of significance among means using the a posteriori Student-Newman-Keuls (S.N.K.) test were conducted. All multiple comparison tests were made at the 5% ($p = 0.05$) level of significance. The S.N.K. test is among the most sensitive of tests for a posteriori comparisons among means and one of the least susceptible to a Type 2 statistical error (Parker 1980). Analyses of variance tables are presented in Appendix 2.

Results

Four hundred and nine captures, 134 billies and 275 nannies, were made from the populations at Craigdews, Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Nether Hindhope and College Valley. The total includes capture of all individuals in the Nether Hindhope population in three consecutive years. In addition, weights of the dry skull plus horn sheaths (head weight) of 49 goats, 26 male and 23 female, were recorded.

1. Total weight

Weights were obtained in November and December from goats at Craigdews, Cairnsmore of Fleet, Moffat Hills and Nether Hindhope. The total weight of new born kids was estimated to be approximately 2.6 kg based on the weights of one new born kid and four foetuses near birth. Weight gain was approximately linear up to the third year for both sexes in all four populations (Figures 2.1a & 2.1b). Billies

Figure 2.1

Mean age specific total weights (± 95% C.L.) of (a) nannies and (b) billies from Craigdews (black histograms), Cairnsmore of Fleet (white histograms), Moffat Hills (south-west to north-east hatching) and Nether Hindhope (south-east to north-west hatching). Numbers circled within each histogram are sample sizes.

Differences between populations for nannies were statistically significant at ages 1 ($p < 0.01$), 2 ($p < 0.05$), 3 ($p < 0.01$) and 6+ ($p < 0.01$). For billies the only statistically significant difference between populations was for age 0 ($p < 0.01$) and for age 3 between Craigdews and the Moffat Hills ($t_3 = 14.24$, $p < 0.002$).


Total weight (kg) →
0
20
40
60
0
1
2
3
4
5
6+
6
16
6
7
2
5
2
10
1
6
3
5
3
8
3
2
nd.
4
4
6
+96·68
2
4
5
4
5
18
5
12
Age (yr) →

(a)


Total weight (kg) →
Age (yr) →
60
40
20
0
0
1
2
3
4
5
6+
12
8
11
3
1
1
2
1
2
5
3
2
2
3
1
2
1
1
2
2
1
1
n.d.
+10165
+6989

(b)

approximately doubled their weight, from between 20 kg and 30 kg to between 40 kg and 45 kg during that time; nannies had lower absolute weights ranging from between 15 kg and 28 kg in their first year to between 25 kg and 46 kg by their third year. Thereafter, growth rates decreased in both sexes. The maximum live weights for billies and nannies were 68.0 kg for a billy in his eighth year from Nether Hindhope, and 55.0 kg for a nanny in her tenth year from the Moffat Hills.

Growth rates of billies were higher than those of nannies ranging from between 8.5 kg/yr to 10.7 kg/animal/yr for the former and between 4.3 kg/yr to 7.2 kg/yr for the latter. Mean age specific weights and growth rates of both sexes were generally lower at Cairnsmore of Fleet and Craigdews than at Nether Hindhope. The weights and growth rates of nannies from the Moffat Hills tended to be intermediate between those from Cairnsmore of Fleet or Craigdews and those from Nether Hindhope (Figure 2.1a & 2.1b, Table 2.1).

Study area	Billies	Nannies
Craigdews	8.5	4.2
Cairnsmore of Fleet	8.4	6.3
Moffat Hills	10.7	7.2
Nether Hindhope	8.0	9.4

Table 2.1. Growth rates in weight (kg/yr) between the first and third autumns or early winters based on means.

Table 2.2

Multiple comparisons among means of age-specific weight (kg) of (a) nannies and (b) billies. Differences not significant at $p = 0.05$ are underlined.

(a) Nannies

Age (yr)

1	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	22.0	24.8	30.0	32.4

2		Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
		31.8	37.0	41.0

3	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	28.7	35.8	36.5	39.3

6+	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	37.8	39.4	45.5	47.4

(b) Billies

0	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	21.1	21.8	23.8	29.5

Significant differences in weight occurred between populations for nannies in their first, second, third and seventh plus years (Figure 2.1a, Appendix 2). Nannies at Craigdews and Cairnsmore of Fleet were significantly lighter ($p < 0.05$) than those at Nether Hindhope. Those from the Moffat Hills were intermediate in weight between those at Craigdews or Cairnsmore of Fleet and Nether Hindhope but never significantly lighter than those from the latter population (Table 2.2).

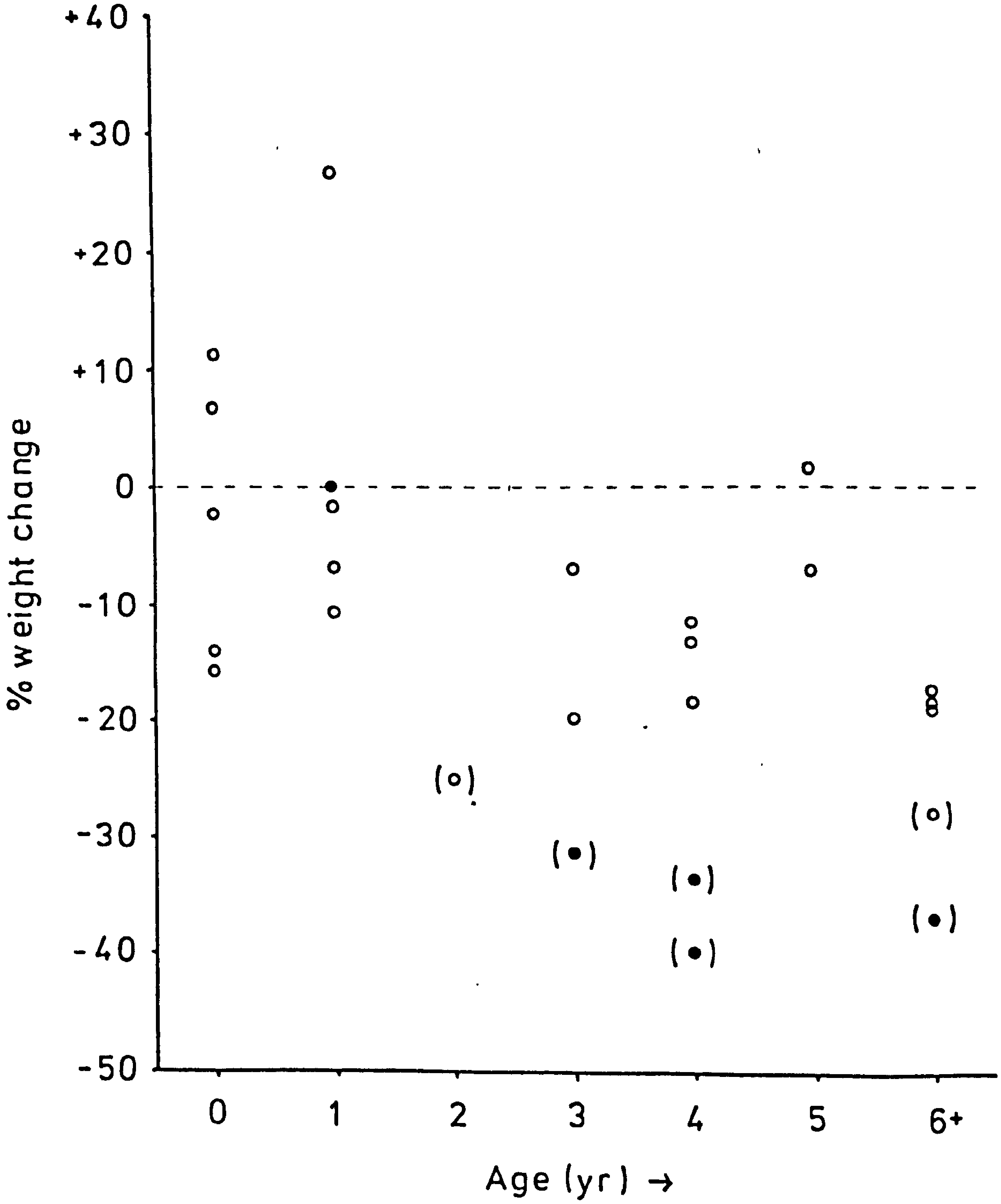
Of the two age classes of billies for which analyses of variance were possible, that is, first and second years, only for the former was there a significant difference between populations. However, billies in their fourth year from the Moffat Hills were significantly heavier ($t_3 = 14.24$, $p < 0.001$) than those of the same age from Craigdews (Figure 2.1b, Appendix 2). The S.N.K. test on mean weights of billy kids showed that those at Nether Hindhope were significantly heavier ($p < 0.05$) than those from other populations. Furthermore, Moffat Hills billy kids were significantly heavier ($p < 0.05$) than those from Craigdews although the difference between the means of the former and billy kids from Cairnsmore of Fleet was not significant (Table 2.2).

Seasonal changes in total weight were investigated for nannies in the Nether Hindhope population that were weighed in November 1979 and again in June 1980. Only one billy, in his second year in the autumn, was caught both times and his weight had not changed. For the nannies, weight loss was up to 20% (Figure 2.2).

The estimated weight loss of goats that died in the late winter through to the spring was much greater than those that survived (Figure 2.2). All these individuals had died in a state of undernutrition as judged by the quality of their tibial marrow (Chapter 4). The data

Figure 2.2

Age-specific weight change of nannies (o) and billies (•) over winter. Symbols in parentheses indicate those goats that died in the spring. Ages are those in autumn.


+40
+30
+20
+10
0
-10
-20
-30
-40
-50
% weight change
0
1
2
3
4
5
6+
Age (yr) →

suggest that individuals losing more than 20% of their total weight over the winter die in the following spring.

2. Heart girth

Heart girth increased rapidly for the first two years in nannies and for the first three or four years in billies (Figures 2.3a & 2.3b). Billies generally had higher growth rates and larger heart girths than nannies of the same age. There were few consistent differences between populations of the same sex (Table 2.3).

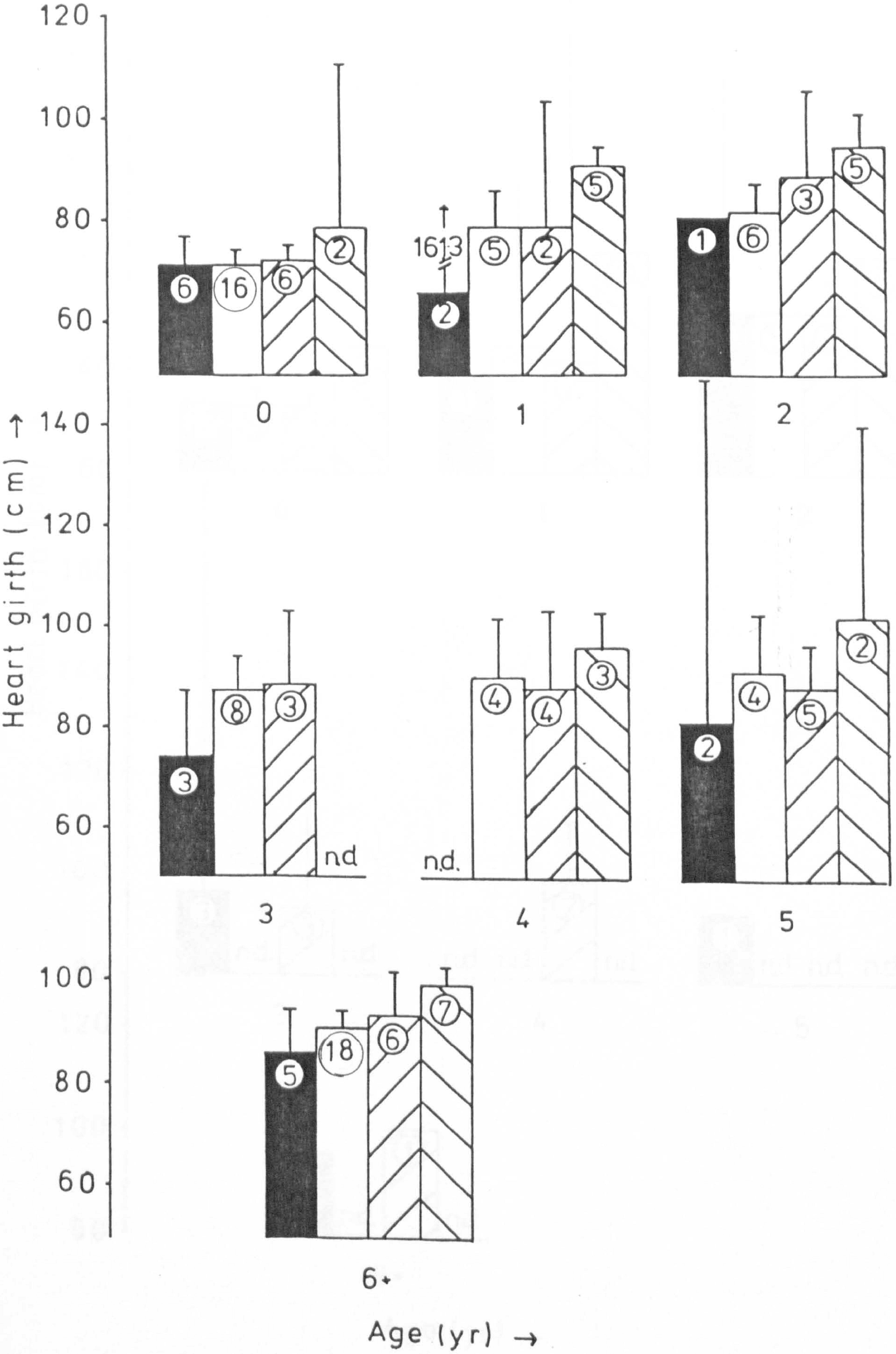
Study area	Billies	Nannies
Craigdews	9.0	5.0
Cairnsmore of Fleet	9.5	6.0
Moffat Hills	9.5	8.5
Nether Hindhope	8.5	8.3

Table 2.3. Growth rates of heart girth (cm/yr) between the first and third autumns or early winters based on means.

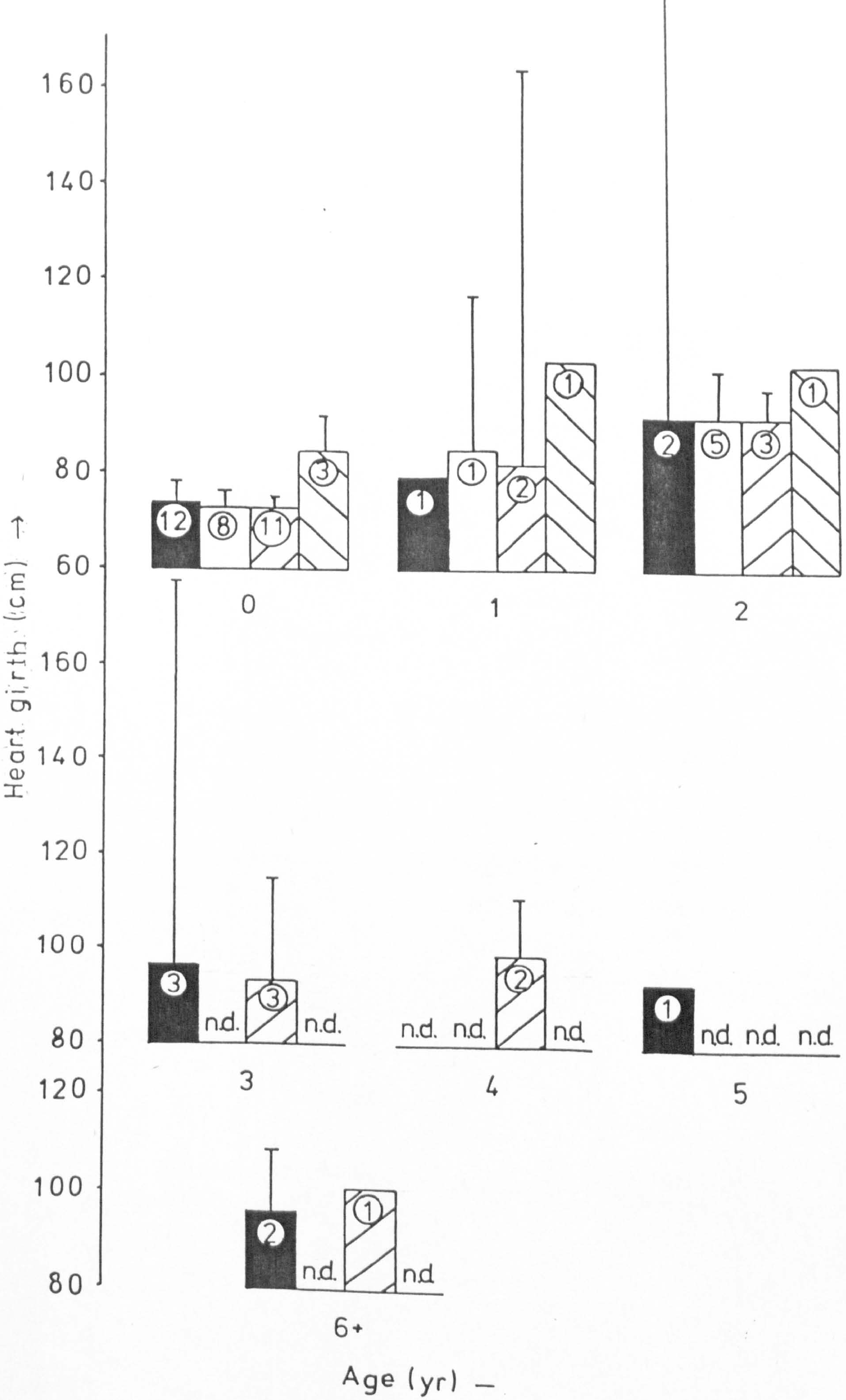
As with total weight, nannies from Craigdews or Cairnsmore of Fleet had particularly small mean heart girths compared to those from Nether Hindhope whilst Moffat Hills nannies were usually intermediate in girth (Figure 2.3a). Significant differences in heart girth occurred between populations for nannies in their first, second, third and seventh plus years (Figures 2.3a, Appendix 2). S.N.K. tests indicated that the mean heart girths of nannies from Nether Hindhope and the Moffat Hills

Figure 2.3

Mean age specific heart girth ($\pm$ 95% C.L.) of nannies (a) and billies (b). Labelling as for total weight (Figure 2.1). Statistically significant differences between populations occurred for nannies aged 1 ($p < 0.01$), 2 ($p < 0.01$), 3 ($p < 0.05$) and 6+ ($p < 0.01$). For billies the only significant difference between populations was for age 0 ($p < 0.001$).


120
100
80
60
140
120
100
80
60
100
80
60
Heart girth (cm) →
6
16
6
2
0
161.3
2
5
2
5
1
1
6
3
5
2
3
8
3
nd
3
n.d.
4
4
3
4
2
4
5
2
5
5
18
6
7
6+
Age (yr) →

(a)


Heart girth (cm) ↑
160
140
120
100
80
60
160
140
120
100
80
120
100
80
12
8
11
3
1
1
2
1
2
5
3
1
3
n.d.
3
n.d.
n.d.
n.d.
2
n.d
1
n.d.
n.d.
n.d
2
n.d.
1
n.d
0
1
2
3
4
5
6+
Age (yr) →

(b)

(a) Nannies

Age (yr)				
1	Craigdews	Moffat Hills	Cairnsmore of Fleet	Nether Hindhope
	65.5	79.0	79.2	90.8
2	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope	
	82.8	89.3	95.0	
3	Craigdews	Cairnsmore of Fleet	Moffat Hills	
	70.0	87.0	88.3	
6+	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	85.8	90.7	93.3	98.7

(b) Billies

0	Moffat Hills	Cairnsmore of Fleet	Craigdews	Nether Hindhope
	72.8	73.0	73.5	85.3

were usually significantly bigger ($p < 0.05$) than those from Cairnsmore of Fleet or Craigdews (Table 2.4). Also, the mean heart girths of Craigdews nannies in their second and fourth years were significantly smaller ($p < 0.05$) than those from other populations (Table 2.4).

Sample sizes were smaller for billies but once again those from Nether Hindhope had larger heart girths than those in other populations. Only for billy kids was there a significant difference between populations (Figure 2.3b, Appendix 2) and the S.N.K. test indicated that those from Nether Hindhope had significantly larger ($p < 0.05$) heart girths than those from other populations. Differences between mean heart girth of billy kids from the Moffat Hills, Cairnsmore of Fleet and Craigdews were not significant (Table 2.4).

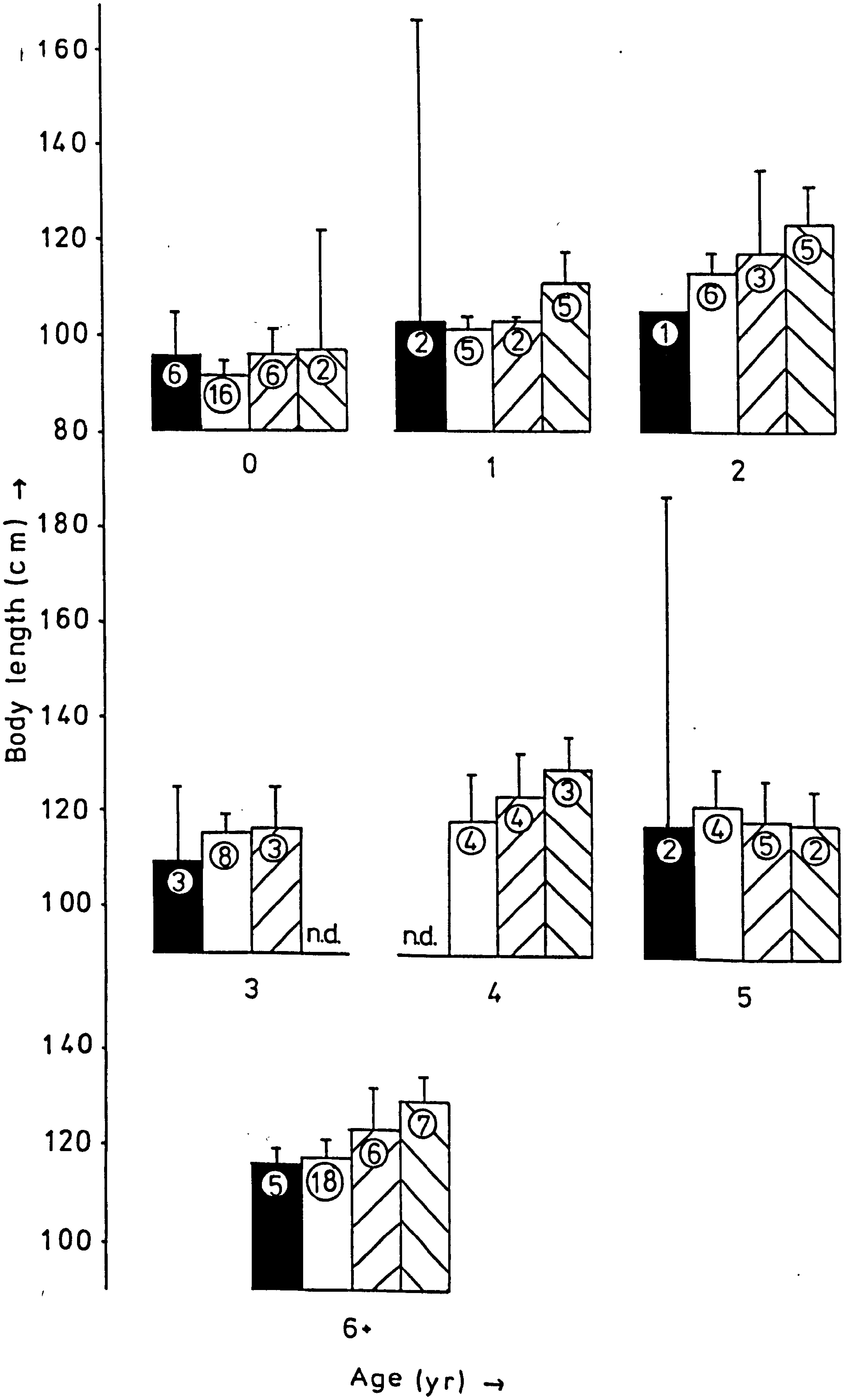
3. Body length

Body length is a direct measure of skeletal growth; this is not the case with heart girth or total weight both of which may vary with the extent of rumen fill and fat reserves. There were nevertheless few differences between the growth curves for body length and those of heart girth or total weight. Mean body length of nannies increased steadily from between 90 cm and 100 cm in their first year to between 100 cm and 120 cm in their third year depending on the population; thereafter, growth declined (Figure 2.4a). The few data for billies showed that they were longer bodied than nannies of similar age and continued to grow until at least their fourth year (Figure 2.4b).

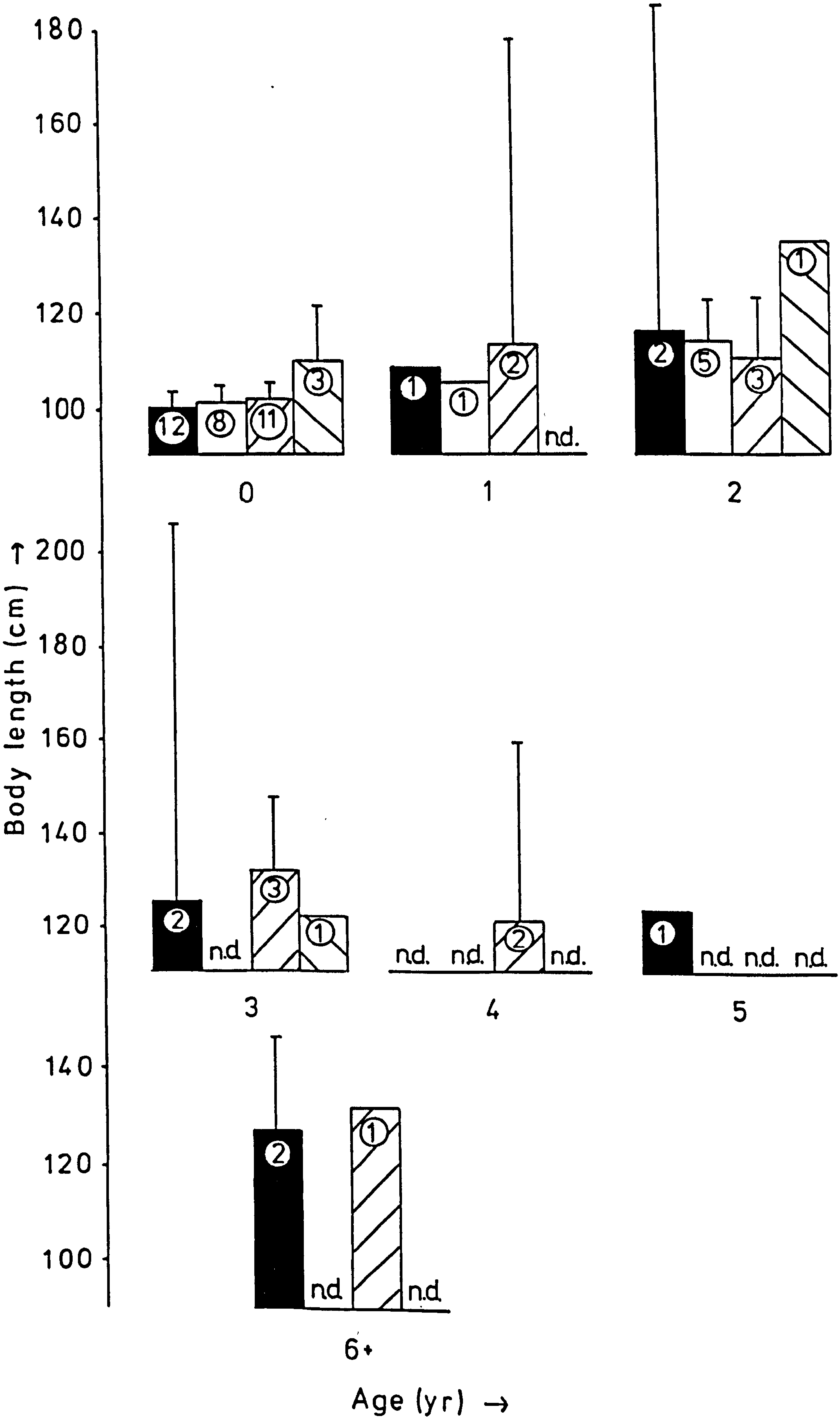
Nannies had higher growth rates than billies for body length and for the former, the highest growth rates were for those at Nether Hindhope (Table 2.5).

Figure 2.4

Mean age specific body lengths (± 95% C.L.) of nannies (a) and billies (b). Labelling as for total weight (Figure 2.1). Statistically significant differences occurred between populations for nannies aged 1 ($p < 0.05$), 2 ($p < 0.05$), and 6+ ($p < 0.001$). For billies, there were no significant differences.


160
140
120
100
80
180
Body length (cm) ↑
Age (yr) →
0
1
2
3
4
5
6+
n.d.
6
16
2
5
1
8
3
4
7
18

(a)


180
160
140
120
100
12
8
11
3
0
1
1
2
n.d.
1
2
5
3
1
2
Body length (cm) ↑
200
180
160
140
120
2
n.d
3
1
3
n.d.
n.d.
2
n.d.
4
1
n.d
n.d.
n.d
5
140
120
100
2
n.d
1
n.d
6+
Age (yr) →

(b)

Study area	Billies	Nannies
Craigdews	4.0	4.5
Cairnsmore of Fleet	6.5	10.5
Moffat Hills	4.0	10.5
Nether Hindhope	12.5	13.0

Table 2.5. Growth rates in body length (cm/yr) between the first autumns or early winters based on means.

As with other measures of size, nannies from Nether Hindhope were generally longer bodied than those from Cairnsmore of Fleet or Craigdews; Moffat Hills nannies tended to have intermediate body lengths. However, differences were not as great as those for total weight or heart girth. Significant differences occurred between populations for nannies in their second, third and seventh plus years (Figure 2.4a, Appendix 2). For the first and last of these age classes, the S.N.K. test revealed that Nether Hindhope nannies had significantly longer bodies ($p < 0.05$) than those at Craigdews or on Cairnsmore of Fleet and on the Moffat Hills for which means did not differ significantly. For nannies in their third year, Nether Hindhope nannies were significantly longer bodied than those from Cairnsmore of Fleet but not the Moffat Hills (Table 2.6).

The mean body lengths of billies showed similar differences but they were less, possibly a result of low sample sizes (Figure 2.4b), and differences between populations were not significant (Appendix 2).

Table 2.6

Multiple comparisons among means of age specific body length for nannies. Differences not significant at $p = 0.05$ are underlined.

Age (yr)

1	Cairnsmore of Fleet	Craigdews	Moffat Hills	Nether Hindhope
	100.6	103.0	103.1	111.0

2	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	113.2	117.3	123.0

6+	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope
	115.8	116.9	123.0	129.4

4. Shoulder height

Shoulder height increased relatively little with age from the first autumn of life. Billies were generally taller and had slower growth rates than nannies (Figures 2.5a & 2.5b, Table 2.7).

Study area	Billies	Nannies
Craigdews	4.0	3.5
Cairnsmore of Fleet	1.5	3.5
Moffat Hills	4.0	4.0
Langholm-Newcastleton Hills	3.5	5.0
Nether Hindhope	1.5	5.0

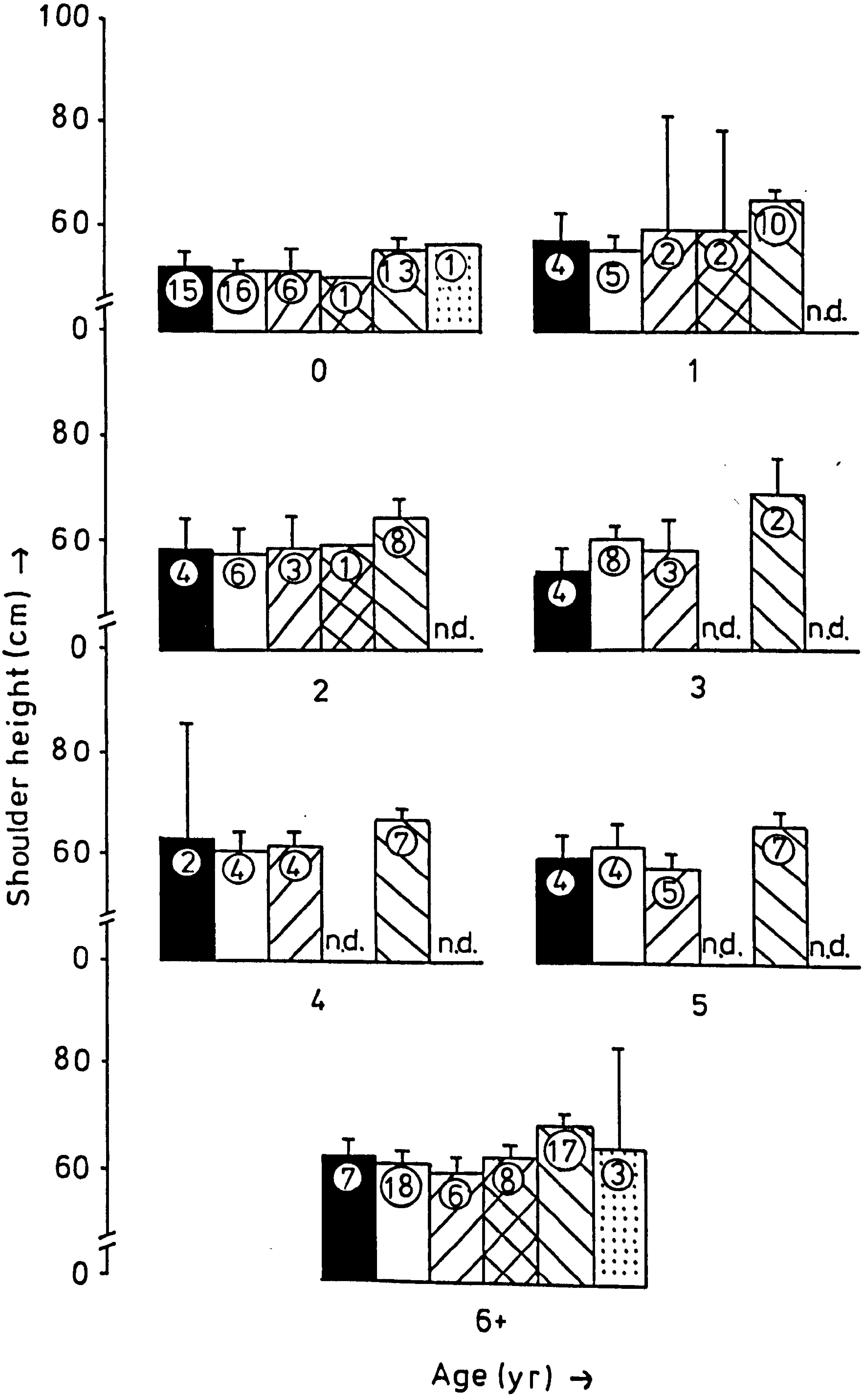
Table 2.7. Growth rates in shoulder height (cm/yr) between the first and third autumns or early winters based on means.

Mean shoulder heights of nannies from Craigdews, Cairnsmore of Fleet, Moffat Hills and Langholm-Newcastleton Hills, were similar and noticeably smaller than those from Nether Hindhope (Figure 2.5a). Analyses of variance revealed significant differences between populations in shoulder height for nannies in their second, third and seventh plus years (Figure 2.5a, Appendix 2). S.N.K. tests indicated that this was because Nether Hindhope nannies were significantly taller ($p < 0.05$) than those from other populations (Table 2.8).

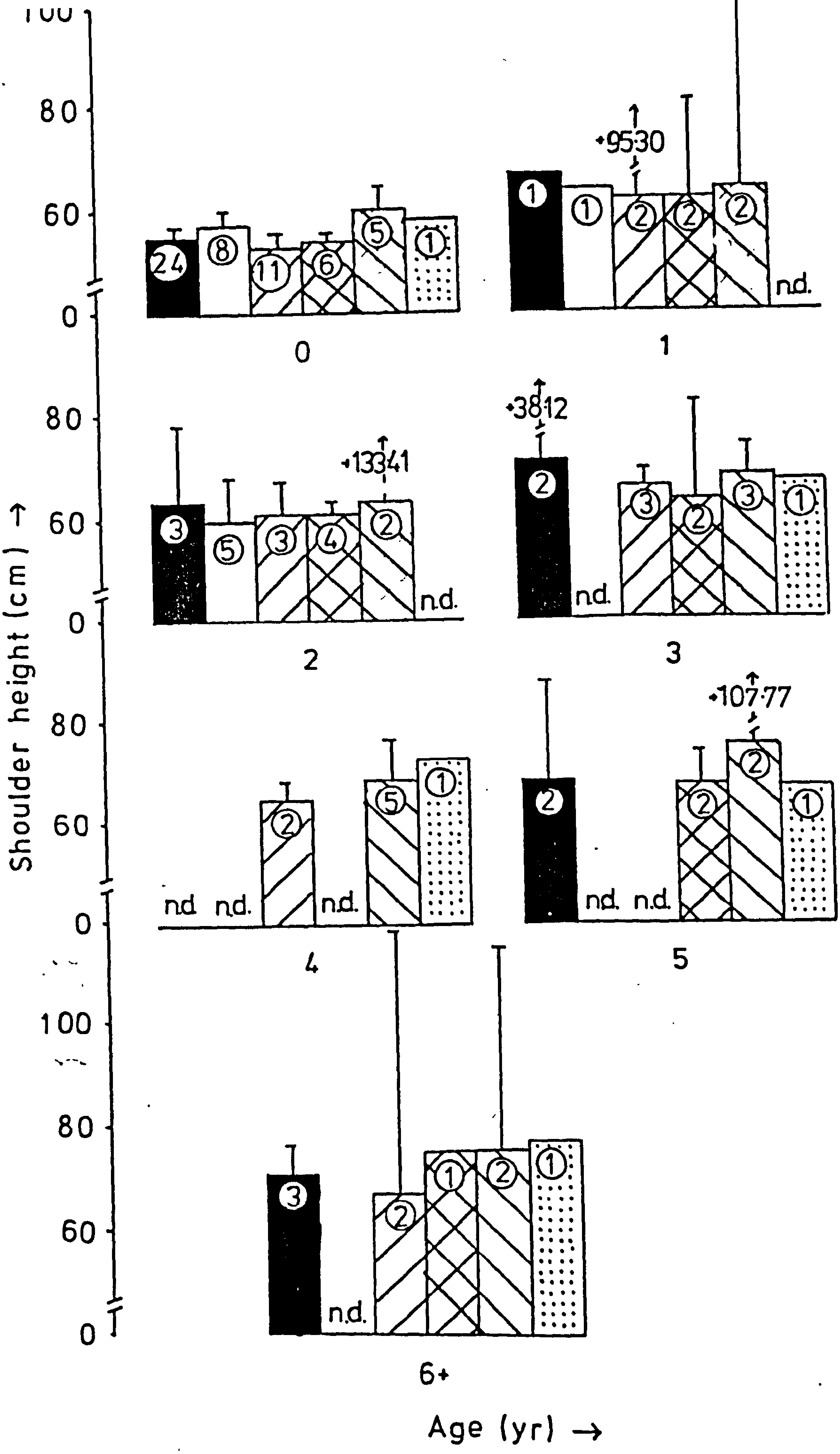
Billies of the same age from different populations show few differences in their shoulder heights and only for kids was there a significant difference (Figure 2.5b, Appendix 2). Comparisons among

Figure 2.5

Mean age-specific shoulder height (± 95% C.L.) for nannies (a) and billies (b). Labelling as for total weight (Figure 2.1) but including the Langholm-Newcastleton Hills (cross hatched histograms) and College Valley (stippled histogram). Statistically significant differences occurred between populations for nannies aged 1 ($p < 0.05$), 2 ($p < 0.05$), 4 ($p < 0.05$), 5 ($p < 0.001$) and 6+ ($p < 0.001$). For billies there were no significant differences.


100
80
60
0
80
60
0
80
60
0
80
60
0
Shoulder height (cm) →
15
16
6
1
13
1
0
4
5
2
2
10
n.d.
1
4
6
3
1
8
n.d.
2
4
8
3
n.d.
2
n.d.
3
2
4
4
n.d.
7
n.d.
4
4
4
5
n.d.
7
n.d.
5
7
18
6
8
17
3
6+
Age (yr) →

(a)


100
80
60
0
Shoulder height (cm) →
Age (yr) →
24
8
11
6
5
1
0
1
1
•95.30
2
2
2
n.d.
1
3
5
3
4
•133.41
2
n.d.
2
•38.12
2
n.d.
3
2
3
1
3
nd
n.d.
2
n.d.
5
1
4
2
n.d.
n.d.
2
•107.77
2
1
5
3
n.d.
2
1
2
1
6+

(b)

Table 2.8

Multiple comparisons among means for age-specific shoulder heights of nannies (a) and billies (b). Differences not significant at $p = 0.05$ are underlined.

(a) Nannies

Age (yr)						
1	Cairnsmore of Fleet 54.8	Craigdews 56.8	Moffat Hills 58.5	Langholm-Newcastleton Hills 58.6	Nether Hindhope 64.6	
2	Cairnsmore of Fleet 57.5	Craigdews 58.8	Moffat Hills 59.0	Nether Hindhope 64.8		
4	Cairnsmore of Fleet 60.5	Moffat Hills 61.5	Craigdews 63.0	Nether Hindhope 67.1		
5	Moffat Hills 57.8	Craigdews 60.2	Cairnsmore of Fleet 62.3	Nether Hindhope 66.3		
6+	Moffat Hills 60.3	Cairnsmore of Fleet 61.6	Langholm-Newcastleton Hills 62.9	Craigdews 63.4	College Valley 65.0	Nether Hindhope 68.8

(b) Billies

Age (yr)					
0	Moffat Hills 53.3	Langholm-Newcastleton Hills 54.2	Craigdews 55.3	Cairnsmore of Fleet 57.1	Nether Hindhope 59.6

means revealed that, as with nannies, billy kids from Nether Hindhope were significantly taller ($p < 0.05$) than those from other populations (Table 2.8).

5. Tail length and ear length

Measurement of both these appendages on live goats was difficult and within the limit of accuracy, (0.5 cm), no consistent differences between populations occurred. Therefore, generalised growth curves for both are presented calculated from pooled samples. Ears were measured for goats from Craigdews, Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Nether Hindhope and College Valley. Data on tail lengths were from Craigdews, Cairnsmore of Fleet, Moffat Hills and Nether Hindhope (Figure 2.6).

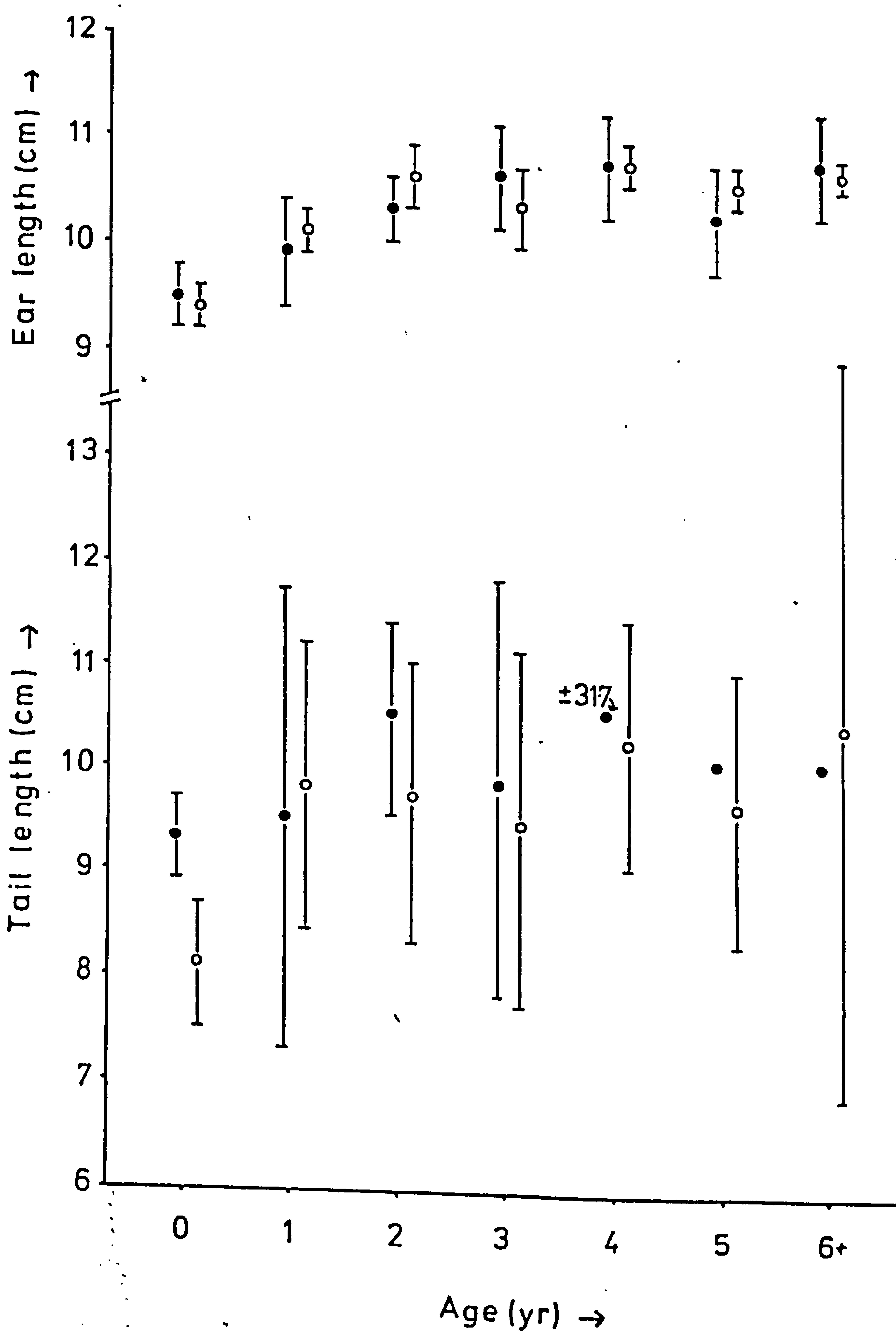
Both ears and tails grew little after the first year and there were no consistent differences between the sexes. Mean ear lengths were all between 9.4 cm and 10.7 cm. Mean tail lengths varied between 8.1 cm and 10.5 cm (Figure 2.6); the large confidence limits for the latter are likely to reflect not only true variability in tail length but, more than other measurements, human error. Tails were particularly difficult to measure with consistency.

6. Horn length and horn increment length

Horn lengths of billies and nannies from six populations were obtained; Craigdews, Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Nether Hindhope and College Valley. For the last population, the horn lengths of some of the goats culled in November 1976 (Chapter 4) were included; these horns had not been removed from their cores so that shrinkage due to dessication was probably small.

Figure 2.6

Mean age-specific ear lengths and tail lengths (± 95% C.L.) of nannies (o) and billies (•). Data from six Southern Upland populations.


Ear length (cm) →
12
11
10
9
Tail length (cm) →
13
12
11
10
9
8
7
6
±3·17
0
1
2
3
4
5
6+
Age (yr) →

Horns of billies grew much faster and were much longer age for age than those of nannies (Figures 2.7a & 2.7b, Table 2.9). Further, horn growth of billies was sustained for longer than that of nannies reaching means of between 570 mm and 720 mm, depending on the population, by the fifth year (Figure 2.7b). The mean horn length of nannies of the same age varied between 190 mm and 250 mm (Figure 2.7a) and increased little thereafter. The result was increasing sexual dimorphism in horn size with age.

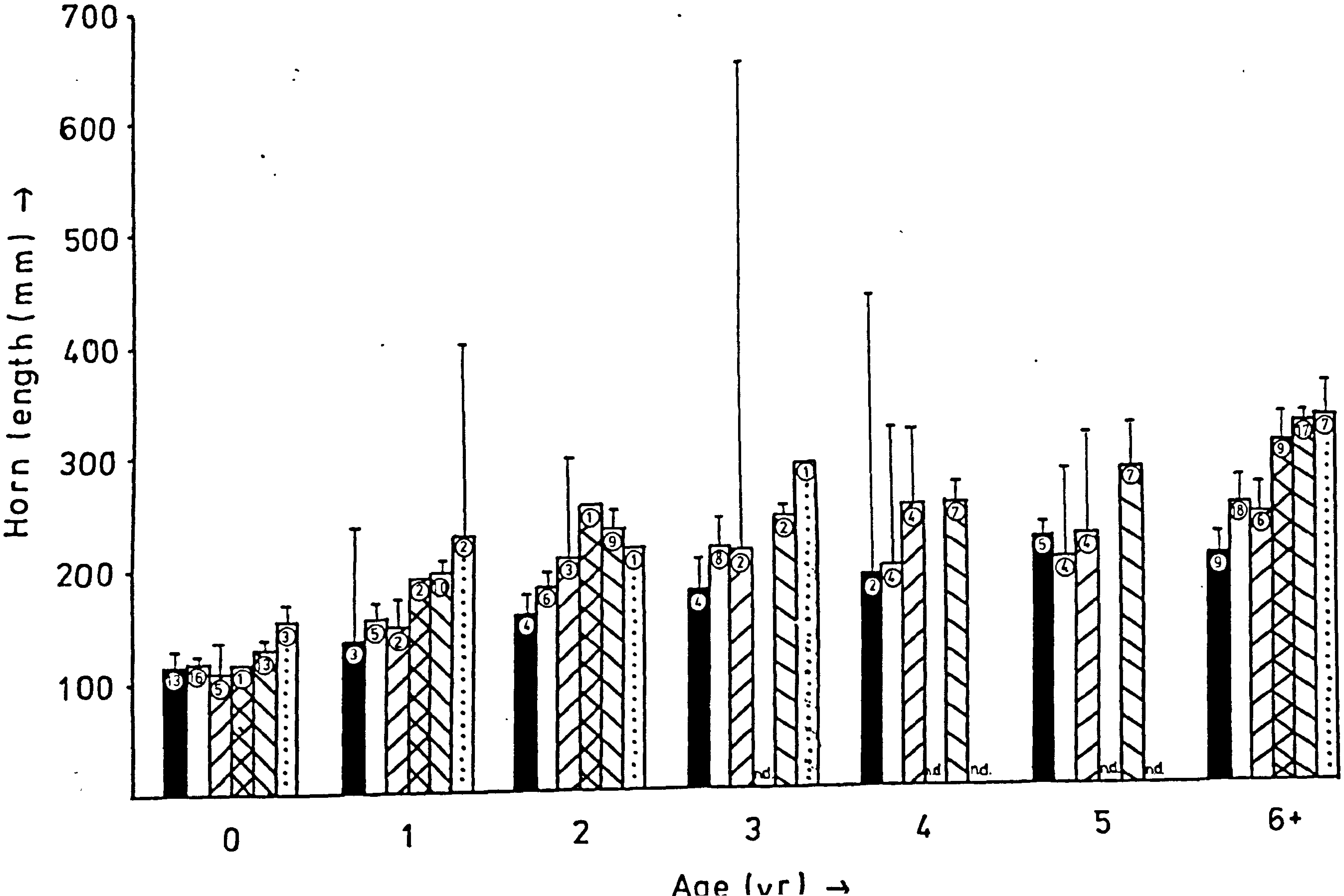
Study area	Billies	Nannies
Craigdews	79.5	22.5
Cairnsmore of Fleet	105.0	32.5
Moffat Hills	111.5	50.0
Langholm-Newcastleton Hills	86.0	70.0
Nether Hindhope	133.5	51.0
College Valley	124.0	32.5

Table 2.9. Growth rates of horn length (mm/yr) between the first and third autumns or early winters based on means.

For nannies, there were clear differences in mean age-specific horn length between populations; in particular those from Craigdews and Cairnsmore of Fleet had the smallest horns and those from College Valley, Nether Hindhope and the Langholm-Newcastleton Hills the largest horns for each age class (Figure 2.7a). Analyses of variance revealed significant differences between populations for nannies in their first, second, third and seventh plus years (Figure 2.7a, Appendix 2).

Figure 2.7

Mean age-specific horn lengths (± 95% C.L.) of nannies (a) and billies (b). Labelling as for shoulder height (Figure 2.5). Statistically significant differences occurred between populations for nannies aged 0 ($p < 0.001$), 1 ($p < 0.01$), 2 ($p < 0.01$) and 6+ ($p < 0.01$). For billies there were significant differences at age 0 ($p < 0.01$) and 1 ($p < 0.01$).


Horn length (mm) →
700
600
500
400
300
200
100
0
1
2
3
4
5
6+
Age (yr) →
13
16
5
1
13
3
3
5
2
2
10
2
4
6
3
1
9
1
4
8
2
nd.
2
1
2
4
4
nd
7
nd.
5
4
4
nd
7
nd
9
8
6
9
17
7

(a)

(b)

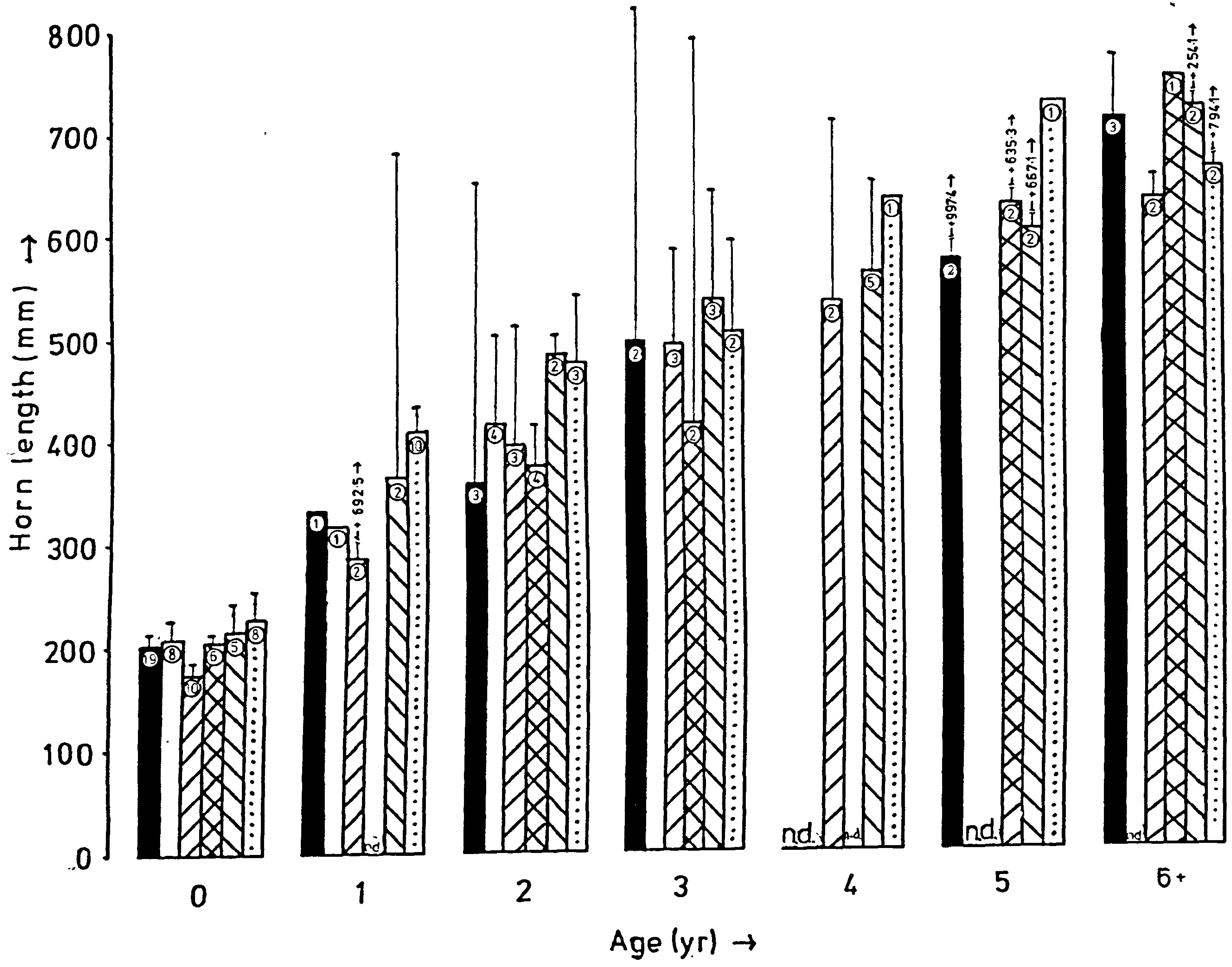

Horn length (mm) →
800
700
600
500
400
300
200
100
0
19
8
10
6
5
8
1
1
2
nd
692·5 →
2
10
3
4
3
4
2
3
2
3
2
3
2
nd.
nd
2
5
1
2
nd.
2
2
1
997·4 →
635·3 →
667·1 →
3
nd
2
1
2
2
2541 →
7941 →
0
1
2
3
4
5
6+
Age (yr) →

Table 2.10

Multiple comparisons among means of age-specific horn lengths of nannies (a) and billies (b). Differences not significant at $p = 0.05$ are underlined.

(a) <u>Nannies</u>

Age (yr)						
0	Moffat Hills	Craigdews	Cairnsmore of Fleet	Nether Hindhope	College Valley	
	109.0	113.2	115.0	129.0	151.3	
1	Craigdews	Moffat Hills	Cairnsmore of Fleet	Langholm-Newcastleton Hills	Nether Hindhope	College Valley
	133.7	146.0	152.0	190.0	193.7	230.0
2	Craigdews	Cairnsmore of Fleet	Moffat Hills	Nether Hindhope		
	158.3	179.3	208.7	231.3		
6+	Craigdews	Moffat Hills	Cairnsmore of Fleet	Langholm-Newcastleton Hills	Nether Hindhope	College Valley
	207.9	243.3	253.9	307.8	322.6	329.9

(b) <u>Billies</u>

0	Moffat Hills	Langholm-Newcastleton Hills	Craigdews	Cairnsmore of Fleet	Nether Hindhope	College Valley
	172.4	200.8	201.2	207.0	215.4	227.5
1	Moffat Hills	Langholm-Newcastleton Hills	Nether Hindhope	College Valley		
	284.5	340.0	365.0	410.3		

The S.N.K. test indicated that these differences were the result of Nether Hindhope and College Valley nannies having significantly longer ($p < 0.05$) horns than those from Cairnsmore of Fleet or Craigdews (Table 2.10).

Differences in horn length between populations for billies, at least for the first three years of life, were similar to those for nannies; Cairnsmore of Fleet and Craigdews billies had smaller horns than those from College Valley and Nether Hindhope. Thereafter mean horn lengths were similar and confidence limits were markedly larger.

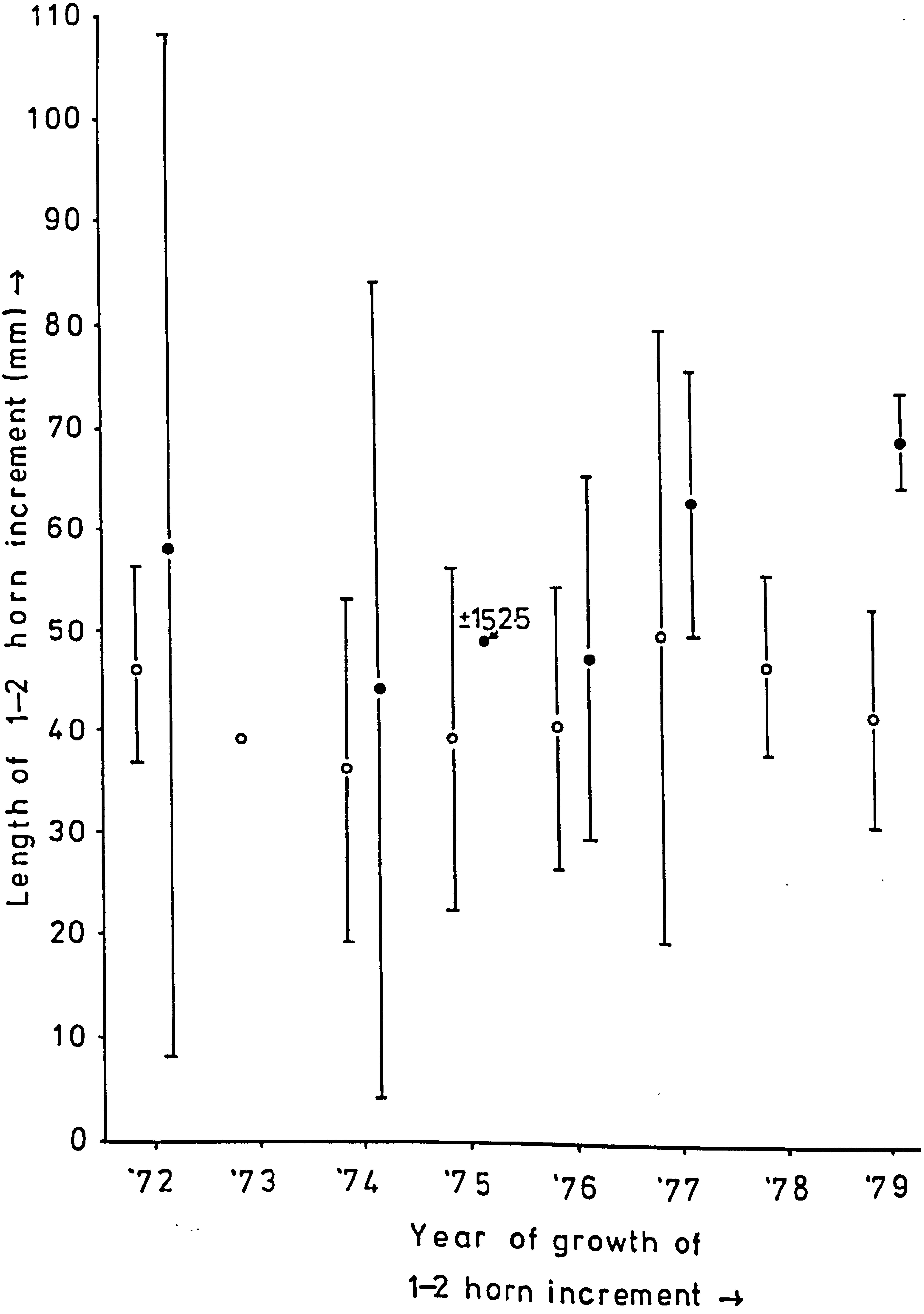
Populations differed significantly only in their first and second years (Figure 2.7b, Appendix 2), and for these two age classes, Moffat Hills billies had significantly shorter ($p < 0.05$) horns than those in other populations (Table 2.10).

A potentially confounding variable in comparisons of body or horn size is the year to year variation in growth rate. This could be investigated in a preliminary way using horn growth and in particular horn increment length of nannies from Cairnsmore of Fleet and Nether Hindhope. Samples of nannies from other populations and those of billies were too small to warrant analyses. Since the first year's horn growth (the 0-1 increment) may have been underestimated due to wear, the mean length of the second year growth (1-2 increment) was compared for different years.

Mean length of the 1-2 increment varied in a similar way between years for nannies at Nether Hindhope and at Cairnsmore of Fleet (Figure 2.8). 1972 and 1977 were 'good growth' years when increment length was longer than in the 'poor growth' years of 1974, 1975 and 1976. In 1979

Figure 2.8

The relationship between the year of growth of the 1-2 (second year) horn increment and its length (mean ± 95% C.L.) for nannies from Cairnsmore of Fleet (o) and Nether Hindhope (●).


110
100
90
80
70
60
50
40
30
20
10
0
Length of 1–2 horn increment (mm) →
±15.25
'72
'73
'74
'75
'76
'77
'78
'79
Year of growth of
1–2 horn increment →

growth was 'poor' on Cairnsmore of Fleet but 'good' at Nether Hindhope. In all cases the sample sizes were small and confidence limits large but the data suggested that variation in horn length may be related not only to the population but also to the years through which an individual has grown.

Sexual dimorphism in size

Two ratios, that of mean male total weight to mean female total weight and mean male horn length to mean female hron length for each age class respectively, were used to examine sexual dimorphism. Billies always weighed more than nannies of the same age and were up to 1.48 times as heavy with an increase with age in the degree of dimorphism. Sexual dimorphism in horn length was much more pronounced and increased markedly with age reaching a maximum of 3.42 for goats in their seventh plus year at Craigdews (Figure 2.9). For other measures of body size, sexual dimorphism was similar in degree to that for weight.

The greater weights of billies compared to nannies of the same age was, in part, due to their relatively heavier horn sheaths plus skull weights (head weight). The proportion of the total weight that was made up of head weight increased more or less linearly for billies to a maximum of 2.6% in the seventh plus year; for nannies the maximum was 1.1% and after the third year no increase in the proportion was evident (Figure 2.10).

Discussion

The data on weights and growth rates described in this chapter had two serious omissions. Firstly, weights of neonates born to nannies of known age and weight were not obtained. Secondly, few data on annual

Figure 2.9

Sexual dimorphism (y axis) expressed as the ratios of mean male total weight to mean female total weight and mean male horn length to mean female horn length for each age class and population. Ratios were calculated only when two or more individuals from each sex had been measured.

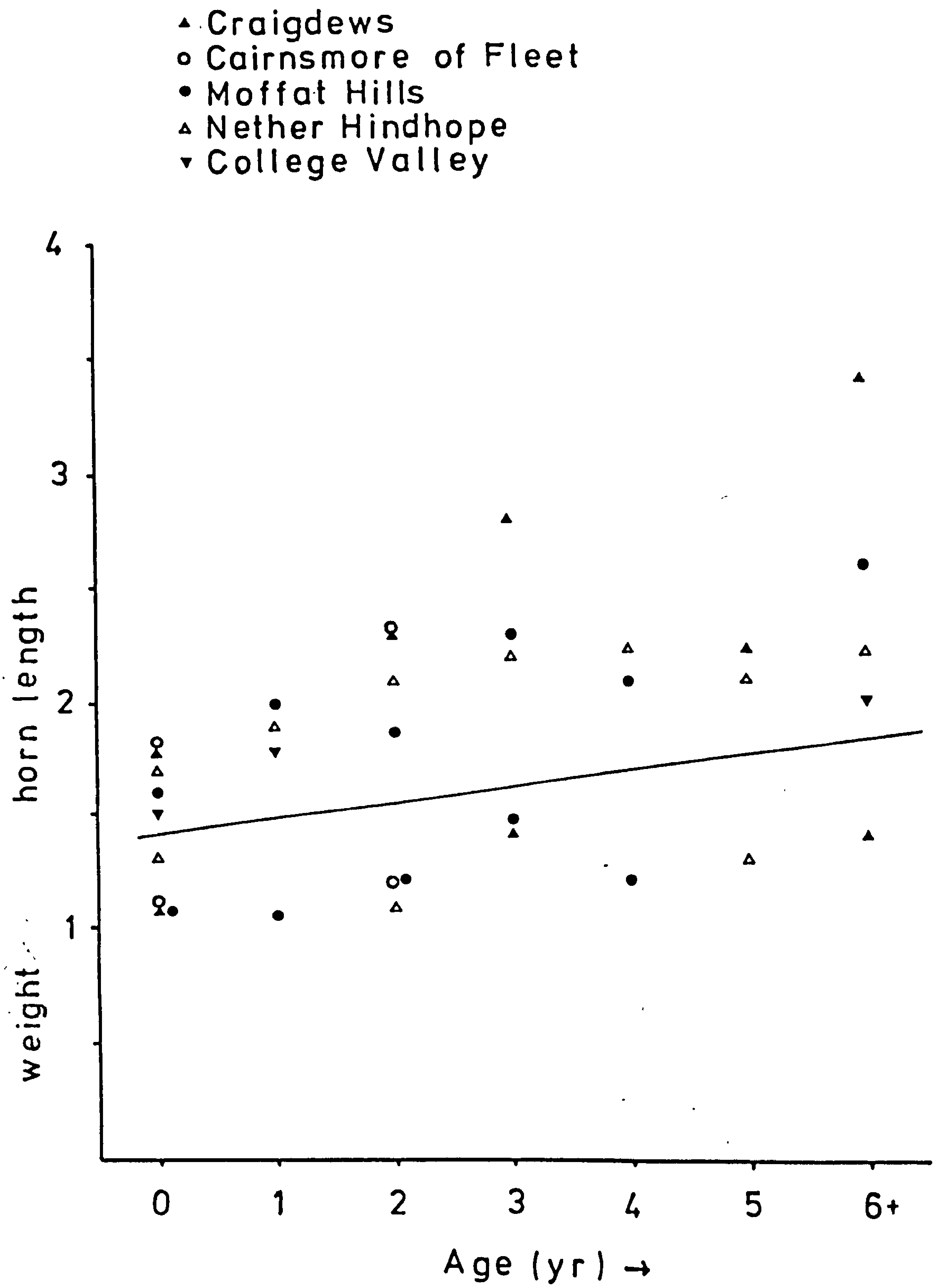
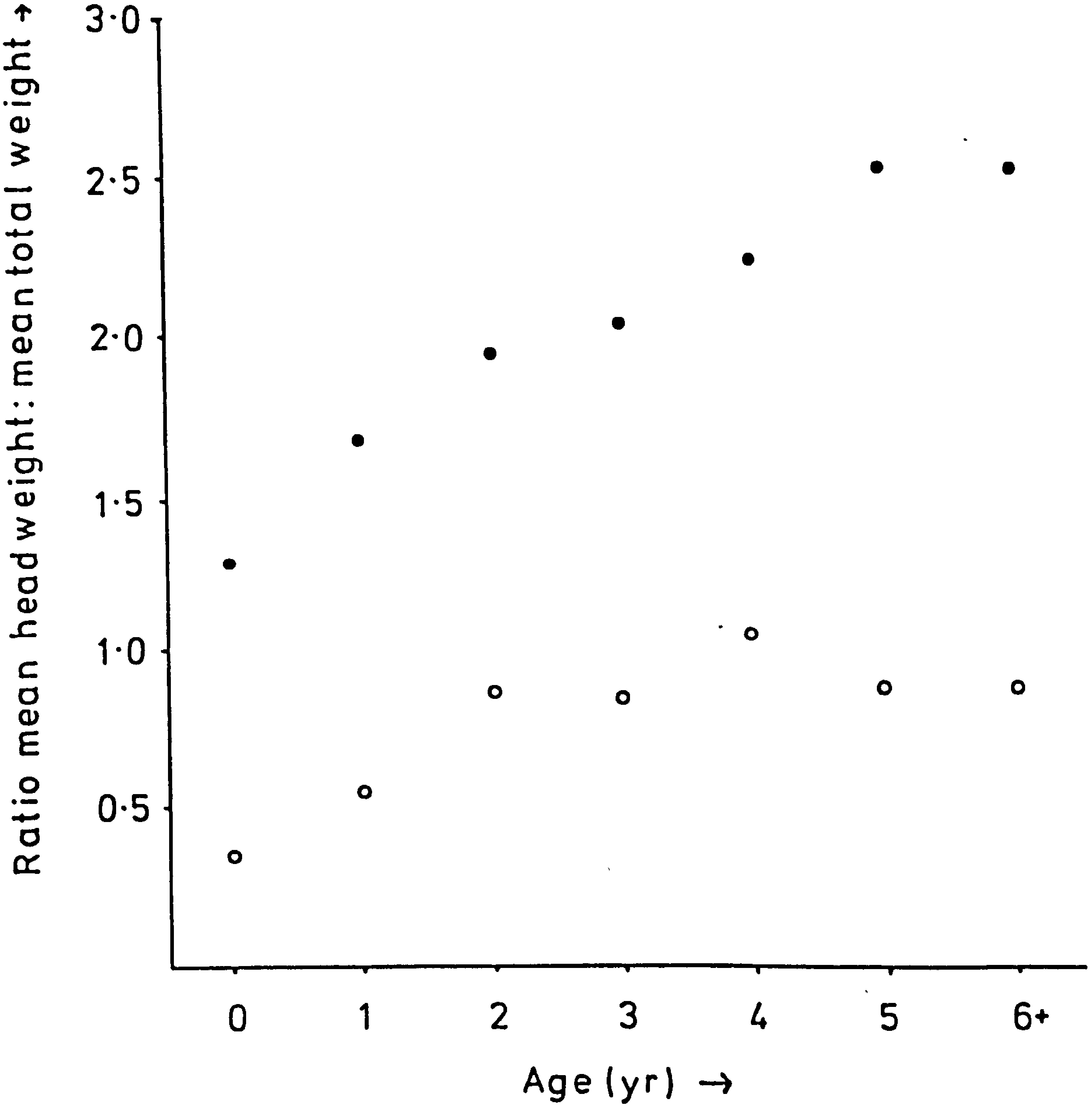

▲ Craigdews
○ Cairnsmore of Fleet
● Moffat Hills
△ Nether Hindhope
▼ College Valley
horn length
weight
4
3
2
1
0
1
2
3
4
5
6+
Age (yr) →

Figure 2.10

The relationship between age and the ratio of mean head weight (weight of dry skull plus horn sheaths) to total weight for billies (•) and nannies (o). Data from several Southern Upland populations.



Ratio mean head weight : mean total weight →
3·0
2·5
2·0
1·5
1·0
0·5
0
1
2
3
4
5
6+
Age (yr) →

fluctuations in growth rates were collected.

The weight of the neonate is an important population parameter in sheep and goat populations. For instance, in feral Soay sheep, the weight of the parous dam was related to the birth weight of the lamb; lambs of low birth weight also had a lower survival rate (Grubb 1974a). Similar dynamics occur in domestic sheep (Anon 1979) and also domestic goats (Ahmed and Tantawy 1960).

For ungulates in temperate or arctic regions, changes in diet and a drop in voluntary food intake occur from summer to winter and early spring (see Chapter 3). Concomitant with these is a marked decrease in weight (Bandy, Cowan & Wood 1970; Doney et al. 1974; Hoefs 1974; Mitchell, McCowan & Nicholson 1976; Wood, Cowan & Nardan 1962). My data for feral goats were insufficient to show an annual periodicity of growth although the considerable weight losses of the Nether Hindhope nannies between November and June indicate that it probably occurred. Weight loss in some of these individuals may have been associated with lactation during which there are great energy demands on the female mammal (Sadleir 1972).

Substantial variation in the total weight of ruminants may occur hourly or daily (Talbot & McCulloch 1965). For this reason single measurements of the weights of feral goats are unsatisfactory. Similarly, since goats from some populations were weighed in November and some in December the observed differences in weight may have been confounded by individuals losing weight between the two months. However, other measures of body size less affected by variations in rumen fill and season such as body length and horn length revealed the same differences between populations as those found for weight. Therefore, I believe the comparisons were valid.

Sexual dimorphism occurred for weight and all other measures of body size with the exception of ear lengths and tail length. Billies sustained growth longer and often grew faster than nannies. This means that comparisons between feral goat populations in terms of 'adult' body size or 'adult' weight are only valid when the population structures are identical. The same conclusion was reached by Caughley (1971) from analysis of two red deer populations in New Zealand.

As few billies in their seventh or older years were caught, it was not established whether growth continued beyond this age. Doney *et al.* (1974), showed that, for feral Soay rams on Hirta, total weight gain continued up to at least the sixth year whereas ewes from the same population reached an asymptote by the fourth year. This is similar to the weight and other growth curves for feral goats in the present study, those from Holy Island (Bareham unpub.) and Wales (Brown 1977), and also for bighorn sheep (Blood *et al.* 1970) and hill sheep (Anon 1979; Slee *in litt.*).

The greater weight gains of billies compared to nannies was associated with increasing weight of the skull and horns and the greater fighting ability in the former. The proportion of total weight that was head weight, up to 2.5%, was similar to that of approximately 2% for wild goats (Schaller 1977). These proportions are very small compared to those for wild American rams which bear 8% to 12% of their body weight as horns alone (Geist 1966). In all male caprinids the large and heavy heads and horns may give rise to greater heat loss and increased energy expenditure in winter. In late winter, when both sexes are probably on a submaintenance diet and decline in weight, as are hill sheep (Eadie 1970), the heavier head weight of billies compared to nannies may contribute to the former's lower survival rate (Chapter 4).

In common with other mammals which have polygynous mating systems, the strong sexual dimorphism exhibited by feral goats is probably linked to sexual selection (Bartholomew 1970; Geist 1971; Grubb 1974b; Jewell 1976; Newsome 1977; Schaller 1977). The theory of sexual selection in males predicts that larger, stronger individuals (although not necessarily the oldest) are more likely to be dominant in male-male competition and enjoy the majority of successful sirings. Hypotheses relating body sizes, horn size and fighting ability are in the process of being tested for feral billies in the Moffat Hills (S. Pickering pers. comm.) but the lifetime reproductive success of billies is unknown because most individuals outlived the duration of the study.

It has not been possible to separate genetic and environmental influences as causes of morphometric variability although circumstantial evidence presented below suggests that variations in body and horn size are primarily the result of varying environmental conditions.

The trend of decreasing body size and horn length from north-east to south-west across the Southern Upalnds parallels a trend in decreasing soil fertility as judged by the composition of the parent rock. Andesitic tuffs and basalts of the Cheviot Hills in which the College Valley and Nether Hindhope populations occur, make some of the most fertile hill pasture in the Southern Uplands (Hunter 1962). The Langholm-Newcastleton Hills have mixtures of shales, sandstones and granite as parent rock and the Moffat Hills shales and greywackes. In both areas the soil fertility is presumed to be lower than that for the Cheviot Hills. The parent rock at Craigdews and on Cairnsmore of Fleet is granite which is nutrient poor giving rise to soils of low fertility. It is inferred that, since the nutritional quality of the vegetation is in large measure dependent on soil fertility, the observed morphometric differences between feral goat populations could be explained by differences in the quality of the food supply.

This appears likewise to be the case for hill sheep. Age-specific total weights of Scottish Blackface hill ewes from hill farms in Argyll and the Cheviots were made available through the courtesy of Dr. R.H. Armstrong. The lower total weights for ewes of the same age from Argyll compared to those in the Cheviots are striking (Figure 2.11).

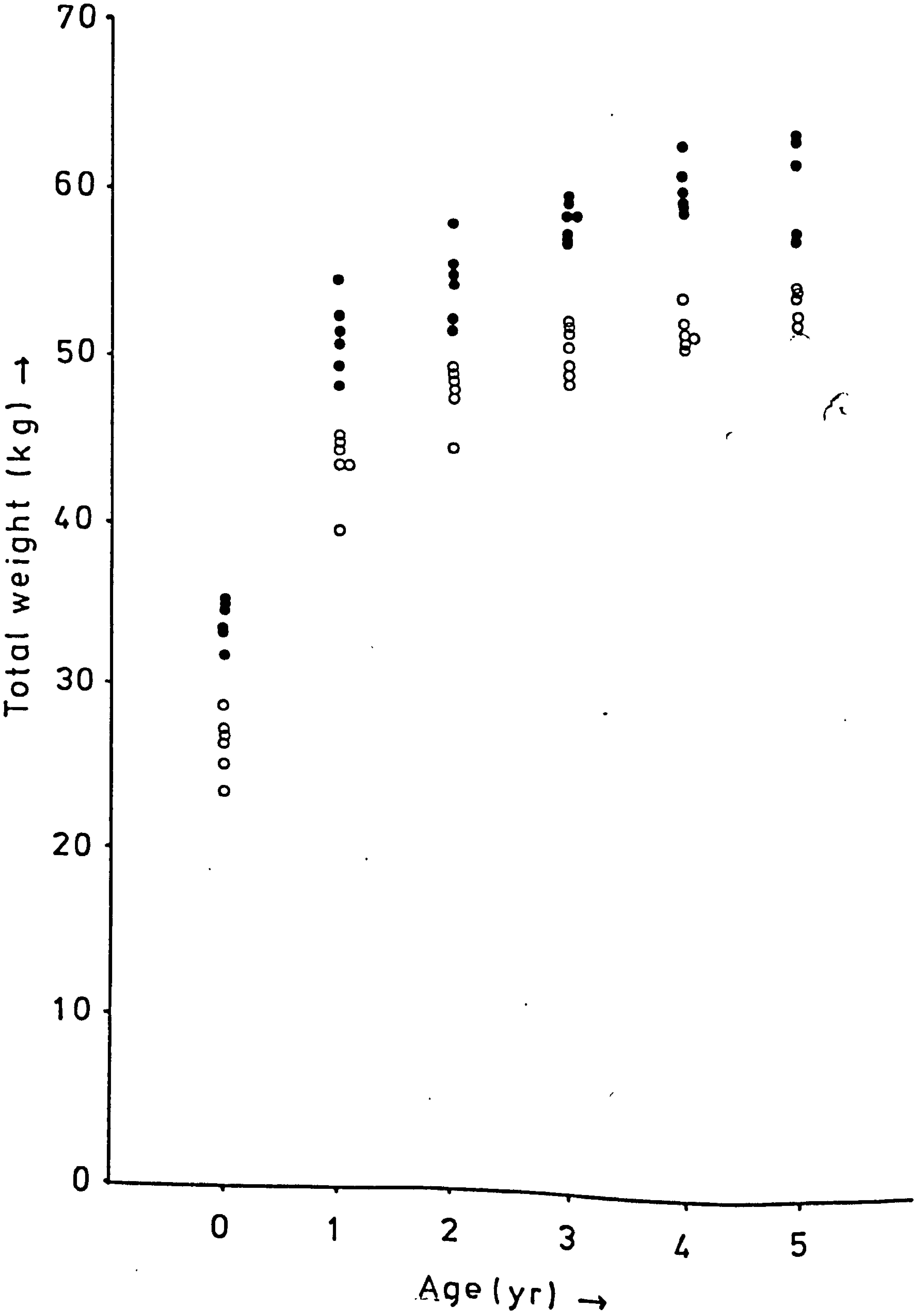
Stocking densities of hill sheep decreased with decreasing soil fertility across the Southern Uplands from north-east to south-west (Chapter 4). This was expected since they reflect the winter carrying capacity of the pasture. The data indicate that an important factor governing the size of hill sheep and feral goats is their nutritional background.

Population density may also have affected body size. Goat density was considerably higher at Craigdews and on Cairnsmore of Fleet than in other populations (Chapter 4) and the former goats were the smallest. Klein and Strandgaard (1972) found that body size and weight of roe deer in Denmark were inversely related to population density. The hypothesis that variation in the size of feral goats are firstly, the result of variation in food supply and secondly variation in population density could be tested by experimental manipulation of populations.

Feral goats in the Southern Uplands had similar ranges of body sizes to those in Wales (Brown 1977; Crook 1969) and on Holy Island (Bareham unpub.); although those on the former were, on average, heavier this may have been the result of sampling at different seasons. Much larger feral goats have been reported than those described in the present study. Whitehead (1972) considered that the normal upper limit

Figure 2.11

Mean age-specific total weights of six cohorts of hill Blackface ewes from Argyll (o) and the Cheviot Hills (●). Data courtesy of Dr. R.H. Armstrong (H.F.R.O.).


70
60
50
40
30
20
10
0
Total weight (kg) →
0
1
2
3
4
5
Age (yr) →

on weight of Scottish feral billies was 76 kg, 8 kg more than the maximum recorded in this study for a billy from Nether Hindhope. The total weight of a feral billy from Ben Venue (Perthshire) of 140 kg (Whitehead 1972) is suspiciously high. Judging by their large horns and the few data available on body size, it is likely that billies from College Valley attain heavier weights than those from other populations.

Horn lengths of trophy billies shot in Scotland and Ireland (Whitehead 1972) are similar to the maximum horn lengths recorded in the present study. Both are longer than the longest horns of wild goats from a high density population on Theodorou Island off Crete (Papageorgiou 1974) but not longer than those of wild goats from Iran (Schaller 1977) where, however, weights were comparable to those of feral goats (Valdez, Alamia, Bunch & Mowlavi 1977).

A preliminary analysis suggested that year to year fluctuations in horn growth could be considerable. They also occurred in feral Soay rams (Grubb 1974b) and wild Dall rams (Bunnell 1978); such factors as environmental quality and population density may be causal and interactive in determining growth rate and may be useful in predicting range quality and secondary production.

Poor nutrition during the long upland winter probably restricts feral goats to a small skeletal frame which prevents attainment of their genetic potential given good nutrition. This likewise appears to be the reason why Scottish red deer are small compared to their conspecifics in Continental Europe and Asia (Suttie 1980).

The coincidental variations in size and soil fertility and the variations in horn growth by different cohorts suggest that environmental influences are strong. However, the populations in the Southern Uplands are likely to have been established by a small number of individuals and founder effects may have occurred which influenced body size. This could be investigated by transferring individuals between populations and monitoring their growth rates.

CHAPTER 3. FEEDING ECOLOGY

Introduction

There is little information on the feeding ecology of feral goats or the extent of overlap in diet and habitat usage between them and hill sheep. This chapter describes the feeding behaviour, habitat usage and diet of feral goats and hill sheep in several of the study areas.

How and why herbivores select particular forages are important questions of behaviour and ecology. As Ewer (1968) noted, the way herbivores feed, their feeding style (Jarman 1974), has been poorly studied. Without such information a comprehensive comparison of feeding ecologies of sexes or of a species is impossible.

Feeding behaviour may profoundly influence survival rates of individuals. For instance, it is inferred that the great reduction in feeding time of feral rams on St Kilda during the autumn rut in primarily responsible for their survival rates being lower than those of the ewes (Grubb & Jewell 1974).

Differences in feeding behaviour can serve to reduce competition (Selander 1972). Sympatric herbivore species or males and females of the same species may eat the same plant species but use different plant parts or have spatial or temporal differences in feeding behaviour. These variables have been disentangled for some African ungulate and primate species and can be related to interspecific differences in social and spatial organisation (Bell 1970; Clutton-Brock 1974; Clutton-Brock 1977; Geist 1974; Jarman 1974).

Quantification of habitat use, and in particular of the selection of plant communities is essential for assessing impact, constructing predictive models of feeding ecology and for the study of range relationships between herbivores. Sheep and red deer on British uplands select plant communities with the highest digestible energy content; these are the communities on mull soils (Hunter 1962) chiefly Festuca-Agrostis grasslands (Charles, McCowan & East 1977; Colquhoun 1971; Griffiths 1970; Hughes, Dale, Mountford & Ellis-Williams 1975; Rawes & Welch 1969). There is some evidence that feral goats also select these communities (Buckland 1978).

Ungulates, because of their ability to digest and assimilate nutritionally poor forages, are the major converters of plant cellulose into food for human consumption. Furthermore, ungulates are capable of greatly modifying the vegetation that they exploit. It follows that knowledge of their diets is essential for assessing environmental impact.

As a result of their ecological importance and commercial value, hill sheep have been the subject of several studies of feeding ecology. Hunter (1962) and Martin (1964) determined sward preferences and diets respectively of Scottish hill sheep. Arnold (1964) showed that sheep are capable of selecting the most digestible plant growth; in general, they select leaf in preference to stem and green material in preference to dead material. We should expect goats to show similar 'nutritional wisdom' (Arnold & Dudzinski 1979; Lockie 1967) whereby a ruminant selects what it requires from an environment containing a wide variety of different foods of varying quality.

Goats and sheep are frequently classed as browsers and grazers respectively (e.g. Cory 1927; Wilson, Leigh, Hindley & Mulham 1975). Whilst such a classification may be appropriate in environments where the opportunity to browse exclusively exists, it is inappropriate with respect to British uplands since they are characteristically devoid of trees. We may expect a greater similarity in the diets of sheep and goats in these habitats than elsewhere with consequently a higher potential for competition. A large part of this chapter is therefore devoted to describing the diets of sheep and goats where they were sympatric.

Methods

1. Feeding behaviour

The way in which feral goats feed was qualitatively described from opportunistic observations. These data are presented to permit comparison between the feeding behaviour of sheep and goats.

Feeding activity and feeding time budgets were determined by instantaneously scan sampling (Altmann 1974) undisturbed goat or sheep groups every five or ten minutes to record the number of individuals respectively feeding, walking, lying, standing or engaged in social or sexual (socio-sexual) behaviour. The six or three points in each half hour period were lumped and expressed as percentages. Where possible, the activity of known individuals or their groups was recorded in order to determine the duration of rest periods and movements. Group location was recorded every half hour on large scale (1 : 10,560) maps.

Observations were conducted in daylight; during the autumn, winter and early spring, I observed from dawn to dusk. During the late spring and summer, observations began at midday, continued until dusk, started again at dawn and ended at midday. Time budget data from all day or half day observations was supplemented by opportunistic observations from Cairnsmore of Fleet and the Moffat Hills.

2. Habitat use

Opportunistic observations of undisturbed goat and sheep groups during daylight provided data on habitat use. For each individual the following data were recorded using a cassette recorder or a checksheet: time, location, age and sex class (Chapter 4), vegetation type and altitude class. Altitude classes were: 1. (76-151)m; 2. (152-228)m; 3. (229-304)m; 4. (305-380)m; 5. (381-456)m; 6. (457-532)m; 7. (533-609)m; 8. (610-685)m and 9. (686-770)m. Kids and lambs were excluded from analyses since their behaviour was dependent on their dams.

Vegetation types were those assemblages of plant species that could be recognised in the field. Table 3.1 lists the vegetation types, their constituent plant communities and their nearest equivalent associations as described by McVean and Ratcliffe (1962). I compared my ability to identify vegetation types in the field with that of field botanists mapping the vegetation of the Moffat Hills. There was close agreement between us on a range of communities.

Selection ratios were used to compare the use of different vegetation types by billies, nannies and ewes. The selection ratio, which is similar to the Comparative Grazing Index of Hunter (1962), is a measure of the frequency with which a herbivore is observed on a particular vegetation type, correcting for the relative availability of that type in the study area. It is calculated as follows:

$$\text{Selection ratio} = \frac{\text{\% of observations in vegetation type 'X'}}{\text{\% of vegetation type 'X' in the study area}}$$

Table 3.1

The vegetation types, their constituent plant communities and their nearest equivalent associations to those of McVean and Ratcliffe (1962).

Vegetation type	Constituent plant communities	Nearest equivalent association
Dry/moist heath	*Calluna vulgaris* heath	Callunetum vulgaris
	Vaccinium myrtillus heath	Vaccineto-Callunetum
	Calluna/Vaccinium mixtures and mosaics	Vaccineto-Empetretum
Wet heath/blanket mire	*Calluna/Molinia*	Molinieto-Callunetum
	Calluna/Trichophorum	Trichophoreto-Callunetum
	Trichophorum/Eriophorum vaginatum	Trichophoreto-Eriophoretum typicum
	Calluna/Eriophorum vaginatum	Calluna-Eriophoretum
	Nardus/Vaccinium	-
Molinia grassland	*Molinia* grassland	*Molinia-Myrica* nodum
Nardus grassland	*Nardus* grassland *Festuca-Agrostis* grassland where *Nardus* is dominant	Nardetum sub alpinum; Juncetum squarrosi sub alpinum
Freely drained grasslands	*Festuca-Agrostis* grassland *Pteridium aquilinum/Festuca-Agrostis* mixture *Oreopteris/Festuca-Agrostis* mixture	Agrosto-Festucetum
Soligenous mire	*Molinia-Myrica* mire with or without *Juncus acutiflorus*	*Molinia/Myrica* nodum; *Juncus acutiflorus-Acrocladium cuspidatum* nodum
	J. effusus flush	Spagneto-Juncetum effusi
Scree/fern	*Cryptogramma crispa* on scree	-

A ratio of greater than 1.0 indicates selection and a ratio of less than 1.0, avoidance of a particular vegetation type. As the range of values for selection and avoidance ($1.0-\infty$) and (0.0–1.0) respectively are not equivalent, the degree of selection cannot be compared with the degree of avoidance. The problem was overcome by applying a logarithmic transformation to the selection ratio (P. Duncan pers. comm.). This normalises the frequency distribution of selection ratios, removing the positive skew; it was calculated as follows:

$$\text{Transformed selection ratio} = \log_{10}(\text{Selection ratio} + 1).$$

A transformed selection ratio of greater than 0.30 (i.e. $\log_{10} 2.0$) indicates selection, and one less than 0.30 indicates avoidance. Most values now lie between 0.1 and 0.5.

The area occupied by each vegetation type was estimated using the method of internal squares, from vegetation maps prepared for the Nature Conservancy Council (1975, 1976 and 1978, viewed at N.C.C., Edinburgh). Details of the percentage of the study areas occupied by each vegetation type are given in Appendix 3. Error in estimation of areas without allowing for gradient was considered negligible except for dry/moist heaths on the Moffat Hills. Because of the gradient of 30° to 40° on which these communities occur, their area was probably underestimated by 10–15%.

Indices of overlap in altitudinal classes occupied and vegetation type use between billies and nannies or sheep and goats were calculated using the similarity index (S.I.) of Kulcynzski (1927 cited in Bray & Curtis 1957):

$$S.I. = \frac{\Sigma\ 2W}{\Sigma\,(a+b)} \times 100$$

where W is the lesser percentage of observations of the two categories of animal at a particular altitude class or on a particular vegetation type and (a+b) is the sum of the percentages of the given observations. Effectively S.I. represents the percentage of the habitat use that is identical.

3. Dietary analysis

Diets of sheep and goats were estimated by faecal analysis. This technique relies on the specific identification of plant epidermal fragments plus their waxy cuticles which remain intact during digestion and are egested in faeces. Recognition necessitated the preparation of a reference collection of epidermes from upland plant species. Dicotelydons were separated into leaves, stems and flowers and monocotelydons into leaves and stems including flowering stems.

In order to estimate the validity of faecal analysis, rumen samples and rectal faeces were collected from nine goats found dead. If it can be assumed that no marked changes in diet had occurred during the period that the faecal material had been present in the gut, a comparison of the botanical composition of the rumen and of the faeces will indicate the extent of differential digestion. Rumen samples were stored in 10% formalin.

For preparation of ruminal, faecal and plant reference material the same method was used, that of Sparks & Malachek (1968) as modified by Hansen, Foppe, Gilbert, Clark & Reynolds (manuscript, no date).

The justification for using faecal analysis as opposed to other ways of estimating diet, and the detailed methodology of the analysis are given in Appendices 4 and 5 respectively.

Fresh sheep and goat pellets were collected at approximately monthly intervals and either air dried or stored with an equal volume of salt ($NaCl$) prior to analysis. I could not distinguish between sheep, goat, roe deer and red deer pellets on all occasions. Therefore, individual sheep and goats were watched until they defecated, when at least five pellets from each cluster were collected. Collections by this method resulted in small sample sizes of between 2 and 17 clusters obtained each month at each study area.

The diets of sheep and goats at each study area were compared statistically using Spearman's Rank Correlation Coefficient (r_s) for several tied pairs (Siegel 1956). This coefficient was used to compare the order of abundance of plant species/groups in the two diets. A high positive r_s value indicates a strong correlation for the order in which plant species/groups are recorded for the two herbivores; a strongly negative r_s value indicates a low potential for competition. Using r_s one only compares the ranks of plant species/groups by their proportional abundance so that the importance of those species constituting most or least of the sample may be underestimated or overestimated respectively. Dietary overlap was evaluated by using Kulcynzski's Similarity Index, the calculation of which was described earlier.

Results

1. Feeding behaviour

Feral goats, like hill sheep, were versatile and agile feeders. The former were more frequently observed feeding in the field and low canopy layers (Elton & Miller 1954) than the latter, when these layers were available. Sheep were occasionally seen grazing whilst resting on their carpuses on close cropped *Festuca*-*Agrostis* grassland (the ground layer), a posture never adopted by goats.

In College Valley, feral goats readily climb onto low lying branches and occasionally up the sloping trunks of oaks (*Quercus petraea*) in order to browse. The greater climbing ability of goats compared to sheep was obvious in all areas where they were sympatric especially on steep, rocky ground or when crossing dry stone walls. Hill sheep were never observed climbing trees or crossing intact walls, and unlike goats they rarely ventured onto the steepest terrain.

In order to browse vegetation higher than about one metre, goats balance on their hindlegs momentarily or, more often, whilst upright hold their forelegs on branches, tree trunks, walls or fences in order to keep upright. When browsing conifer trees at Nether Hindhope for example, the forelegs were used simultaneously to press branches downwards within reach of the mouth and also to maintain balance. Sheep were never observed foraging whilst on their hindlegs.

Spiny, fibrous or woody material was frequently horned (Geist 1971) by all age-sex classes of goats. Often some of the horned vegetation was then eaten. After horning thistle (*Cirsium*), the stems were bitten about halfway down and ingested from the bitten end upwards, which meant that the flowerhead was ingested with all the spines directed away from the mouth. On one occasion, a billy was observed to eat the flowerheads alone; he quickly rejected the half chewed material which had clearly been an irritant.

Horning of bracken (Pteridium) and heather (Calluna) prior to being eaten had no obvious function. Like thistle stems, bracken was most frequently bitten at a stem with fronds and ingested from the bitten edge upwards.

Examination of 10 to 15 year old pine (Pinus) trees at Nether Hindhope after they had been bruised and barkstripped by goats showed that the freshest shoots were selected and that the cut was sometimes clean and sometimes rough edged. Bark stripping was extensive between the heights of one and two metres, where areas of bark up to 40 cm x 60 cm had been removed. Most strips were pulled up vertically and chewed upwards although some slanted, outwards at the top giving a splayed effect to the barkstripped area. I could detect no differences between barkstripping of pines by goats at Nether Hindhope and that by red deer in the Galloway forests.

In common with hill sheep, feral goats paw at snow in order to expose forage; goats also clear away snow with their horns, a behaviour not possible for most sheep, because of their lack of horns or because of the shape of their horns. On several occasions goats and sheep were observed to feed on lichen on otherwise bare rocks.

On the Moffat Hills, goats were most marked in their selection of certain parts of the dry/moist heath communities. The lower edge of these vegetation zones was selected and in particular, the borders of patches of dry heath (Callunetum vulgaris) where Vaccinium myrtillus was dominant. Goats foraged much less in the middle of the communities dominated by Calluna and appeared to avoid dry heath that had been subject to winter browning.

Diurnal feeding activity of nannies and ewes is illustrated in Figures 3.1a to 3.1d. The feeding activity pattern of kids after the neonatal period was similar to that of nannies and is not illustrated.

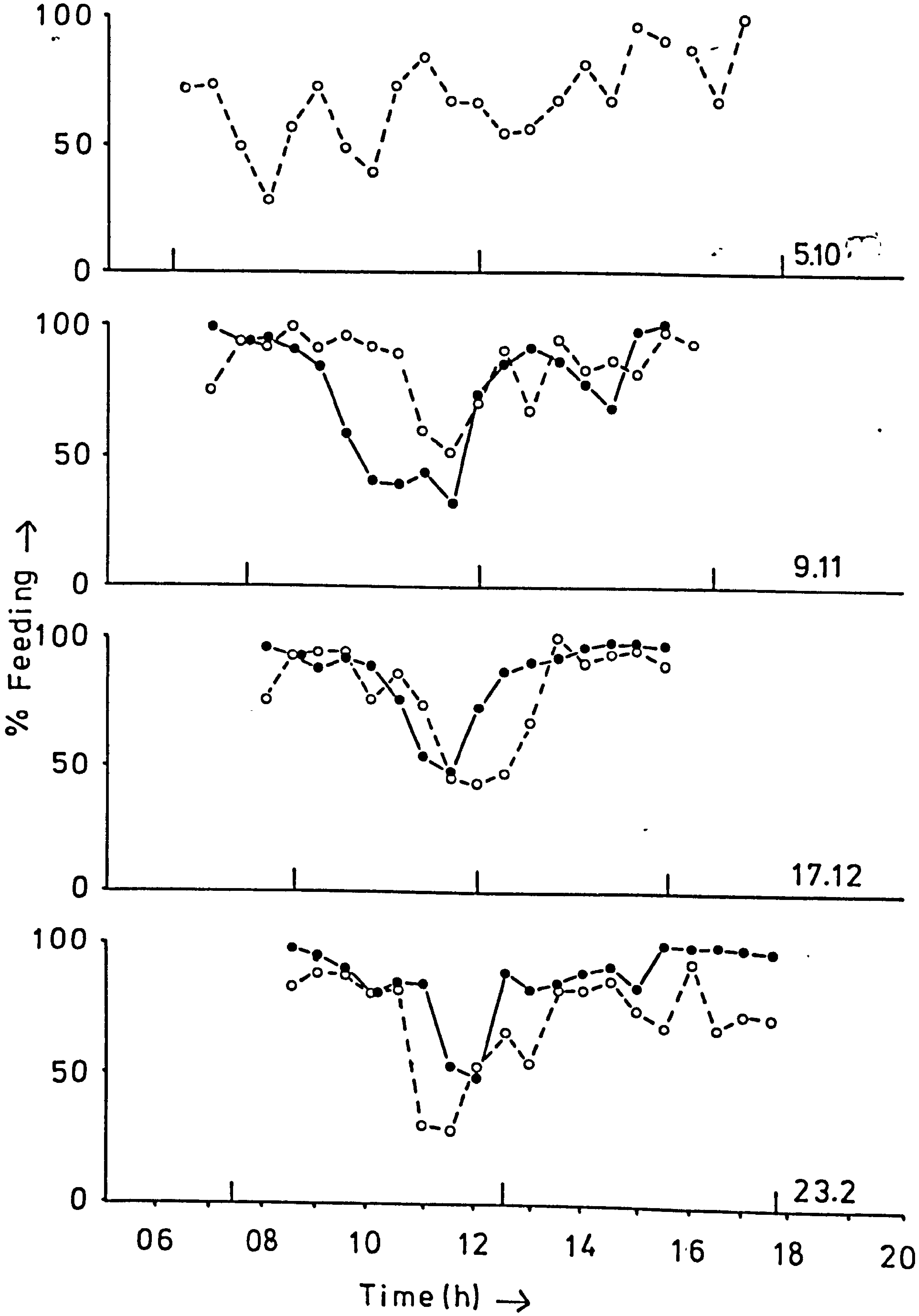
On all days, feeding was the predominant activity of ewes and nannies especially during the first three hours after sunrise and the last three hours before sunset. However, nannies at Nether Hindhope on 19.5.78 were lying from 0445 h until 0630 h with the percentage of feeding records increasing thereafter (Figure 3.1b).

For the observation days in late autumn, winter and early spring, feeding activity of both nannies and ewes tended to be least one or two hours before the middle of the day. During these periods most individuals were resting (lying or standing) and often ruminating. On any given day, the rest periods of ewes and nannies were at least partially synchronous. For instance, the observations on the Moffat Hills on 9.11.78, 17.12.78 and 23.2.79 all on the same heft of goats (Chapter 5) and the same hefts of sheep, revealed a considerable degree of synchrony between the feeding activity patterns; one major rest period between 0900 h and 1300 h occurred for each herbivore on each day (Figure 3.1a).

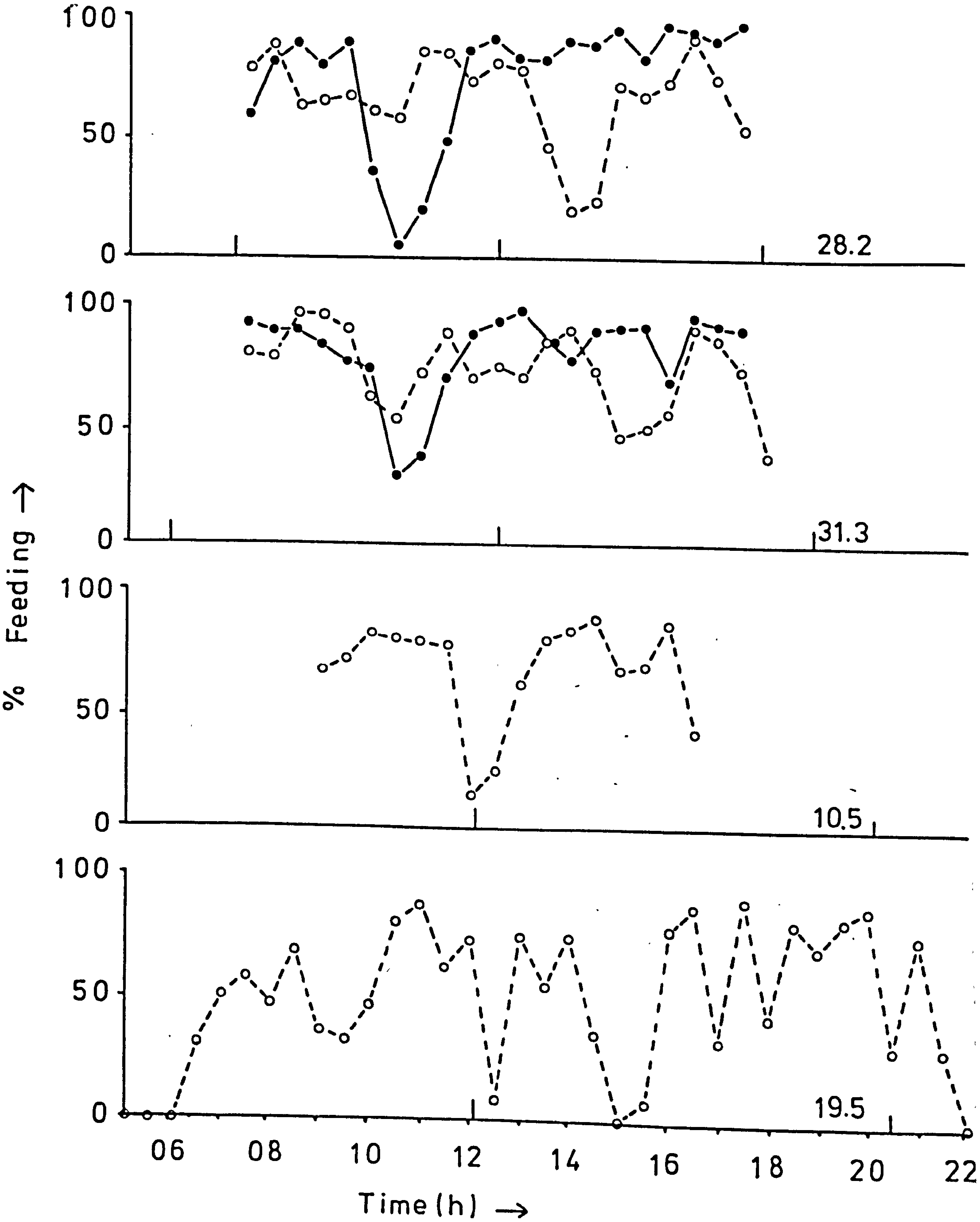
On the 28.2.78 and 31.3.78 at Nether Hindhope, the rest periods of ewes and nannies were out of phase but they occurred at very similar times on the two days from 0900 h to 1230 h for nannies and from 1300 h to 1700 h for ewes (Figure 3.1b). The coincidence of the major rest

Figure 3.1

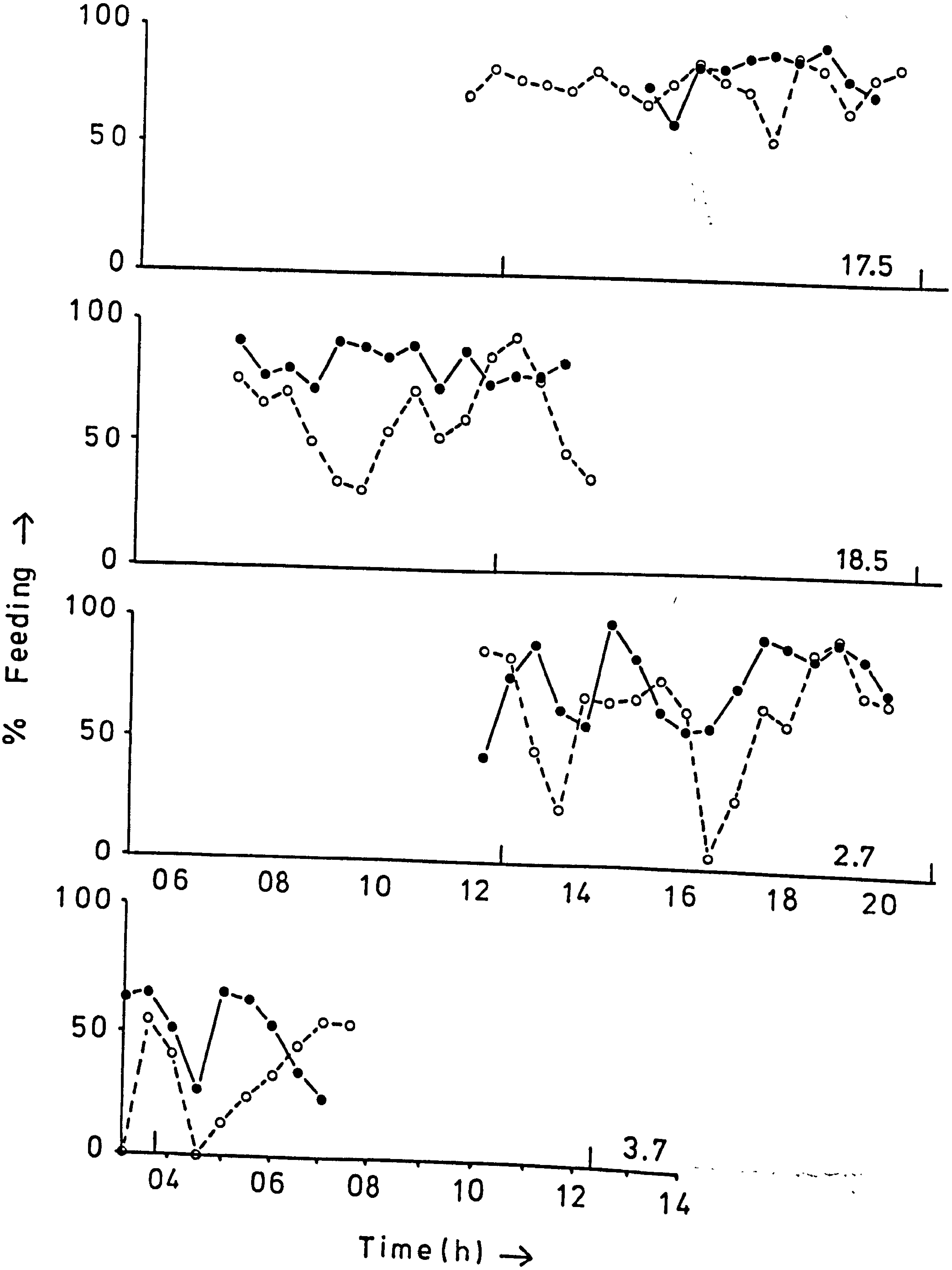
The feeding activity patterns of nannies (o) and ewes (●) determined from whole or half day observations. Vertical bars on the x axis indicate sunrise, midday and sunset times. Sample sizes (total number of individual records per observation bout) are given in Figure 3.2, except for 10.5 and 19.5 when they were 1395 and 2020 respectively. (a): Moffat Hills between 5.10.78 and 23.2.79. (b): Nether Hindhope between 28.2.78 and 19.5.78. (c): Cairnsmore of Fleet 17-18.5.78 and Moffat Hills 2-3.7.79. (d): Moffat Hills 17-18.4.80.



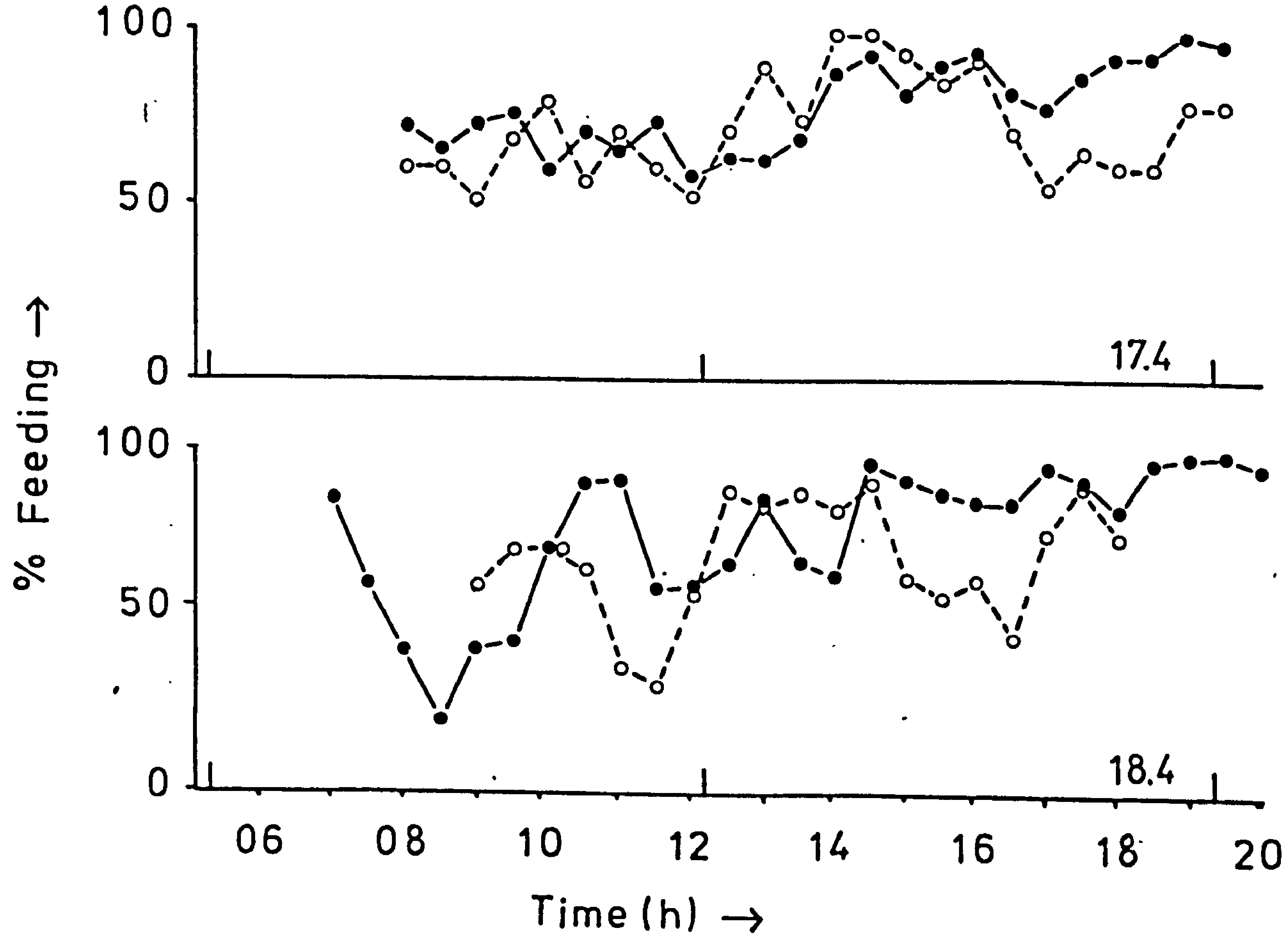
(a)


100
50
0
28.2
100
50
0
31.3
100
50
0
10.5
100
50
0
19.5
% Feeding →
06
08
10
12
14
16
18
20
22
Time (h) →

(b)


100
50
0
17.5
100
50
0
18.5
100
50
0
2.7
06
08
10
12
14
16
18
20
100
50
0
3.7
04
06
08
10
12
14
% Feeding →
Time(h) →

(c)



(d)

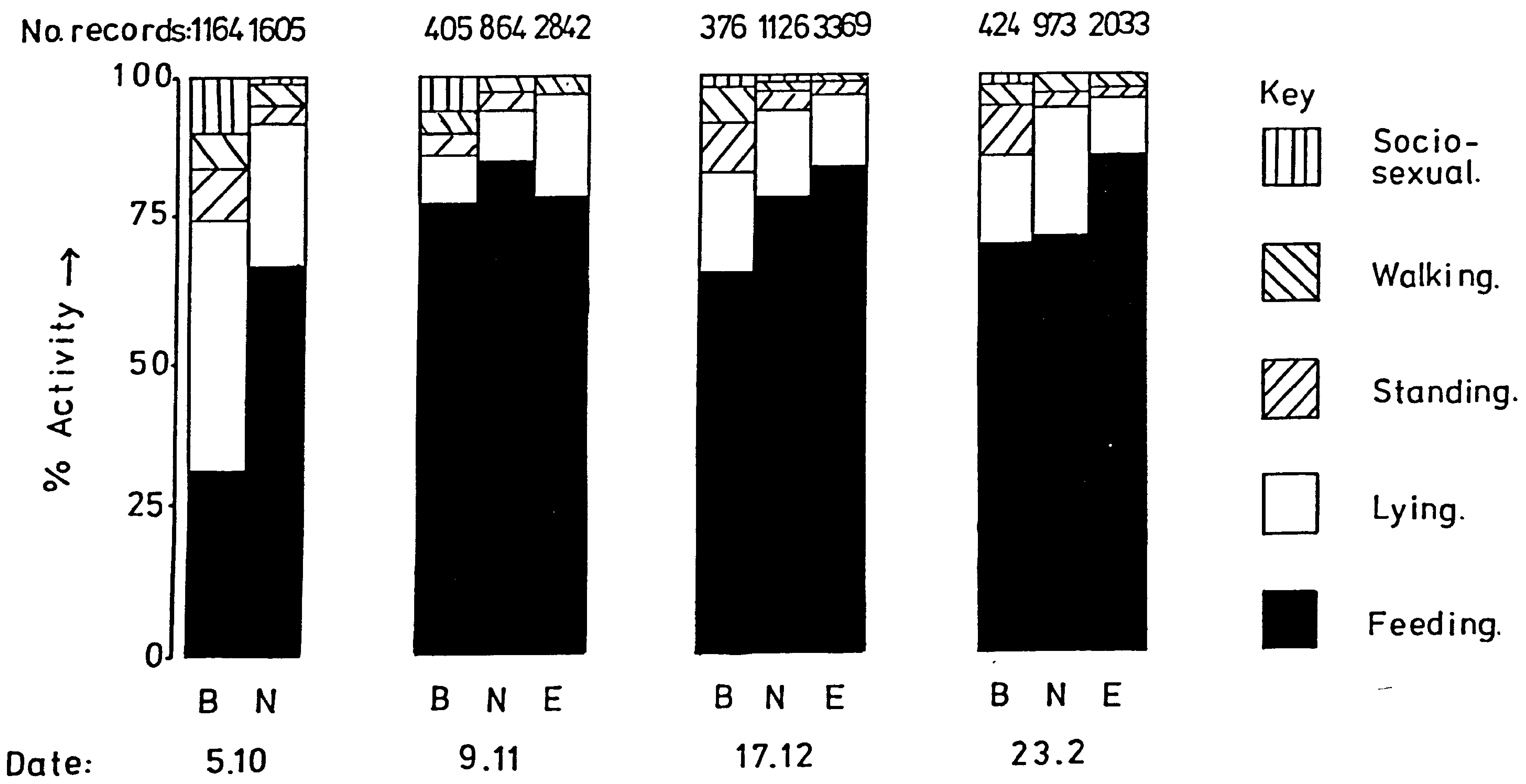
periods of ewes is notable because I observed individuals from different hefts on the two days; the nannies were for the most part the same individuals.

For the observation days in late spring and summer, rest periods just before the middle of the day were either less marked or did not occur. For example, at Nether Hindhope on 10.5.78, nannies showed a clear drop in feeding activity between 1130 h and 1330 h with a minimum at 1200 h. On 19.5.78, however, the same individuals had two main lulls in feeding activity, one around 1230 h and another between 1400 h and 1600 h (Figure 3.1b). Similarly, observations on Cairnsmore of Fleet and on the Moffat Hills on two consecutive days in mid May 1978 (Figure 3.1c) and in mid April 1980 (Figure 3.1d) respectively, indicated that day to day variation in feeding activity can be considerable at these times of year for both sheep and goats.

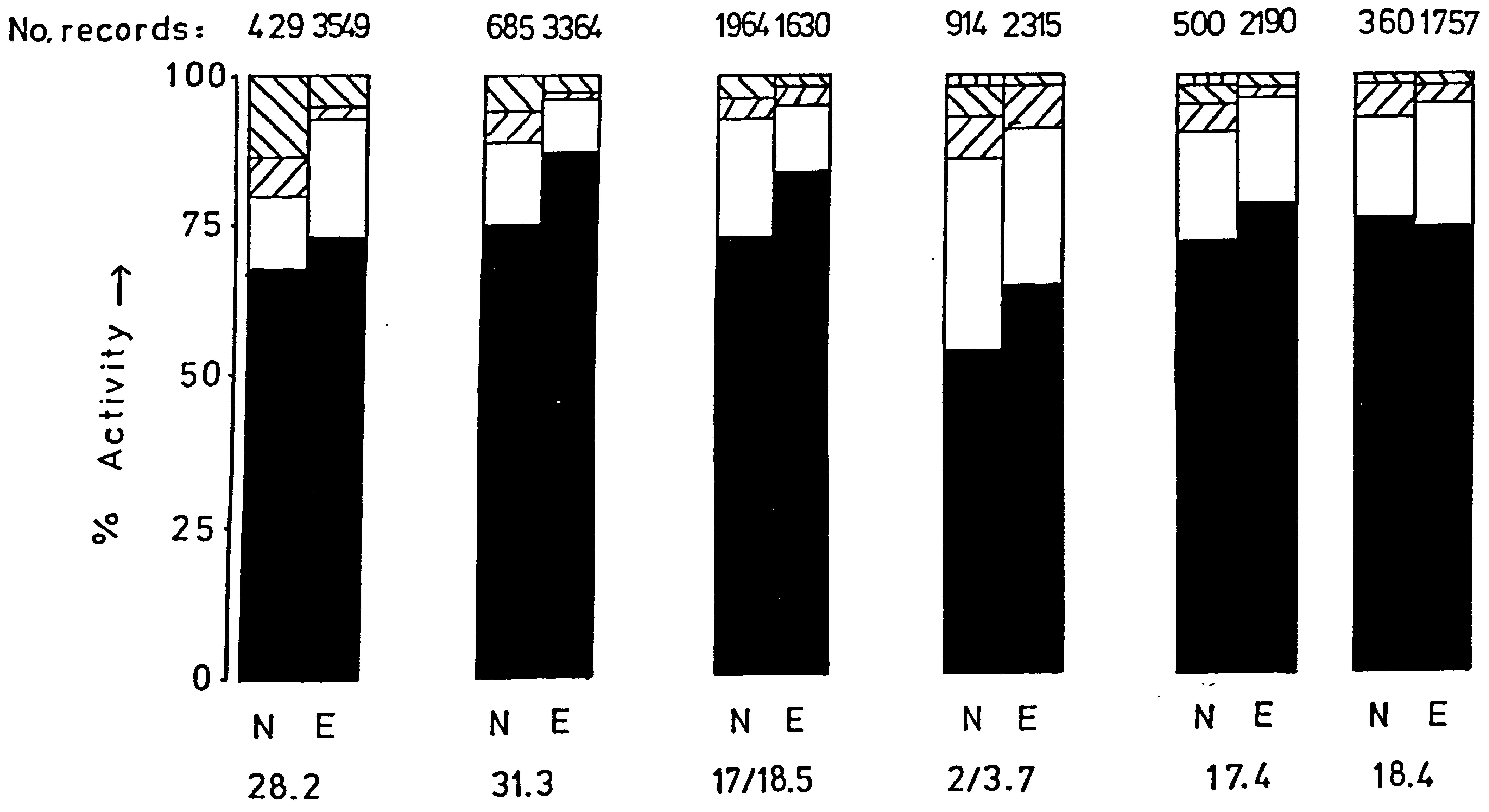
Whilst the feeding activity patterns of billies were similar to those of nannies, the former usually fed for less of the day than the latter. Similarly, with the exception of two of the observation days, 9.11.78 and 18.4.80, nannies fed for less of the day than ewes. For example, the percentage of time spent feeding by billies on 5.10.78, 9.11.78, 17.12.78 and 23.2.79 on the Moffat Hills ranged between 34% and 78% compared to between 72% and 85% for nannies and between 79% and 86% for ewes (Figure 3.2a). On 5.10.78 the goats were rutting so that their feeding time budgets are not comparable to those of other days; billies fed for much less of this day than nannies, and spent more time lying, walking and engaged in socio-sexual behaviour compared to other days. Comparison of feeding time budgets is illustrated further in Figure 3.2b. As morning observations on 3.7.79 were disrupted by shepherding it is likely that the percentage of time feeding was

<u>Figure 3.2</u>

Time budgets of billies (B), nannies (N) and ewes (E) on observation days from (a) the Moffat Hills and (b) several study areas using the same data base as for Figure 3.1.


No. records: 1164 1605
405 864 2842
376 1126 3369
424 973 2033
100
75
50
25
0
% Activity →
B N
B N E
B N E
B N E
Date:
5.10
9.11
17.12
23.2
Key
Socio-sexual.
Walking.
Standing.
Lying.
Feeding.

(a)


No. records:
429 3549
685 3364
1964 1630
914 2315
500 2190
360 1757
100
75
50
25
0
% Activity →
N E
N E
N E
N E
N E
N E
28.2
31.3
17/18.5
2/3.7
17.4
18.4

(b)

underestimated for both herbivores.

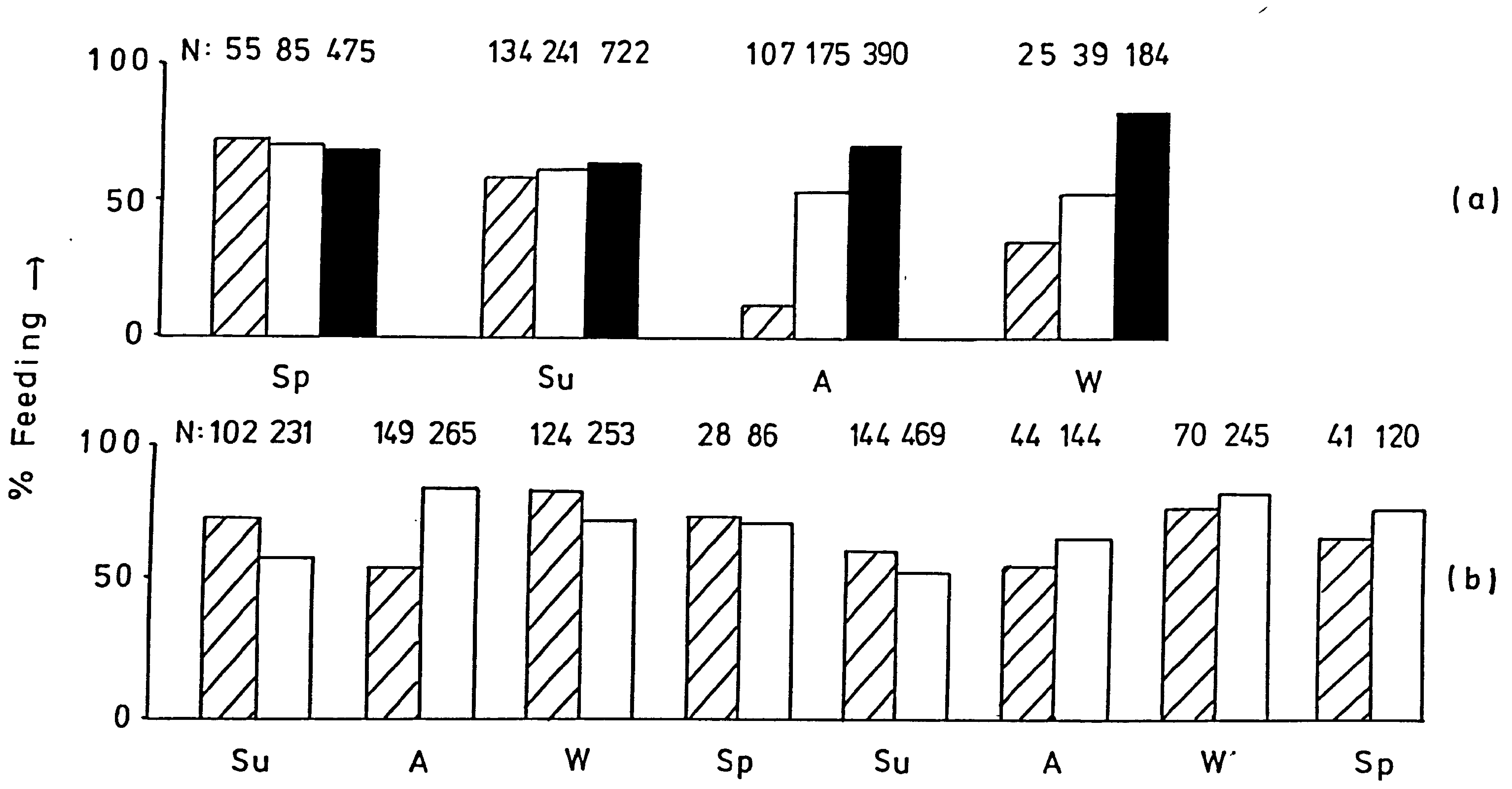
The feeding time budgets calculated from observation days can be compared on an annual basis with those calculated from opportunistic observations (Figure 3.3). On Cairnsmore of Fleet in autumn and winter, ewes fed for considerably more of the day than nannies or billies; the proportion of time spent feeding was similar for all three herbivores in spring and summer. For winter, sample sizes were low but it was observed that billies (and to a lesser extent nannies) spent more time standing, invariably in the sun, than at other seasons. Heavy snow cover at the time (observations in January) restricted the movements of goats and sheep, but ewes were forced to move on to snow free slopes by the shepherd.

On the Moffat Hills, billies fed proportionately most in winter and least in autumn. Nannies fed proportionately more than billies in autumn and proportionately less in summer (Figure 3.3b). Comparison of feeding time budgets calculated from observation days and from opportunistic observations revealed two similarities; firstly, ewes usually fed more than nannies or billies and secondly, billies dramatically reduced their feeding time budgets during the autumn.

The mean duration of rest periods was calculated from observations of individual goats. For this analysis, only those periods during which the goat was undisturbed and always visible have been used. Goats were not infrequently disturbed by walkers, shepherding activities or aeroplanes during their rest periods; further, they often became less visible when lying in sheltered positions. Given these sources of error the length of rest periods were regarded as minima.

Figure 3.3

Feeding time budgets of billies (hatched histograms) nannies (white histograms) and ewes (black histograms) on (a) Cairnsmore of Fleet between spring 1978 and winter 1978-79 and (b) the Moffat Hills (billies and nannies only) between summer 1978 and spring 1980. N = number of observations.


% Feeding →
100
50
0
N: 55 85 475
134 241 722
107 175 390
25 39 184
Sp
Su
A
W
(a)
100
50
0
N:102 231
149 265
124 253
28 86
144 469
44 144
70 245
41 120
Su
A
W
Sp
Su
A
W'
Sp
(b)

By using t tests, it was shown that there were no significant differences between the mean durations of rest periods of billies and nannies; the data for both sexes were therefore pooled. The mean duration of rest periods calculated for three observation days at Nether Hindhope and for five on the Moffat Hills was 20 to 35 minutes and 17 to 34 minutes respectively (Figure 3.4). The means did not differ between days for each study area except for the Moffat Hills between December 1978 and February 1979 ($t_{87} = 3.0335$, $p < 0.01$). The means were, however, consistent between study areas; also, the ranges of the rest period durations were very similar at 5 to 120 minutes and 5 to 130 minutes at Nether Hindhope and on the Moffat Hills respectively.

From systematic plots of the locations of goat groups the mean distance travelled per observation day was calculated (Table 3.2). These represent minima because they were estimated on a flat plane and because the movement of individuals around a location was not taken into account. The mean distances travelled per day were much greater at Nether Hindhope at between 1390 m and 2540 m than on the Moffat Hills at between 300 m and 750 m. However, the records were taken at different seasons.

Goats at Nether Hindhope tended to travel in a circuit during the day covering a wide range of altitudes, whereas those on the Moffat Hills tended to move along contours frequently crossing the location where they were first sighted.

2. Habitat use

Habitat use was quantified on Cairnsmore of Fleet, Moffat Hills

Figure 3.4

Rest period duration ($\bar{x} \pm 95\%$ C.L.) of goats at Nether Hindhope (o) and on the Moffat Hills (●).

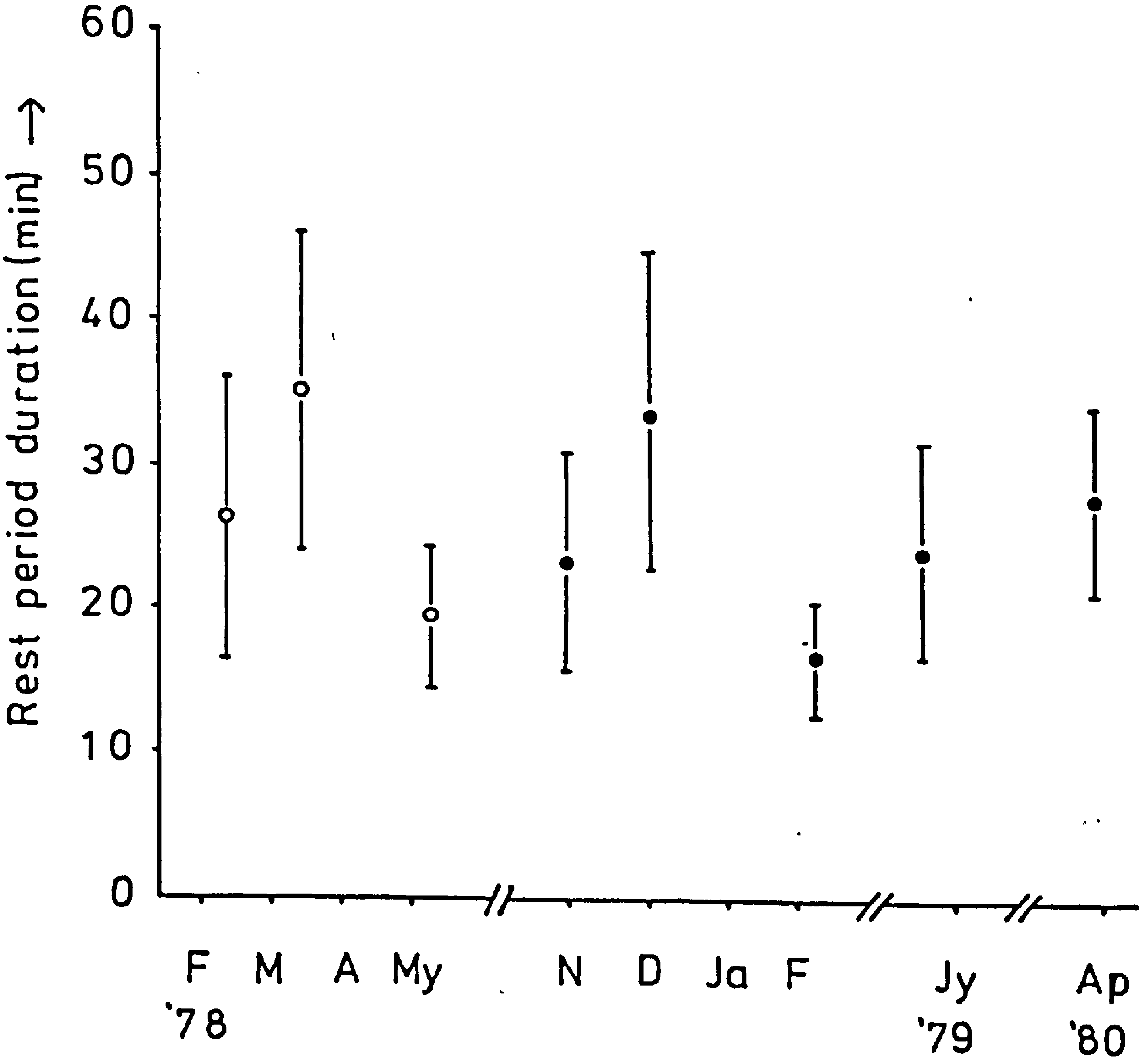

Rest period duration (min) →
60
50
40
30
20
10
0
F
'78
M
A
My
N
D
Ja
F
Jy
'79
Ap
'80

Table 3.2

The mean (± 1.S.E.) distances travelled in metres by goat groups during whole day observations.

Study area	Date	Mean distance (m) travelled per day (± 1.S.E.)	No. groups
Nether Hindhope	28.2.78	2540 ± 286	4
	31.3.78	1390 ± 160	3
Moffat Hills	5.10.78	490 ± 9	2
	9.11.78	750 ± 23	4
	17.12.78	640 ± 65	2
	23.2.79	300 ± 33	5

and the Langholm-Newcastleton Hills. The results from each study are described separately.

(i) Cairnsmore of Fleet

The use of vegetation types by sheep and goats on the eastern block of the N.N.R. was investigated during May, July, August, October and November 1978. Goats were also observed in June 1978 and January 1979, but at this time shepherding activities prevented observations of the sheep.

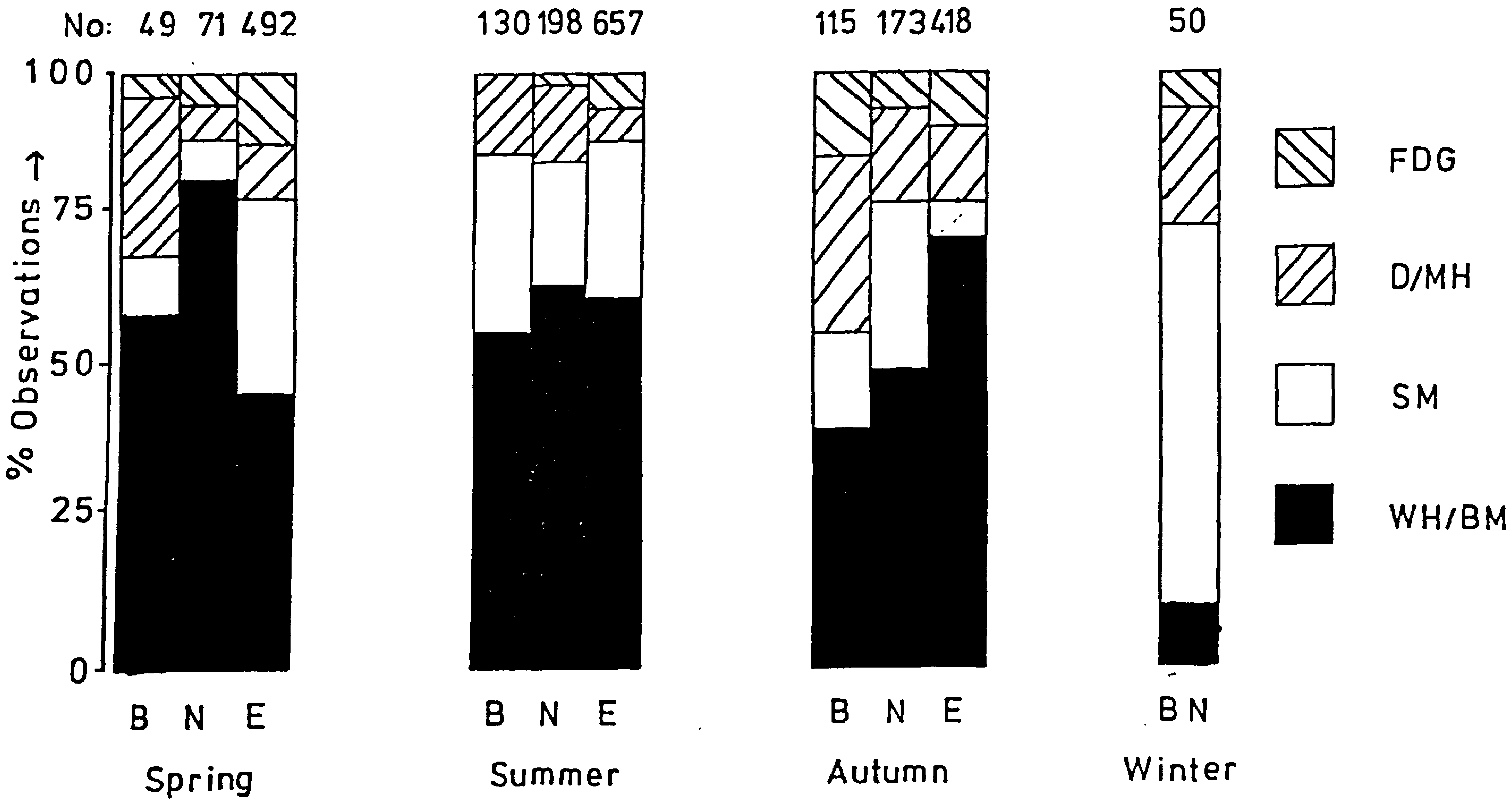
The proportion of observations of ewes on wet heath/blanket mire increased from spring to autumn (Figure 3.5a) and in the latter season, these communities were selected (Figure 3.5b) although not strongly. Over the same period the use of wet heath/blanket mire by both billies and nannies decreased. Nannies used these communities more than billies (Figure 3.5a) and they were selected by the former in spring. In winter they were avoided (Figure 3.5b).

Soligenous mires were used by ewes with decreasing frequency from spring, through summer, to autumn (Figure 3.5b). Little use was made of these communities by nannies and billies in spring but more in summer and autumn (Figure 3.5a). All three herbivores selected soligenous mires in summer and nannies did so in autumn. The pooled data for nannies plus billies in winter indicated that soligenous mires were strongly selected at this season (Figure 3.5b).

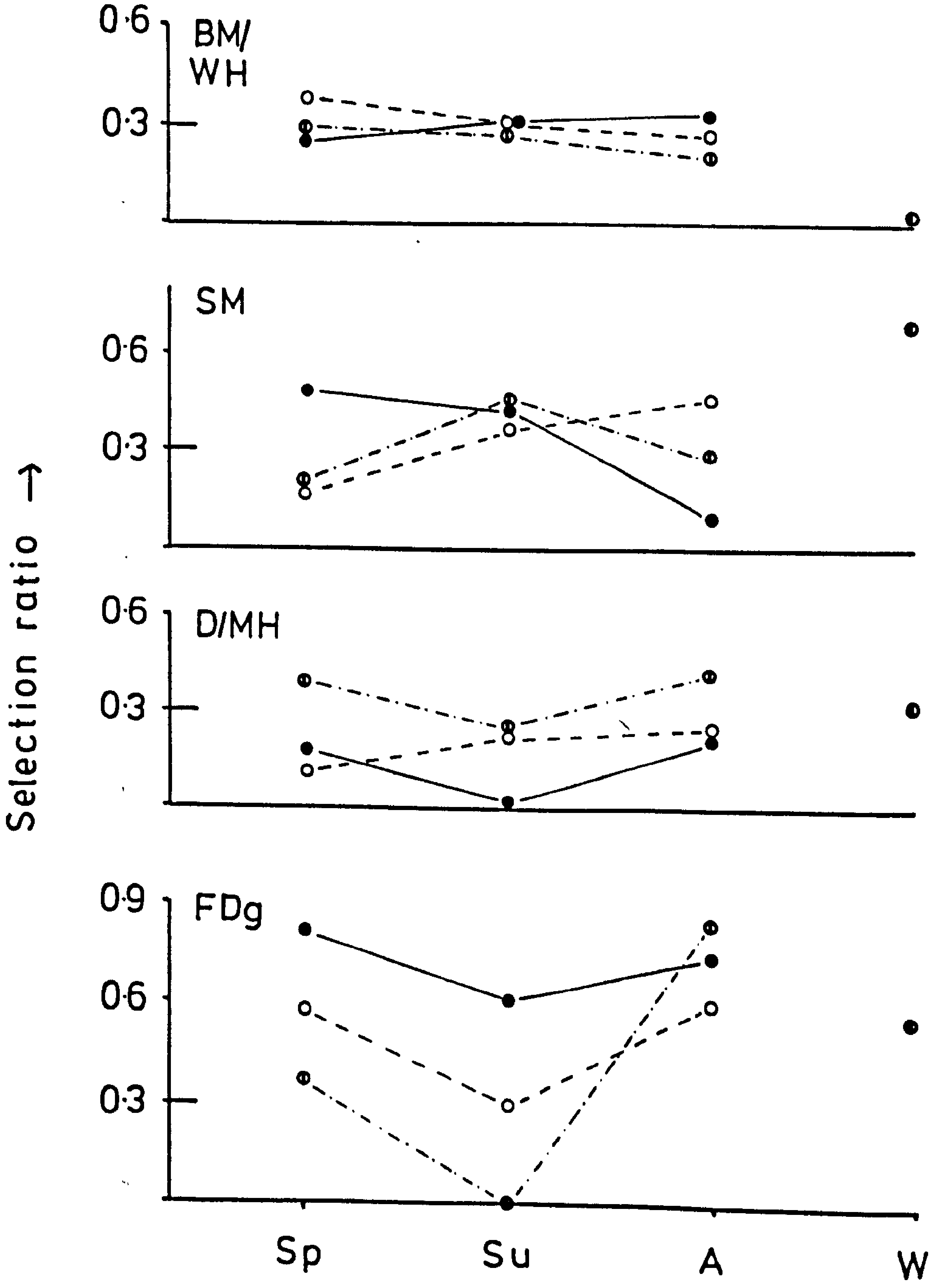
Use of dry/moist heaths by nannies and ewes in spring, summer and autumn was slight (Figure 3.5a) and these communities were avoided (Figure 3.5b). Billies used dry/moist heaths more frequently; in spring and autumn these communities accounted for 27% and 31% respectively of

Figure 3.5

The use of vegetation types (a) and the selection ratios (b) by billies (B, ⦶) nannies (N, o) and ewes (E, •) on Cairnsmore of Fleet between spring 1978 and winter 1978-79. No. = number of observations. FDG = freely drained grassland; D/MH = dry/moist heath, SM = soligenous mire; WH/BM = wet heath/blanket mire.


No: 49 71 492
130 198 657
115 173 418
50
100
75
50
25
0
% Observations →
B N E
Spring
B N E
Summer
B N E
Autumn
B N
Winter
FDG
D/MH
SM
WH/BM

(a)


0·6
BM/
WH
0·3
SM
0·6
0·3
Selection ratio →
0·6
D/MH
0·3
0·9
FDg
0·6
0·3
Sp
Su
A
W

(b)

the sightings (Figure 3.5a) and they were selected (Figure 3.5b). The proportion of observations of all three herbivores on freely drained grasslands was always less than 15% (Figure 3.5a). Nevertheless, they were strongly selected by ewes in spring and autumn and to a lesser extent in summer (Figure 3.5b). Billies and nannies selected these communities in spring, autumn and winter but not during summer (Figure 3.5b). Overlaps between billies and nannies and between sheep and goats in use of vegetation types were highest during the summer. Overlap was lowest between sheep and goats during spring (Table 3.3).

	Spring	Summer	Autumn
Sheep/Goat	69	91	72
Billies/Nannies	75	91	77

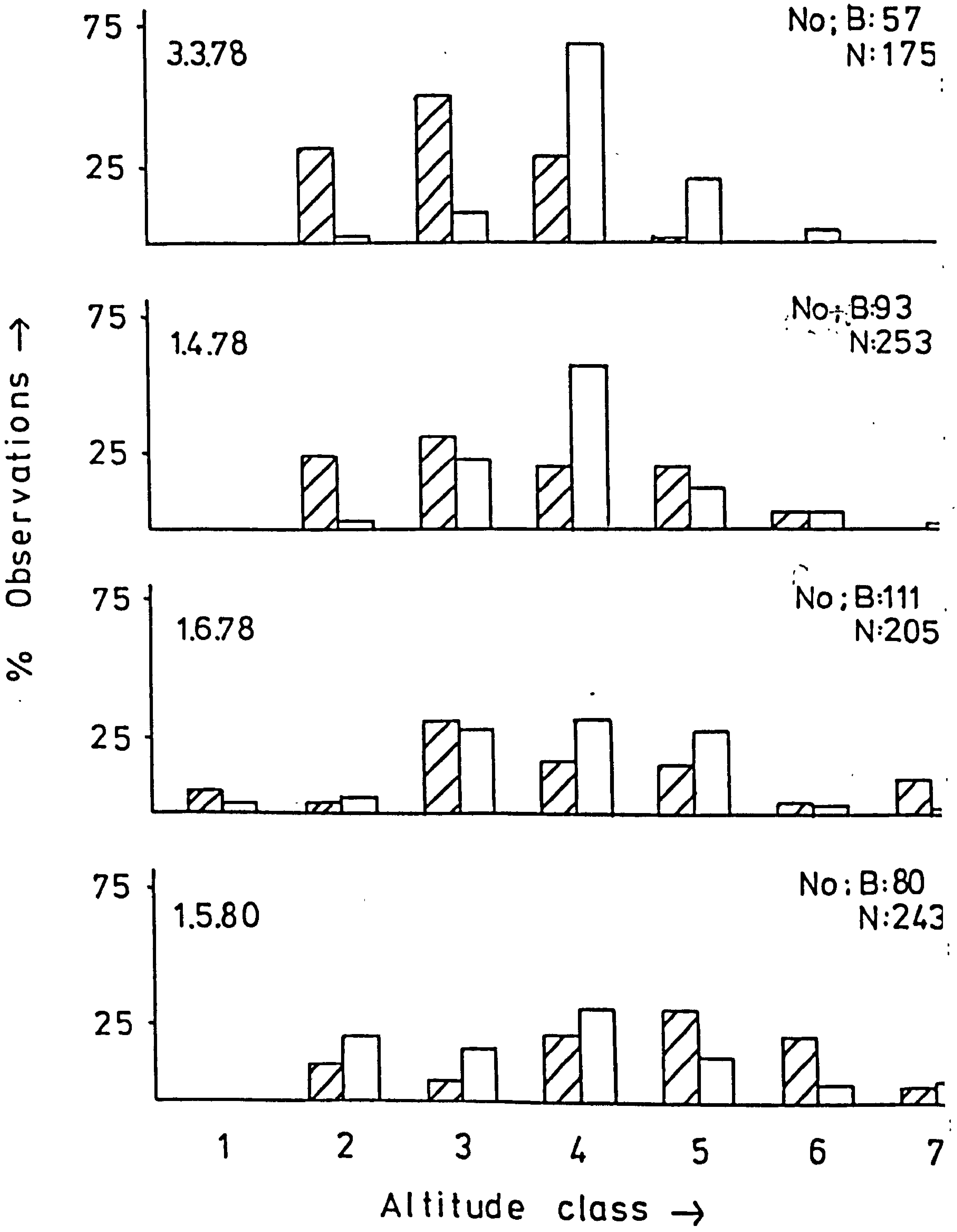
Table 3.3. Similarity Indices of vegetation type use by sheep (ewes) and goats (billies and nannies) on Cairnsmore of Fleet during 1978.

During the complete censuses of March, April and June 1978, billies were observed at consistently lower altitudes than nannies (Figure 3.6). For each census the modal altitude class for nannies was 4 (305-380) m and that for billies 3 (229-304) m. Overlap between the altitudinal distributions increased from 35% in March, 62% in April to 73% in June.

In May 1980 nannies and billies occupied similar altitudinal ranges with approximately the same frequencies (Figure 3.6) and an overlap of 66%. The modal altitude class for nannies was 4 as in 1978 but for

Figure 3.6

The use of altitude classes by billies (B, hatched histograms) and nannies (N, white histograms) on Cairnsmore of Fleet. No. = number of individuals.


75
25
3.3.78
No; B: 57
N: 175
75
25
1.4.78
No; B:93
N:253
75
25
1.6.78
No; B:111
N:205
75
25
1.5.80
No: B:80
N:243
1
2
3
4
5
6
7
Altitude class →
% Observations →

billies it was higher at class 5 (381-456). Up to 40 billies were believed to have been culled at low altitudes prior to the 1980 census, hence the proportion of billies at higher altitudes was increased.

(ii) Moffat Hills

On these hills I collected data on use of vegetation-types and on altitudinal range of goats between late May 1978 and April 1980. The altitudinal range available to goats was between 150 m and 830 m.

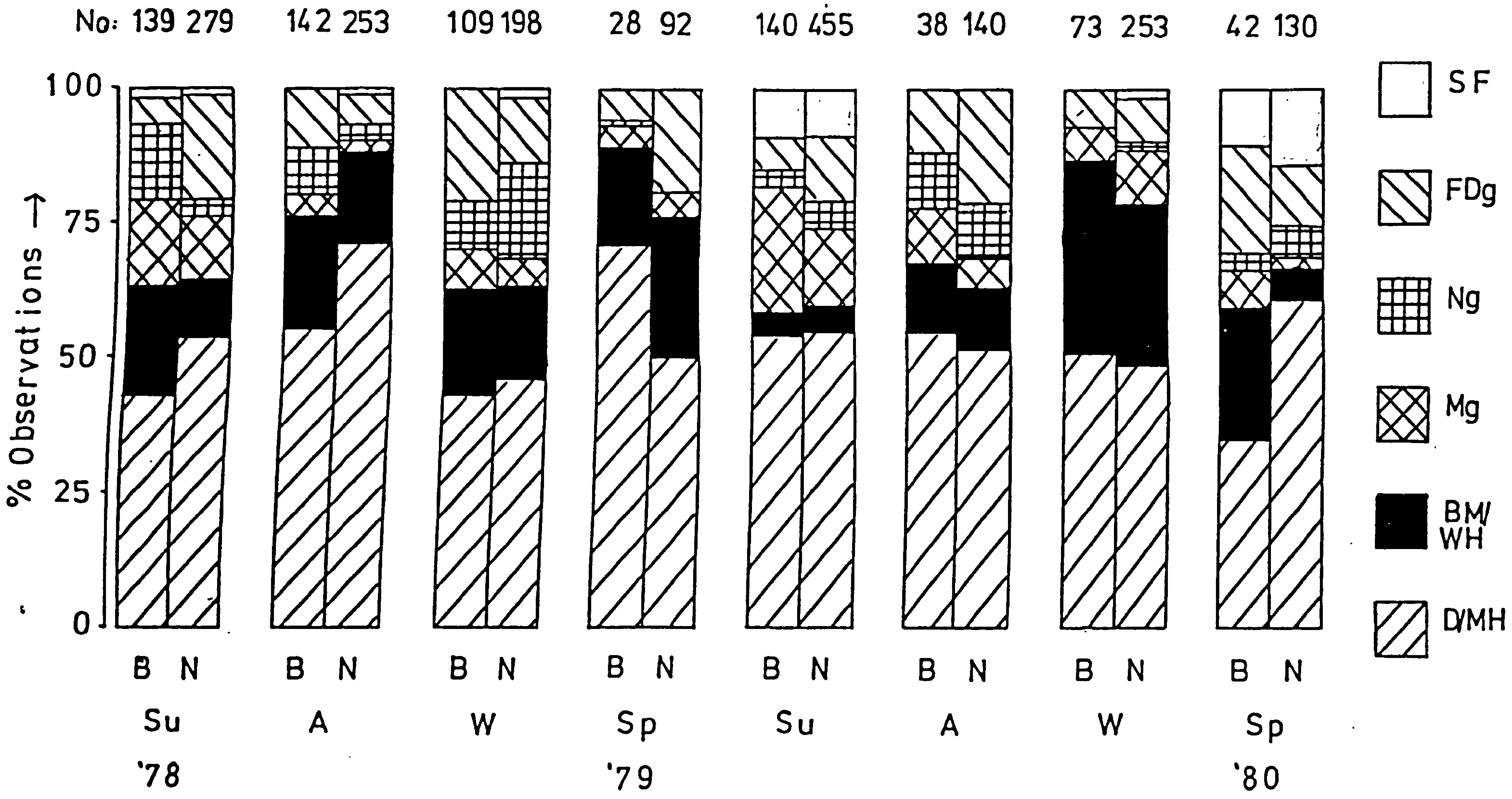
Goats were observed most frequently on dry/moist heaths throughout the year (Figure 3.7a) and these communities were always selected (Figure 3.7b). There were no major differences in the degree of selectivity between the sexes. Percentage use of blanket mire/wet heath mire by either sex was never greater than 36% and variable (Figure 3.7a); they were weakly selected by nannies in spring 1979 and winter 1979-80 and by billies in autumn 1978 (albeit weakly), in winter 1979-80 and in spring 1980 (Figure 3.7b). As a wide range of plant associations were represented by this vegetation type on the Moffat Hills it is possible that a pattern of selection of individual communities was obscured.

Over two years the Molinia grasslands were used more and more strongly selected during the summer than in other seasons, particularly by billies (Figures 3.7a & 3.7b). These communities were also selected by both sexes at other seasons and particularly by nannies in the winter of 1979-80.

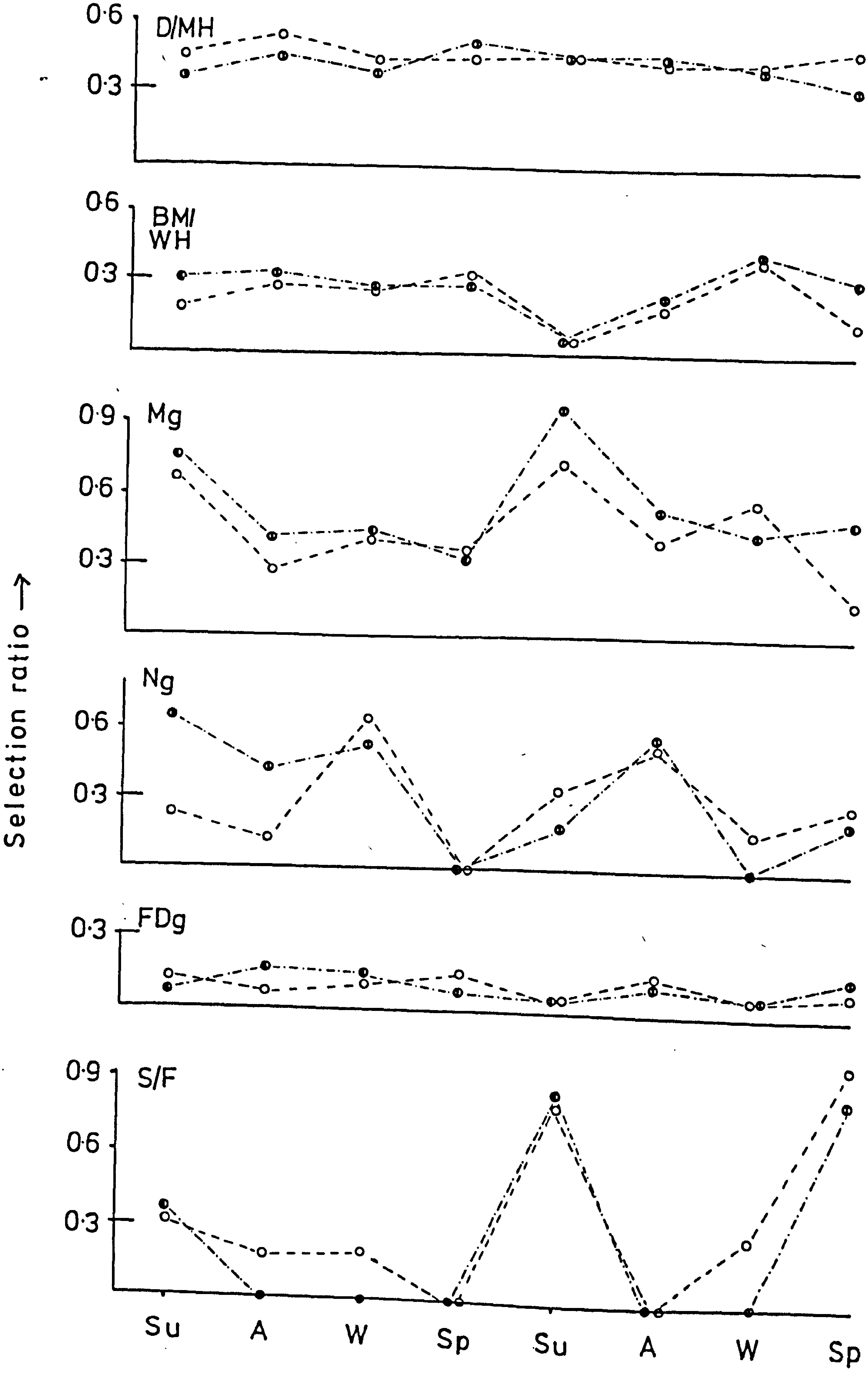
Use of Nardus grasslands was variable (Figure 3.7a) but they were selected by billies in the summer and autumn of 1978 and in autumn 1979, and by nannies in the autumns of 1978 and 1979 (Figure 3.7b).

Figure 3.7

The use of vegetation types (a) and the selection ratios (b) for billies (B, ●) and nannies (N, o) on the Moffat Hills between summer 1978 and spring 1980. No. = number of individuals. SF = scree/fern; FDg = freely drained grassland; Ng = *Nardus* grassland; Mg = *Molinia* grassland; BM/WH = blanket mire/wet heath; D/MH = dry/moist heath.

No: 139 279
142 253
109 198
28 92
140 455
38 140
73 253
42 130
100
75
50
25
0
% Observations →
B N
Su
'78
A
W
Sp
'79
Su
A
W
Sp
'80
SF
FDg
Ng
Mg
BM/WH
D/MH

(a)


0·6
D/MH
0·3
0·6
BM/
WH
0·3
0·9
Mg
0·6
0·3
Selection ratio →
Ng
0·6
0·3
0·3
FDg
0·9
S/F
0·6
0·3
Su
A
W
Sp
Su
A
W
Sp

(b)

Freely drained grasslands were never selected and use of these communities was low throughout the year (Figures 3.7a & 3.7b). Scree/fern communities were strongly selected during the spring of 1980 and summer of 1979 (Figures 3.7a & 3.7b). Most of the scree is dominated by mosses and the fern (Cryptogramma crispa), the latter commences growth in early or mid April and is frequently eaten by goats.

Seasonal overlap in the use of vegetation types by billies and nannies was lowest in summer 1978, spring 1979 and spring 1980 (Table 3.4), although at all times it was greater than 70%.

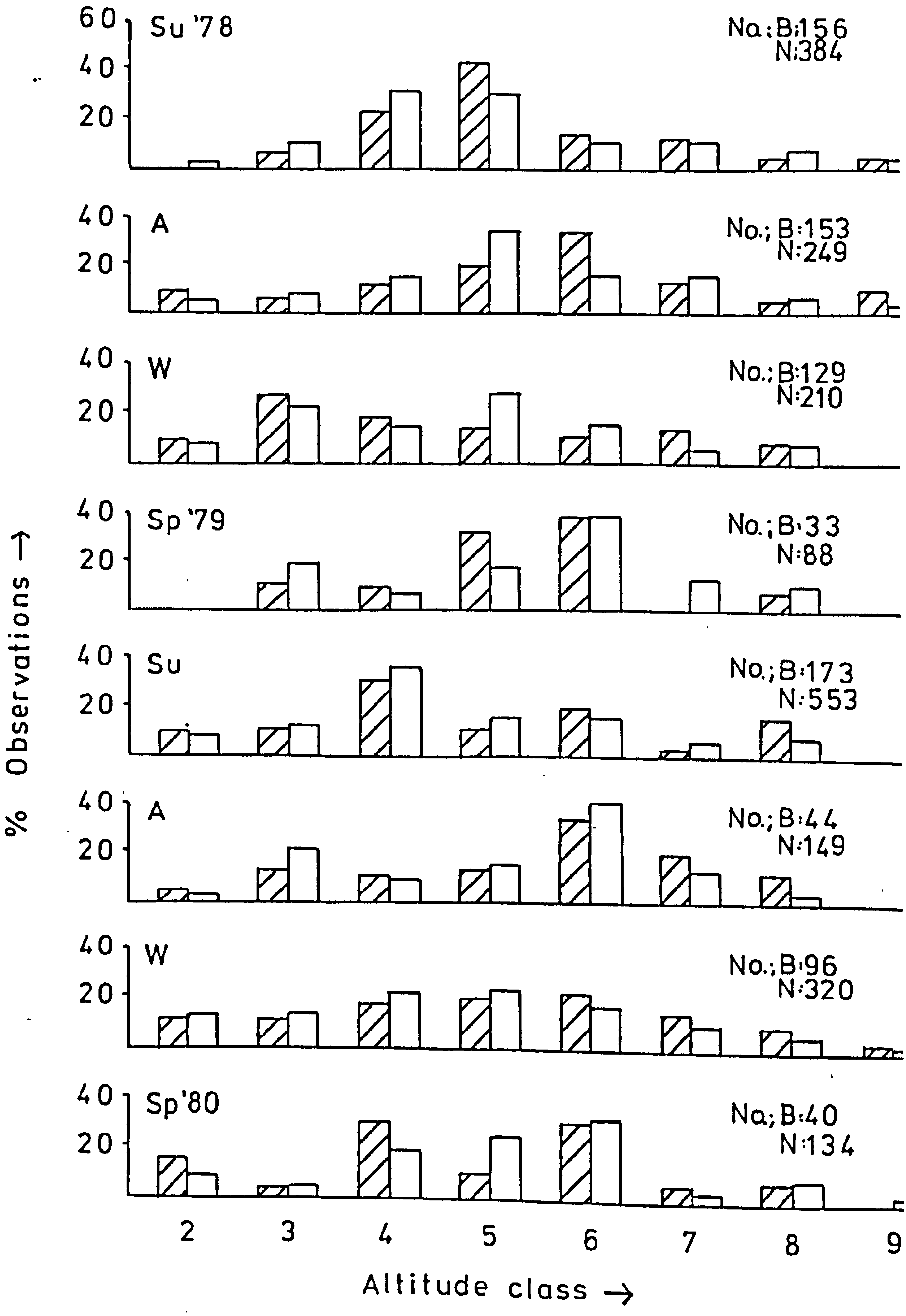
Year	1978				1979			1980
Season	Su	A	W	Sp	Su	A	W	Sp
Billies/Nannies	76	84	89	79	88	92	92	72

Table 3.4. Similarity indices for overlap in the use of vegetation types by billies and nannies on the Moffat Hills.

Both sexes were observed most frequently between the altitudes of 305 m abd 532 m (altitude classes 4 to 6) (Figure 3.8), which corresponds approximately to the zone of dry/moist heath communities, an unsurprising observation. During the winters of 1978-79 and 1979-80, peaks in the distributions of either sex were not evident; proportionately more goats were recorded at lower altitudes than in most other seasons indicating some downward movement from the high crags.

Figure 3.8

The use of altitude classes by billies (B, hatched histograms) and nannies (N, white histograms) on the Moffat Hills. No. = number of individuals.


60
40
20
Su '78
Na.;B:156
N:384
40
20
A
No.;B:153
N:249
40
20
W
No.;B:129
N:210
40
20
Sp '79
No.;B:33
N:88
40
20
Su
No.;B:173
N:553
40
20
A
No.;B:44
N:149
40
20
W
No.;B:96
N:320
40
20
Sp'80
Na.;B:40
N:134
% Observations →
2
3
4
5
6
7
8
9
Altitude class →

From summer to autumn in each year the modal altitude class increased in both sexes (Figure 3.8), proportionately more goats using higher altitudes in the latter season. The altitudinal distribution of nannies in the springs of 1979 and 1980 was similar, with a modal altitude class of 6 (475 m - 532 m) in each case; that for billies was dissimilar possibly as a result of sample sizes being small or of behavioural differences following severe (1978-79) and relatively mild (1979-80) winters. Overlap between the sexes in their use of altitude classes varied between 71% and 87% (Table 3.5).

Year	1978				1979			1980
Season	Su	A	W	Sp	Su	A	W	Sp
Billies/Nannies	81	71	83	80	87	85	86	79

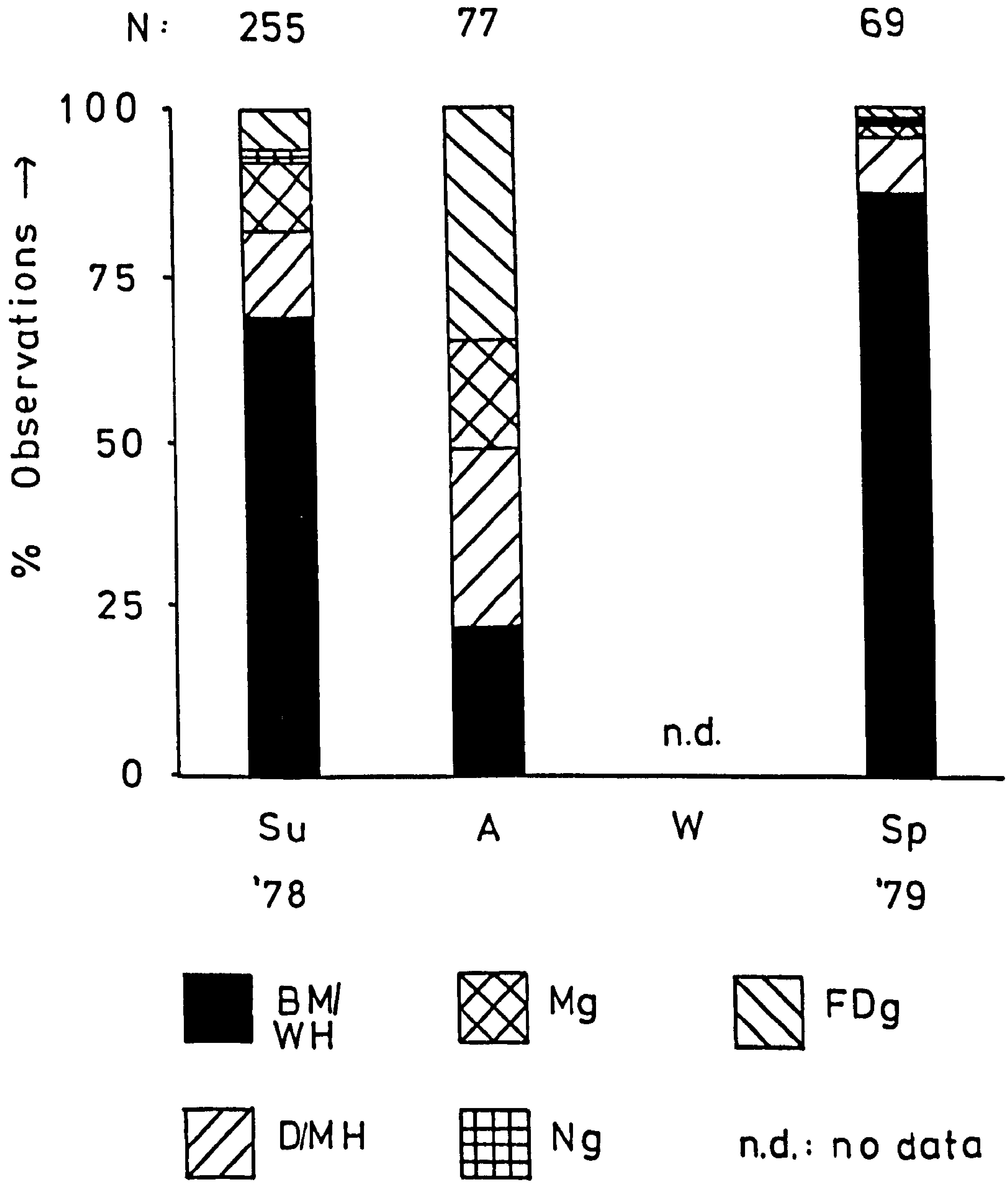
Table 3.5. Similarity indices for overlap between the altitudinal range over which billies and nannies were observed on the Moffat Hills.

(iii) Langholm-Newcastleton Hills

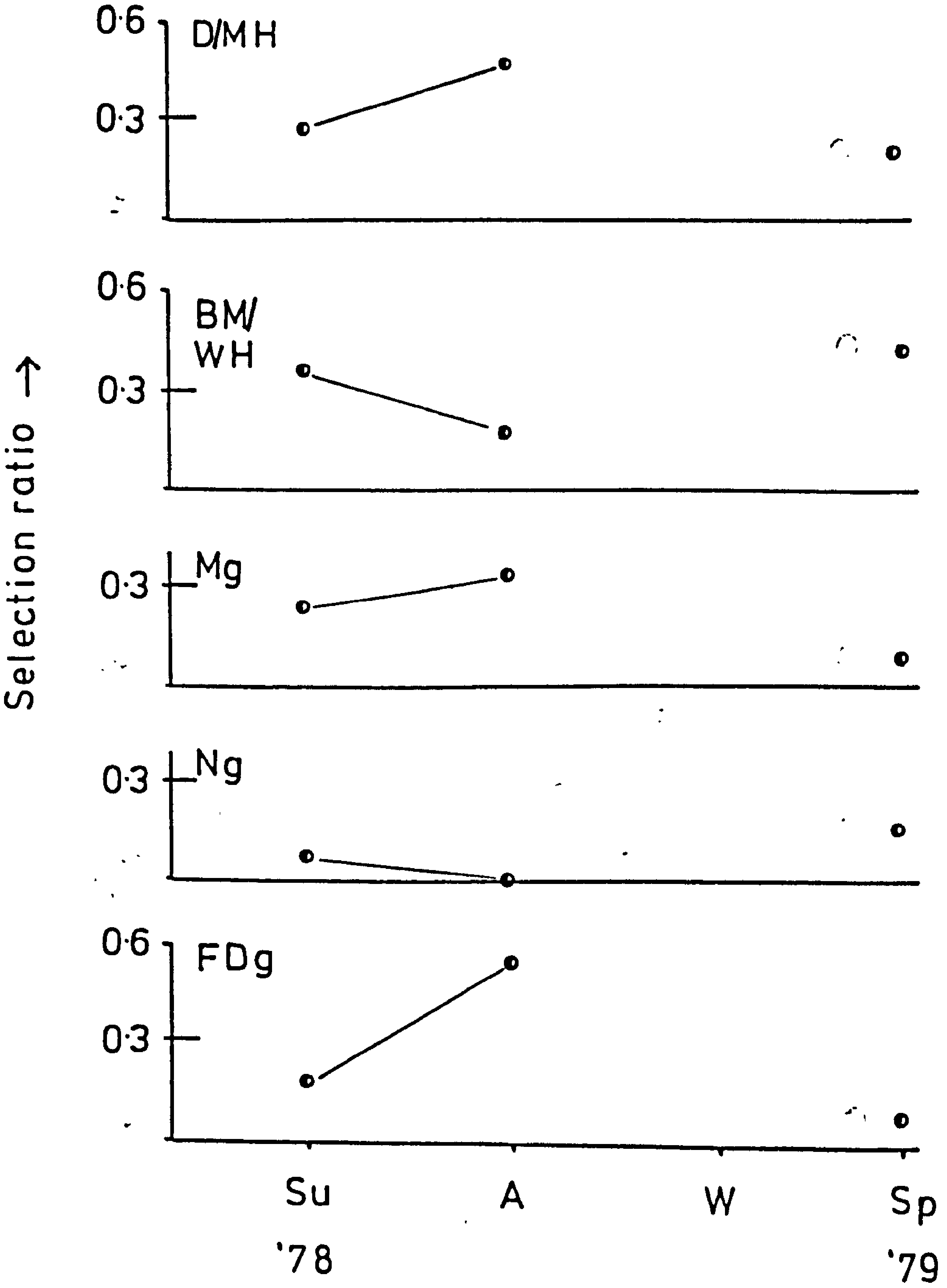
Use of vegetation types on these hills was quantified in summer and autumn 1978 and in spring 1979. The altitudinal ranges of goats were recorded in these seasons and the springs of 1978 and 1980. The range of altitude available was between 150 m and 568 m. As the sample sizes were generally not large enough to allow comparisons of vegetation type use between the sexes in autumn 1978 and spring 1979, the data were pooled.

Figure 3.9

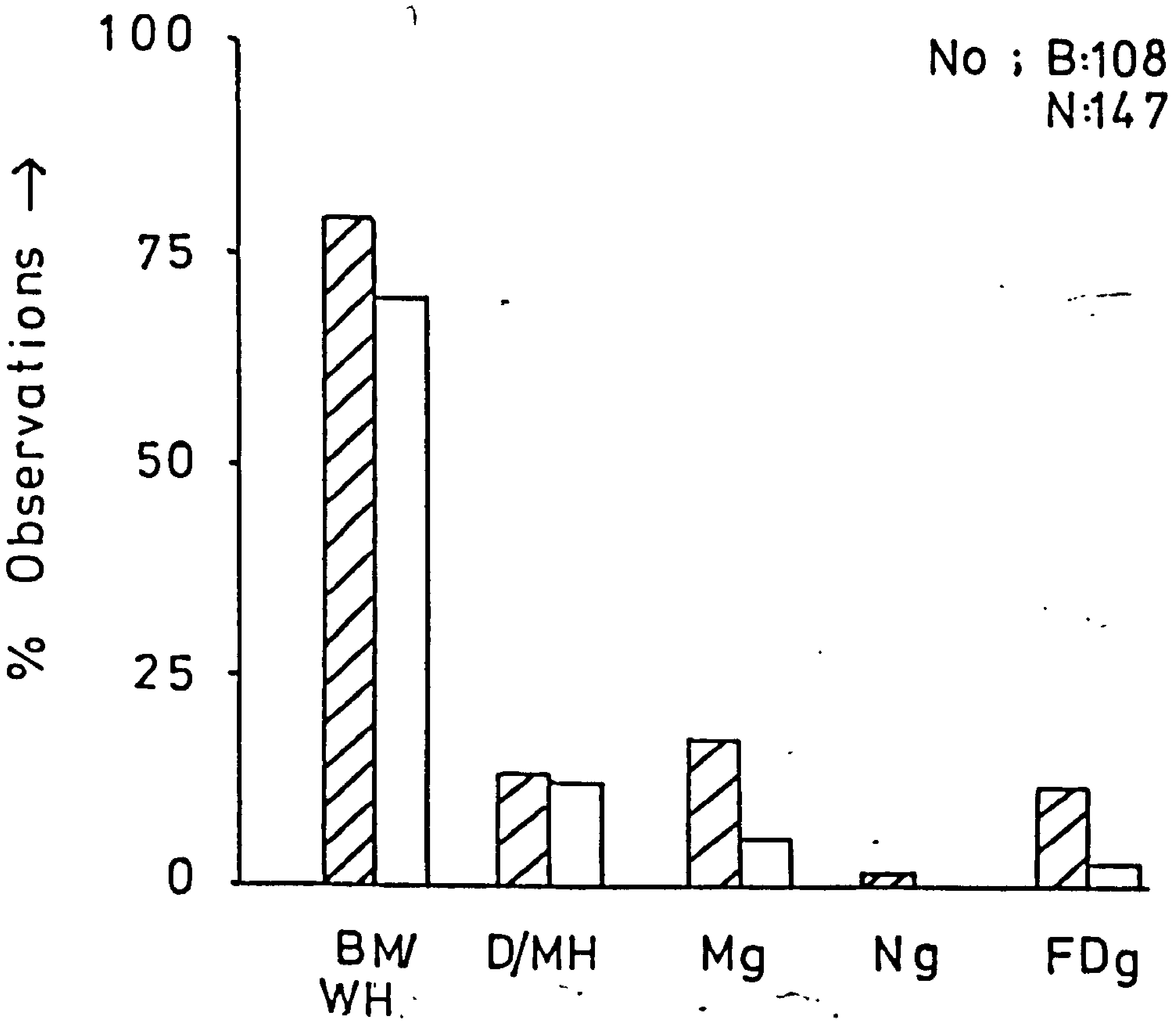
The use of vegetation types (a) and selection ratios (b) for goats (billies & nannies) on the Langholm-Newcastleton Hills; (c), the use of vegetation type by billies (B, hatched histograms) and nannies (N, white histograms) during the summer of 1978. No. = number of individuals. BM/WH = blanket mire/wet heath; Mg = *Molinia* grassland; FDg = freely drained grassland; D/MH = dry/moist heath, Ng = *Nardus* grasslands.


N: 255 77 69
100
75
50
25
0
% Observations →
n.d.
Su '78
A
W
Sp '79
BM/WH
Mg
FDg
D/MH
Ng
n.d.: no data

(a)


Selection ratio →
0·6
0·3
D/MH
0·6
0·3
BM/
WH
0·3
Mg
0·3
Ng
0·6
0·3
FDg
Su
'78
A
W
Sp
'79

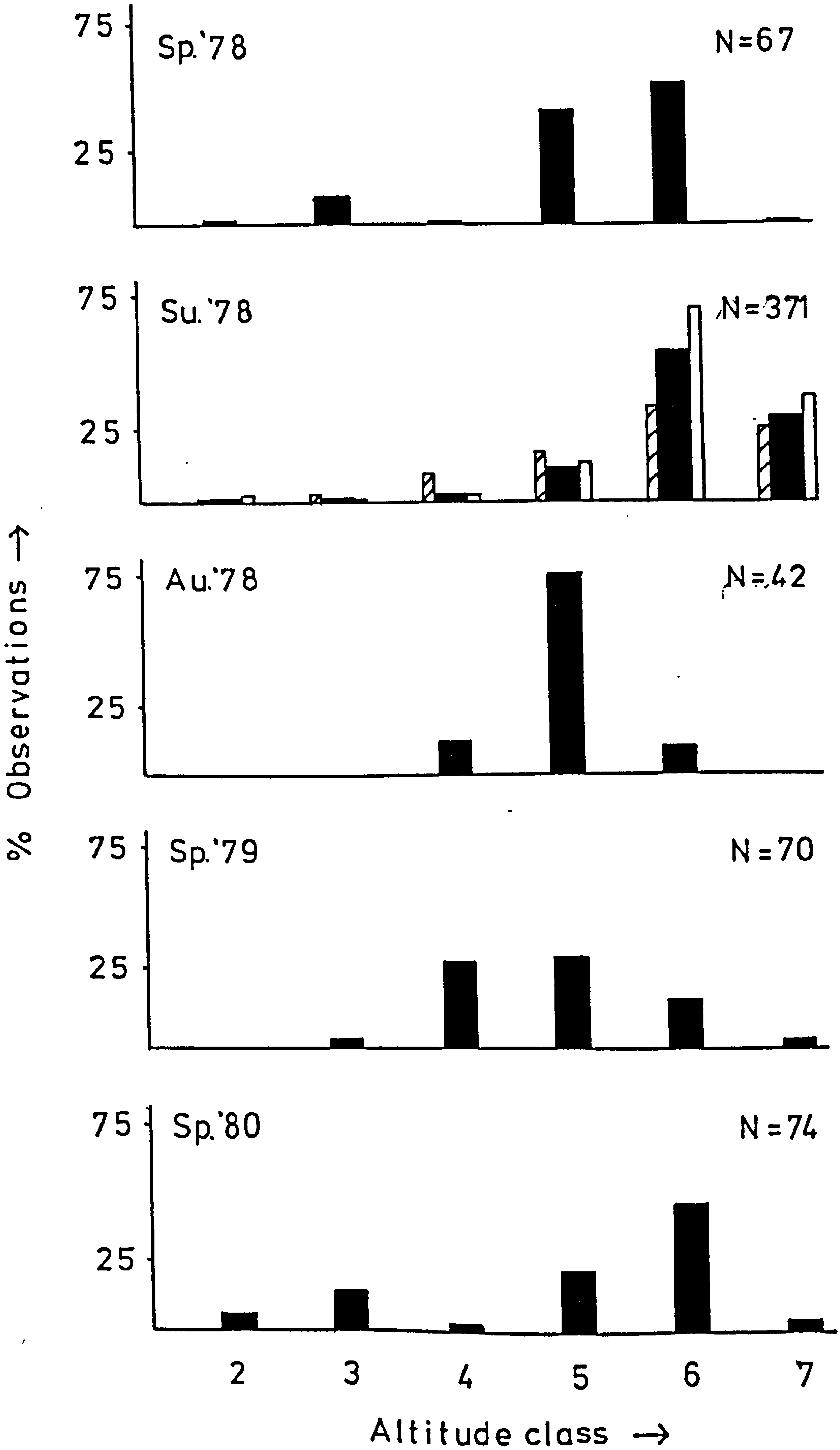
(b)



(c)

Figure 3.10

The use of altitude classes by goats (black histograms) on the Langholm-Newcastleton Hills. For summer 1978, for which the sample size (No.) was largest, observations of billies (hatched histograms) and nannies (white histograms) have been separated.



Sp.'78
N=67
Su.'78
N=371
Au.'78
N=42
Sp.'79
N=70
Sp.'80
N=74
75
25
% Observations →
2
3
4
5
6
7
Altitude class →

In summer 1978 and spring 1979 goats were most frequently observed on blanket mire/wet heath communities (Figure 3.9a) when they were selected (Figure 3.9b). During autumn 1978 there were proportionately more observations on dry/moist heaths, Molinia grasslands and freely drained grasslands (Figure 3.9a) and only in this season were these types selected (Figure 3.9b). The proportion of observations of goats on Nardus grasslands was low and these communities were avoided (Figures 3.9a & 3.9b).

Billies and nannies showed few differences in their use of vegetation types in summer 1978 (Figure 3.9c). However, billies used wet heath/blanket mire less than nannies but used Molinia and freely drained grasslands more. Overlap between the sexes in vegetation-type use was 75%.

The majority of goats were observed at altitudes between 305 m and 609 m (Figure 3.10). In spring 1978 and spring 1980 the modal altitude class was 6 (457 m to 532 m); in spring 1979 most goats were at lower altitudes than in other springs and I was informed that many had used the lowest altitudes during the severe winter of 1978-79 when fieldwork had been impossible. During the summer of 1978, billies were observed more frequently than nannies at altitudes of 381 m to 456 m or less; the majority of nannies (67%) were observed within the altitude class 457 m to 532 m (Figure 3.10).

3. Dietary analysis

In dietary analyses mosses and herbs were not identified as to genus or species level. Similarly, fern species were considered as a single group. However, in this case since the presence of fern epidermal fragments was invariably accompanied by the characteristic trichomes of

Pteridium aquilinum, it is believed that this species accounted for most, if not all, of the fern records. Species within the genera Erica, Luzula, Eriophorum, Carex, Poa, Festuca and Agrostis were not identified and Juncus species other than J. squarrosus were not separated. Thus in the following descriptions, dietary items are referred to as plant species/groups.

(i) Comparison of the botanical composition of ruminal and rectal pellet Samples

The number of plant species/groups in ruminal and rectal pellet samples was similar (Table 3.6). This indicates that the composition of the gut contents had not changed markedly during the retention time of material present in the rectum. Differences in the frequency of occurrence of groups between ruminal and rectal pellet samples were more variable (Table 3.7). The percentages of mosses and ferns show no consistent difference but those for conifers and ericaceous shrubs were usually higher in faecal samples than in ruminal samples; the reverse was true for sedges/rushes, grasses and herbs. This suggested that in faecal analyses woody forages such as ericaceous shrubs would be overestimated and conversely, herbs and monocotelydons underestimated.

(ii) The annual diets of sheep and goats

Diets were estimated on Cairnsmore of Fleet N.N.R. between January 1978 and March 1979 at Nether Hindhope between February 1978 and December 1978 and on the Langholm-Newcastleton Hills between May 1978 and January 1979.

The number of different plant species/groups identified in faecal

Table 3.6

Comparison of the number of plant species/groups in ruminal and rectal faeces samples from the same goats.

	No. plant species/groups	
Individual	Rumen	Rectal pellets
CV1	6	6
H1	8	5
H2	9	10
H3	7	7
RF1	10	11
RF2	12	13
M1	14	11
M2	6	5
C1	11	10

Table 3.7

The frequency of occurrence of plant species/groups in ruminal and rectal faeces samples from the same goats. Ru = ruminal samples; Re = rectal faeces samples.

Individual	CV1		H1		H2		H3		RF1		RF2		M1		M2		C1	
Plant species/group	Ru	Re	Ru	Re	Ru	Re	Ru	Re	Ru	Re	Ru	Re	Ru	Re	Ru	Re	Ru	Re
Mosses	14	13	0	1	1	2	3	4	6	4	2	7	10	9	0	1	4	5
Ferns	16	24	14	13	2	4	3	3	1	1	0	0	5	1	0	0	0	0
Conifers	0	0	63	85	55	55	68	70	0	0	0	0	1	0	0	0	0	0
Dwarf shrubs	1	0	0	0	2	2	1	2	19	31	12	28	51	69	92	94	76	86
<u>Ulex</u>	23	26	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Herbs	24	20	0	0	0	0	0	0	63	59	1	1	6	3	1	0	1	1
<u>Myrica</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0
Sedges/rushes	1	1	8	1	0	1	0	1	0	1	50	49	19	10	0	0	5	3
Grasses	23	16	17	1	40	36	26	20	6	4	34	11	11	10	8	4	5	5

Table 3.8

Comparison of the mean ($\bar{x}$) number of plant species/groups ($\pm$ 1.S.E.) in sheep and goat monthly composite faecal samples from each study area. N = number of months. For none of the study areas was there a significant difference between sheep and goats: Cairnsmore of Fleet, $t_{22} = 1.60$, $p > 1.0$; Langholm-Newcastleton Hills, $t_{12} = 0.24$, $p > 1.0$; Nether Hindhope, $t_{17} = 1.74$, $p > 1.0$.

Species	Cairnsmore of Fleet		Langholm-Newcastleton Hills		Nether Hindhope	
	$\bar{x}$	N	$\bar{x}$	N	$\bar{x}$	N
Sheep	12.9 (±0.74)	12	15.3 (±0.76)	6	15.2 (±0.86)	9
Goat	14.9 (±0.67)	12	15.8 (±1.00)	8	13.2 (±0.76)	10

samples provided a comparison of the diversity of each herbivore's estimated diet. There were no significant differences between the mean number of plant species/groups in samples from sheep and goats on each range (Table 3.8) indicating that diversity was similar.

Plant species/groups with a frequency of occurrence of less than 10% in all months were considered unimportant dietary items and are not included in the following descriptions. Appendix 6 gives the full data.

(a) Cairnsmore of Fleet N.N.R.

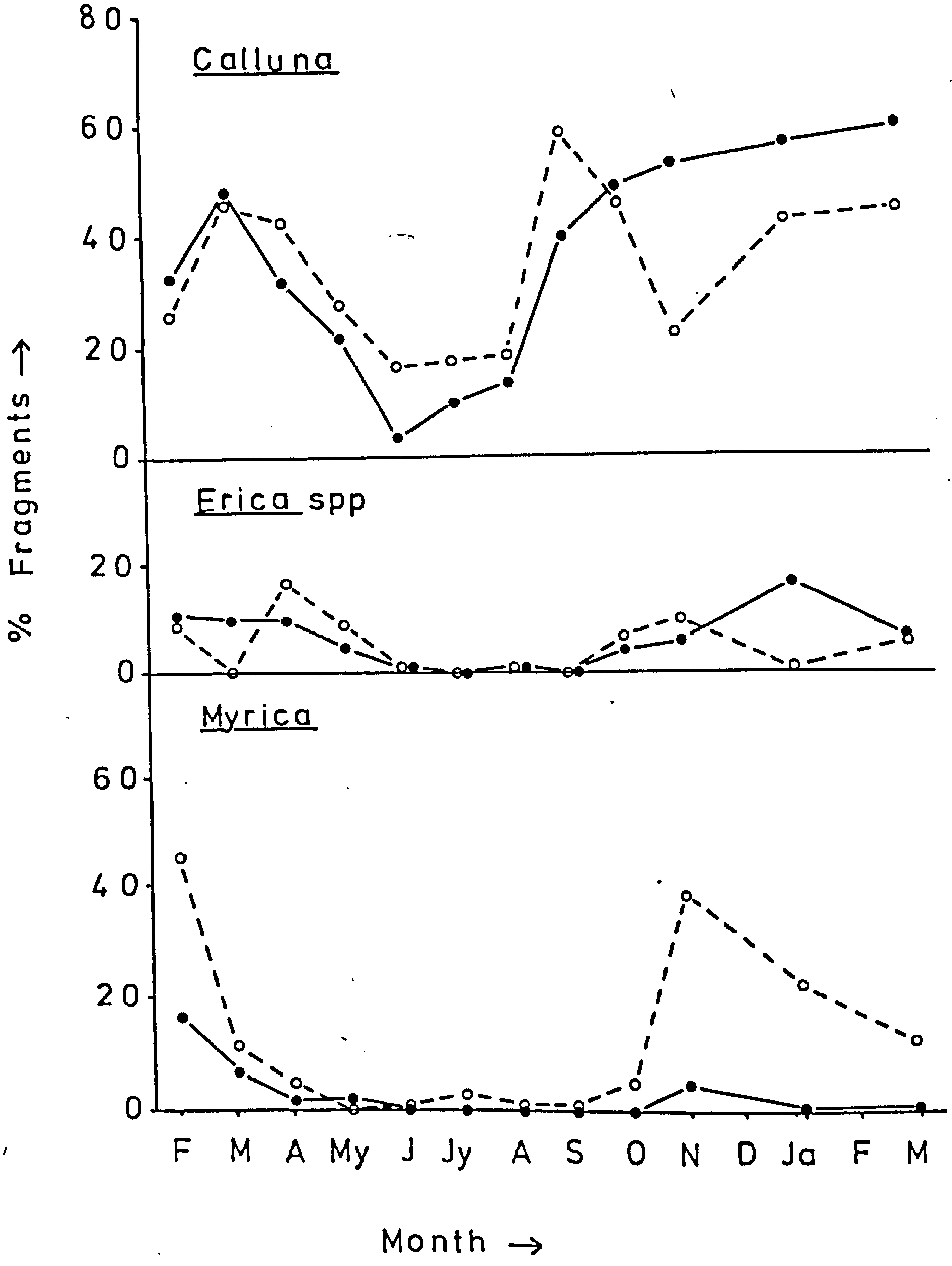
The frequency of occurrence of the main dietary items are illustrated in Figure 3.11. Ericaceous shrubs were the most important dietary items for both herbivores on this study area. The percentage of Calluna fragments was highest in the late autumn, winter and early spring months for both sheep and goats with maxima of 60% in March 1979 and 59% in September 1978 for sheep and goats respectively. In the summer months percentages were 20% or less for both herbivores (Figure 3.11). The occurrence of Erica spp. (E. tetralix and E. cinerea) showed a similar pattern to that of Calluna but percentages were much lower (Figure 3.11).

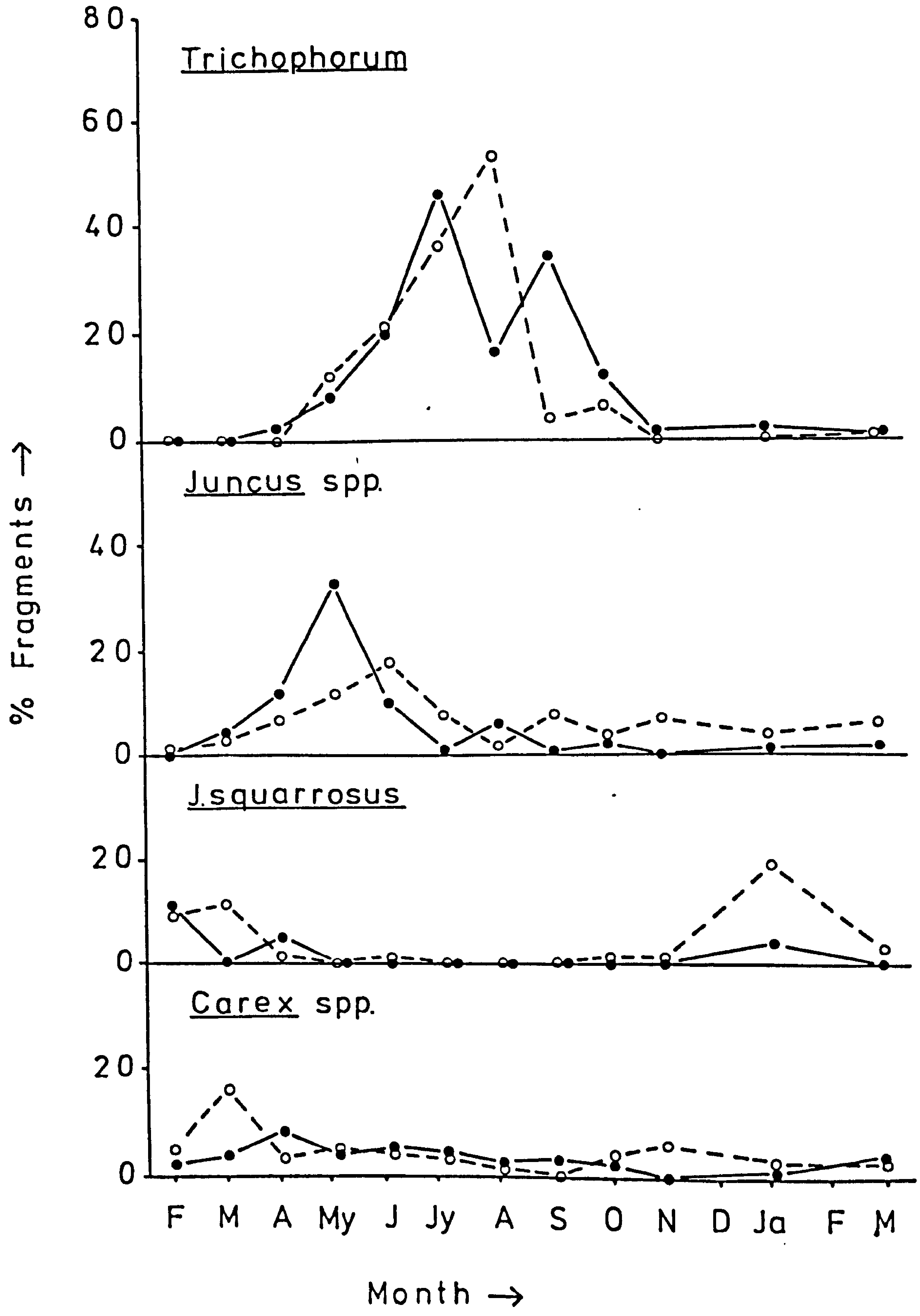
The frequency of occurrence of Myrica gale was for goats, highest in late autumn, winter and early spring with very few fragments recorded in faeces from April through to October (Figure 3.11). Sheep apparently ate very little Myrica at any time of year since the percentage of fragments was normally less than 10% (Figure 3.11).

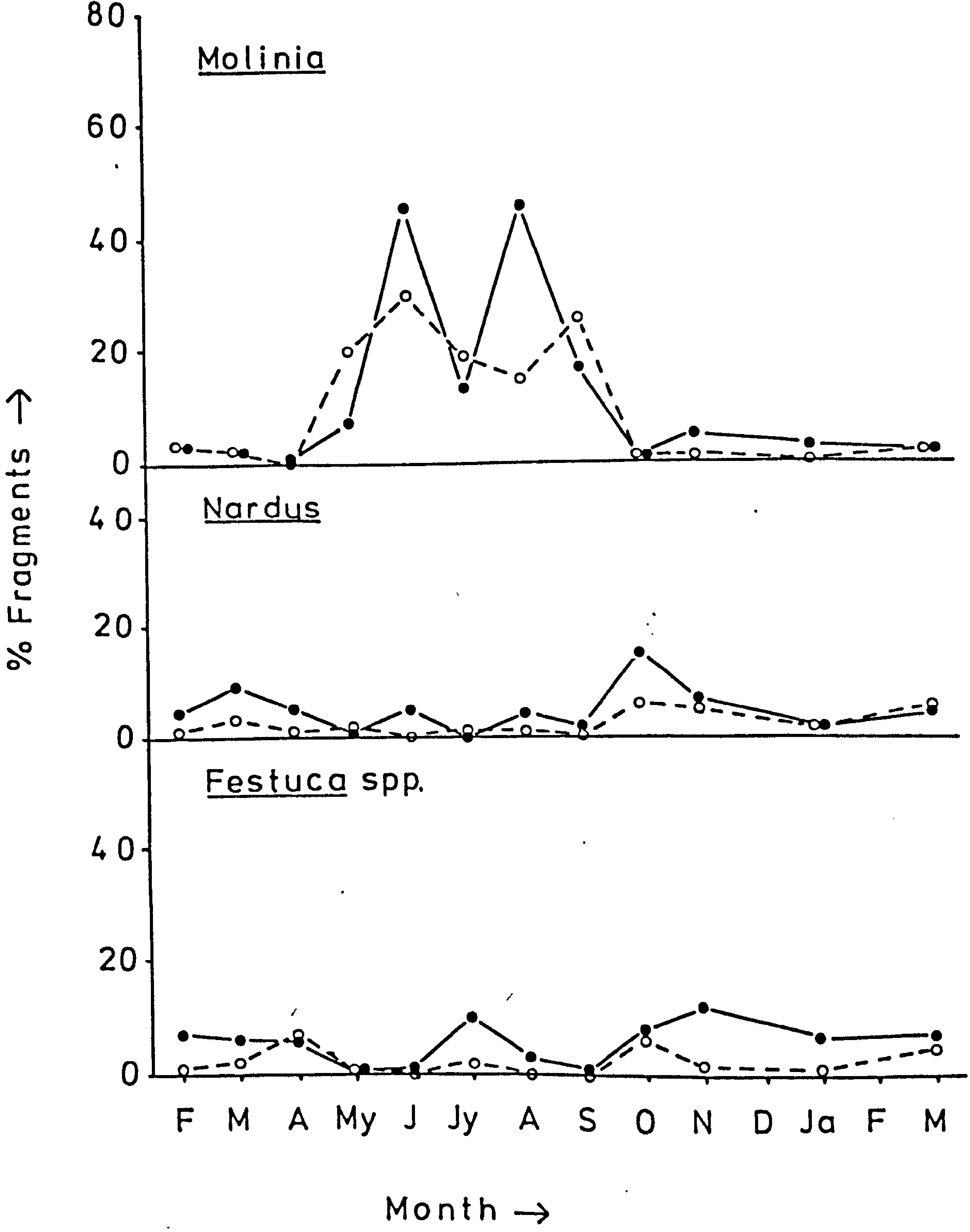
Trichophorum caespitosum was heavily used by both herbivores in summer and early autumn with maximum percentages of 46% in July and 53%

Figure 3.11

The frequency of occurrence of plant species/groups in the faeces of sheep (●) and goats (o) on Cairnsmore of Fleet N.N.R. from February 1978 to March 1979.


80
60
40
20
0
Calluna
Erica spp
20
0
Myrica
60
40
20
0
% Fragments →
F
M
A
My
J
Jy
A
S
O
N
D
Ja
F
M
Month →


Trichophorum
Juncus spp.
J.squarrosus
Carex spp.
% Fragments →
80
60
40
20
0
40
20
0
20
0
20
0
F
M
A
My
J
Jy
A
S
O
N
D
Ja
F
M
Month →


80
60
40
20
0
Molinia
40
20
0
Nardus
Festuca spp.
40
20
0
% Fragments →
F
M
A
My
J
Jy
A
S
O
N
D
Ja
F
M
Month →

in August recorded for sheep and goats respectively. The percentage of fragments of Trichophorum at other seasons was less than 5% for both herbivores.

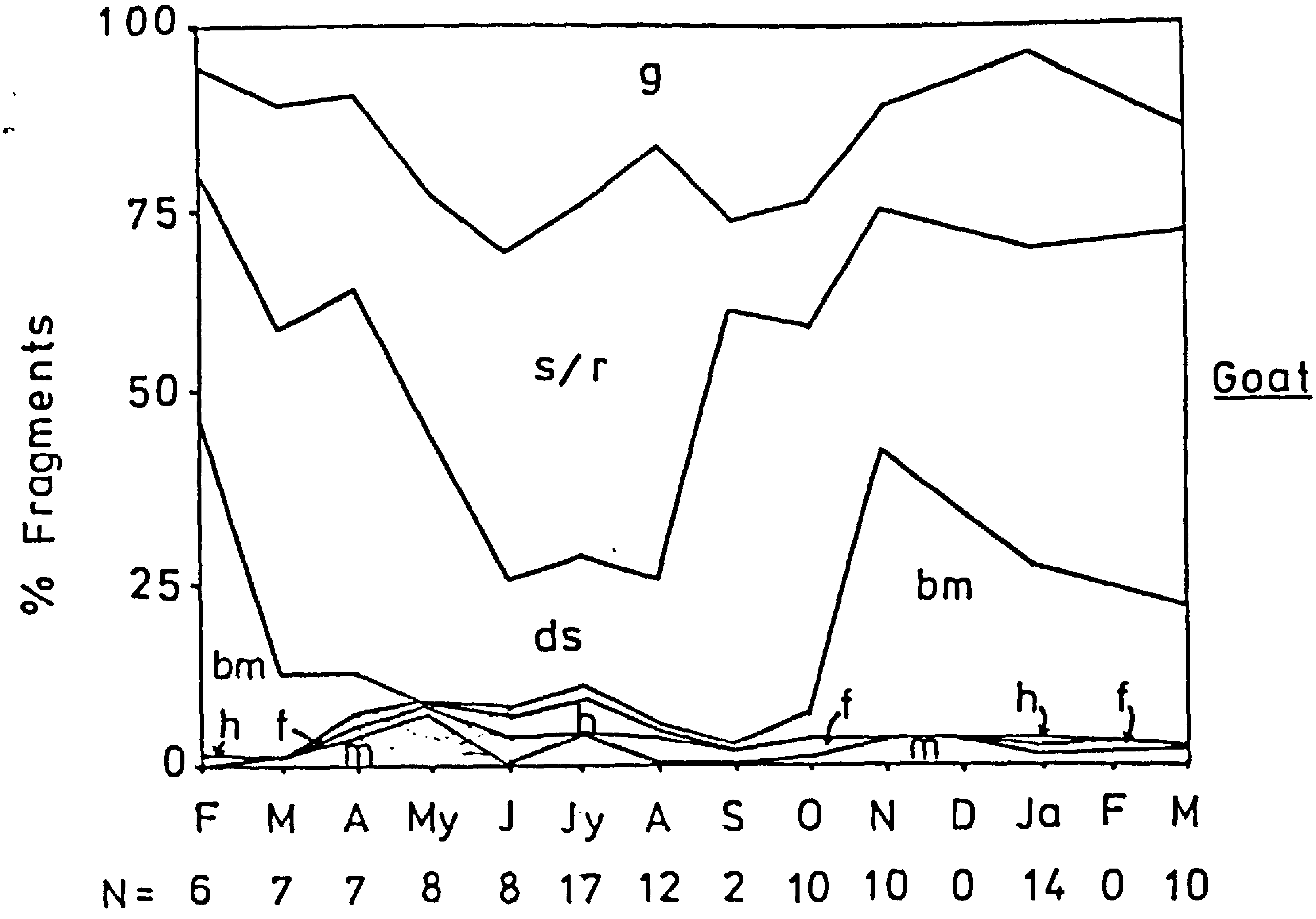
Juncus spp. (predominantly J. effusus and J. articulatus) were recorded most frequently in spring and early summer, with peaks of 33% in May and 18% in June for sheep and goats respectively. From July to April values were below 10% for both herbivores. The seasonal variation in use of J. squarrosus was noticeably different from that of other Juncus spp. in that the highest percentages of fragments of the former were recorded in winter (Figure 3.11).

Carex spp. (including C. echinata, C. panicea and C. nigra) constituted less than 10% of the fragments in sheep and goat faeces in all months except for March 1978, when 16% was recorded for goats. There was little seasonal variation in frequency of occurrence (Figure 3.11).

Only three grass genera, Molinia, Festuca and Nardus occurred to any significant extent in faecal samples (Figure 3.11). Molinia caerulea was recorded predominantly in summer with highest percentages occurring in June and August for sheep (46%) and in June for goats (30%). Marked drops in the frequencies of occurrence in July for sheep and July/August for goats coincided with an increased proportion of Trichophorum in their respective samples. Nardus stricta was recorded at greater than 10% only in the sheep samples for October although the value for March 1978 was 9%. The frequency of occurrence of Festuca spp. (predominantly F. ovina but possibly some F. rubra) was never greater than 5% for goats and only greater than 10% for sheep in November. As with Carex spp., seasonal variation in the proportion of Festuca spp. was not evident for either herbivore.

Figure 3.12

Comparison of the frequency of occurrence of plant groups in the faeces of sheep and goats from Cairnsmore of Fleet N.N.R. between February 1978 and March 1979. g = grasses; s/r = sedges/rushes; ds = dwarf shrubs; bm = bog myrtle (*Myrica*); h = herbs; f = ferns and m = mosses. N = number of pellet clusters sampled.


100
75
50
25
0
% Fragments
g
s/r
ds
bm
bm
h
f
m
h
f
m
h
f
Goat
F M A My J Jy A S O N D Ja F M
N= 6 7 7 8 8 17 12 2 10 10 0 14 0 10

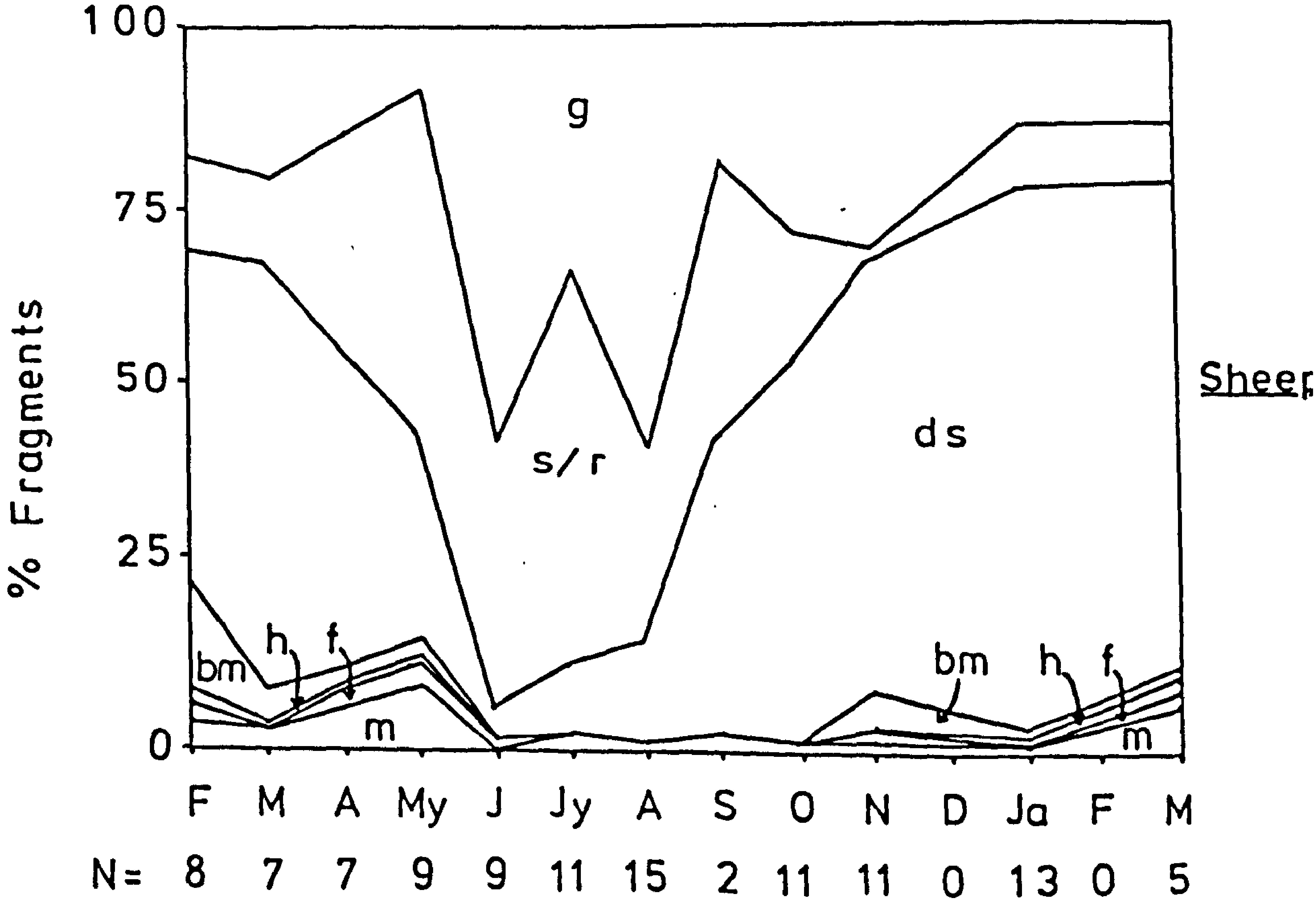

100
75
50
25
0
% Fragments
g
s/r
ds
bm
h
f
m
bm
h
f
m
Sheep
F M A My J Jy A S O N D Ja F M
N= 8 7 7 9 9 11 15 2 11 11 0 13 0 5

Table 3.9

Spearman's rank correlation coefficients (r_s) and similarity indices (S.I.) for comparison of the diets of sheep and goats on Cairnsmore of Fleet N.N.R. $^{*}p < 0.05$, $^{**}p < 0.01$.

Year	Month	r_s	S.I.
1978	February	$+0.68^{**}$	71.2
	March	$+0.43^{*}$	80.1
	April	$+0.69^{**}$	75.6
	May	$+0.82^{**}$	62.8
	June	$+0.51^{*}$	76.3
	July	$+0.46^{*}$	74.6
	August	+0.35	95.9
	September	+0.33	66.0
	October	$+0.73^{**}$	83.5
	November	$+0.28^{**}$	52.0
	December	n.d.	
1979	January	+0.16	58.9
	February	n.d.	
	March	$+0.61^{**}$	84.3

The composition of sheep and goat faeces throughout the year is summarised in Figure 3.12 where species of grasses, sedges and rushes and dwarf shrubs have been grouped. Ferns, mosses and herbs not described in the text are also included. Both herbivores showed a similar pattern of use of different plant groups as estimated from faecal analysis. In summer when abundant fresh forage was available, grasses, rushes and sedges were the main dietary items. In winter, dwarf shrubs and Myrica predominated.

Significant positive correlations between the order of abundance of different plant species/groups in sheep and goat faecal samples occurred in all months except in August, September, November and January 1979. Overlap between the estimated diets of sheep and goats was always greater than 50% and exceeded 80% in March 1978, October 1978 and March 1979 (Table 3.9). There were, nevertheless, important differences between sheep and goats in their monthly diets. In particular, during the summer, the percentages of grasses was much higher in samples from sheep than in those from goats. In winter, sheep faeces had higher percentages of dwarf shrubs but lower percentages of Myrica than those of goats (Figure 3.12).

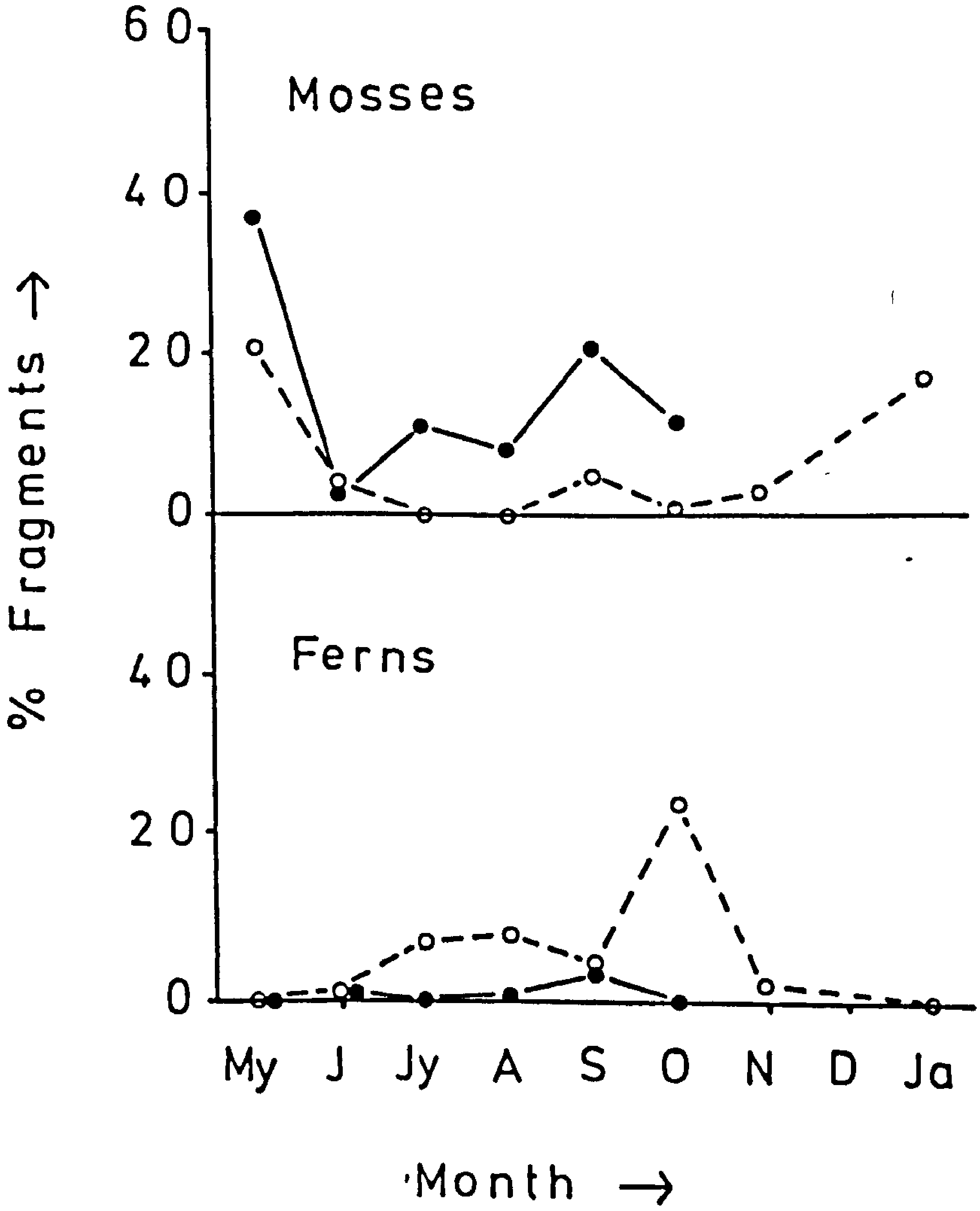
(b) Langholm-Newcastleton Hills

Mosses formed an important component of sheep and goat faeces from these hills (Figure 3.13) accounting for 37% and 21% of the fragments in sheep and goat samples respectively, collected in May. Thereafter, percentages were lower although they increased to 21% for sheep in September and 17% for goats in January.

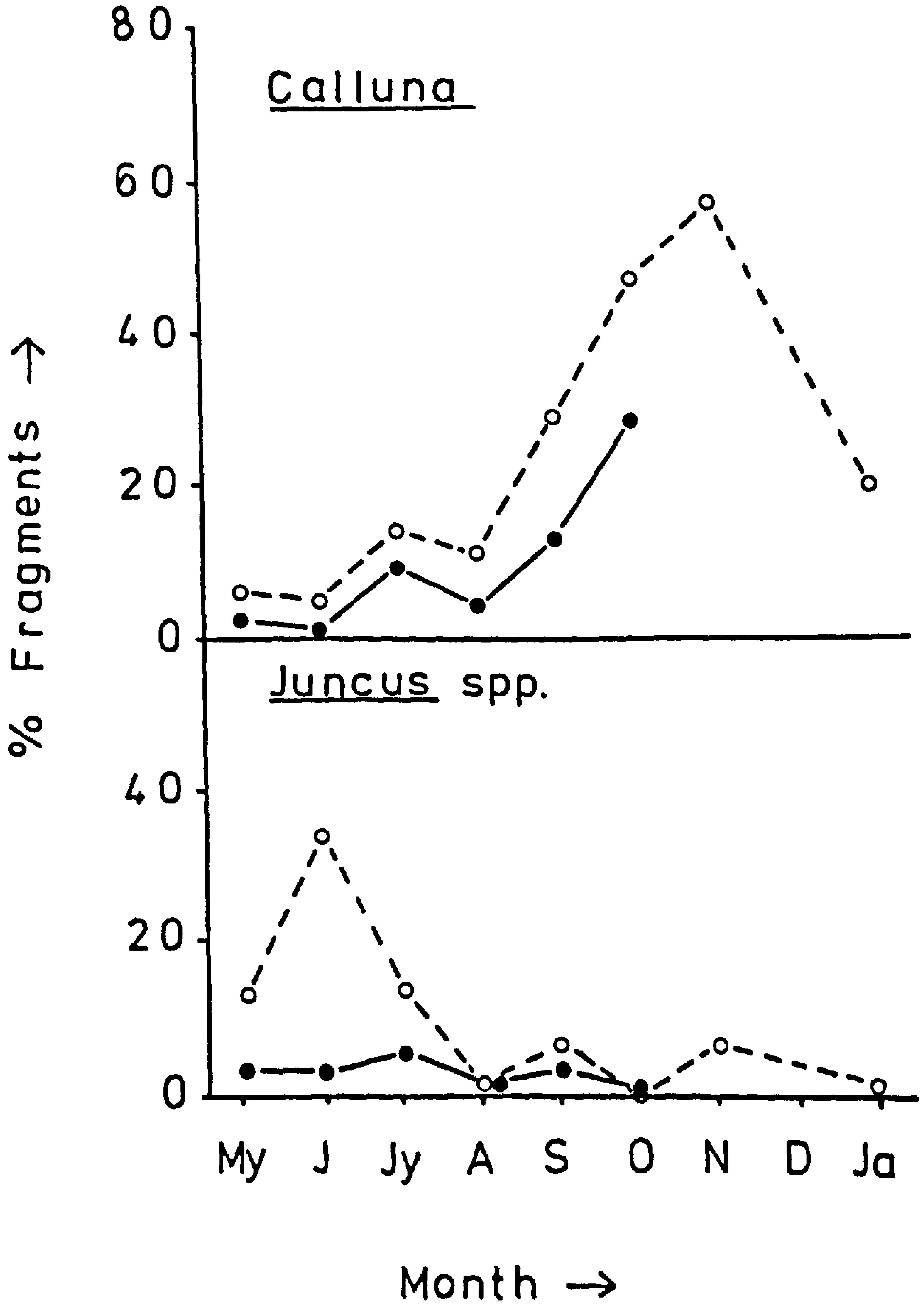
The proportions of fern fragments (probably all Pteridium) were

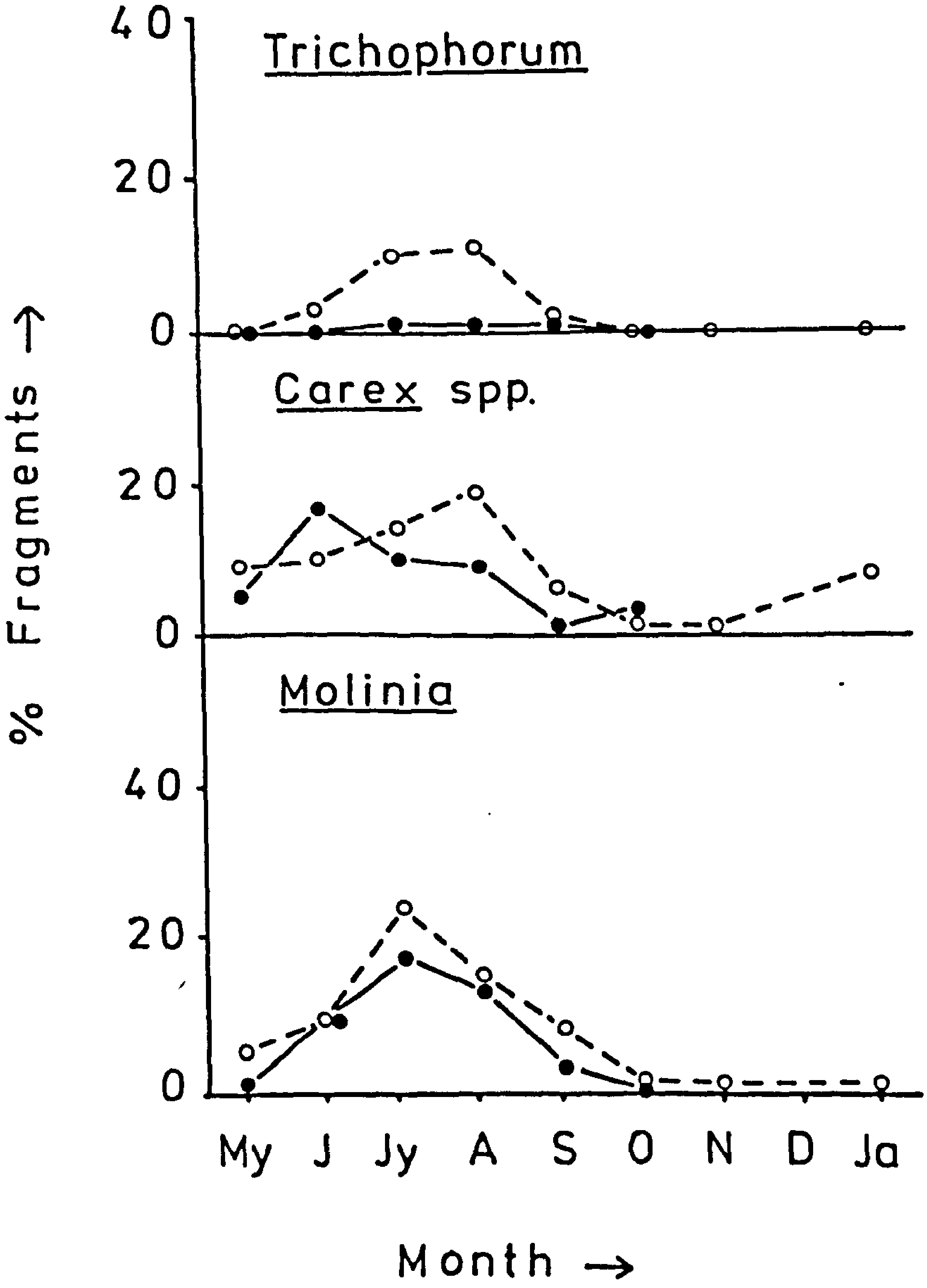
Figure 3.13

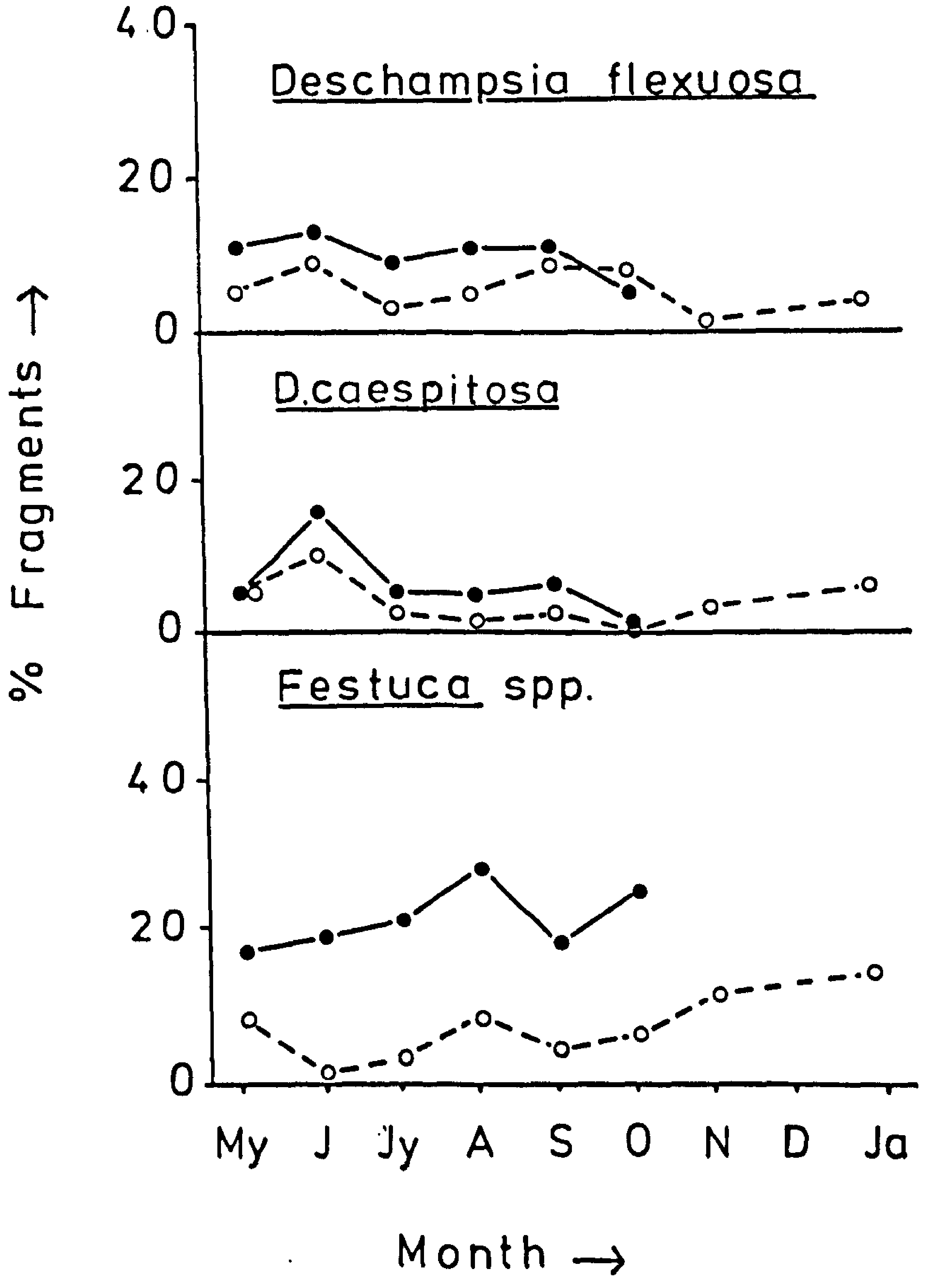
The frequency of occurrence of plant species/groups in the faeces of sheep (•) and goats (o) from the Langholm-Newcastleton Hills from May 1978 to January 1979.



60
40
20
0
40
20
0
Mosses
Ferns
% Fragments →
My
J
Jy
A
S
O
N
D
Ja
Month →


80
60
40
20
0
40
20
0
Calluna
Juncus spp.
% Fragments →
My
J
Jy
A
S
O
N
D
Ja
Month →


Trichophorum
Carex spp.
Molinia
% Fragments →
40
20
0
20
0
40
20
0
My
J
Jy
A
S
O
N
D
Ja
Month →


40
Deschampsia flexuosa
20
0
D.caespitosa
20
0
Festuca spp.
40
20
0
% Fragments →
My
J
Jy
A
S
O
N
D
Ja
Month →

unimportant for both herbivores except for goats in October when they constituted 24% of the sample (Figure 3.13). A noticeably increased proportion of fern fragments was also recorded in goat faeces at Nether Hindhope at about the same time.

The only dwarf shrub of importance in the diets was Calluna. The proportions of this in samples from both herbivores increased from May to October (Figure 3.13) as they did in samples from Cairnsmore of Fleet. The decline in frequency of occurrence of Calluna in January 1979 may have been the result of the low sample size of three pellet clusters sampled.

The frequency of occurrence of Juncus spp. (including J. effusus and J. articulatus) in sheep samples was less than 10% throughout the sampling period. For goats, however, an early summer peak in frequency of occurrence was recorded similar to that recorded for goats on Cairnsmore of Fleet and at Nether Hindhope (Figure 3.13).

The occurrence of Trichophorum in goat samples was important only in the summer months when a maximum of 11% was recorded. Sheep samples never contained more than 5% of Trichophorum (Figure 3.13). The increase in the frequency of occurrence of Trichophorum for goat samples during the summer months parallelled that of sheep and goats on Cairnsmore of Fleet where, however, frequencies were much higher.

Carex spp. (including C. nigra and C. echinata) formed a significant proportion of sheep and goat samples. For the former, percentages were highest, up to 17%, in early summer and for the latter highest percentages, up to 19%, occurred in July and August, values declining thereafter (Figure 3.13).

The frequency of occurrence of Molinia was greatest in summer for both herbivores (Figure 3.13), as for Cairnsmore of Fleet, and to a lesser extent for Nether Hindhope. This grass was an important dietary item for sheep and goats in that season.

Deschampsia flexuosa constituted between 5% and 13% of the sheep samples from May to October and 1% to 9% of goat samples from May to January 1979. For neither herbivore was there a marked pattern of seasonal variation although there was apparently little use of the grass by goats in winter (Figure 3.13). The frequency of occurrence of D. caespitosa was lower than 10% for both herbivores except in June when goat and sheep samples contained 10% and 16% respectively (Figure 3.13).

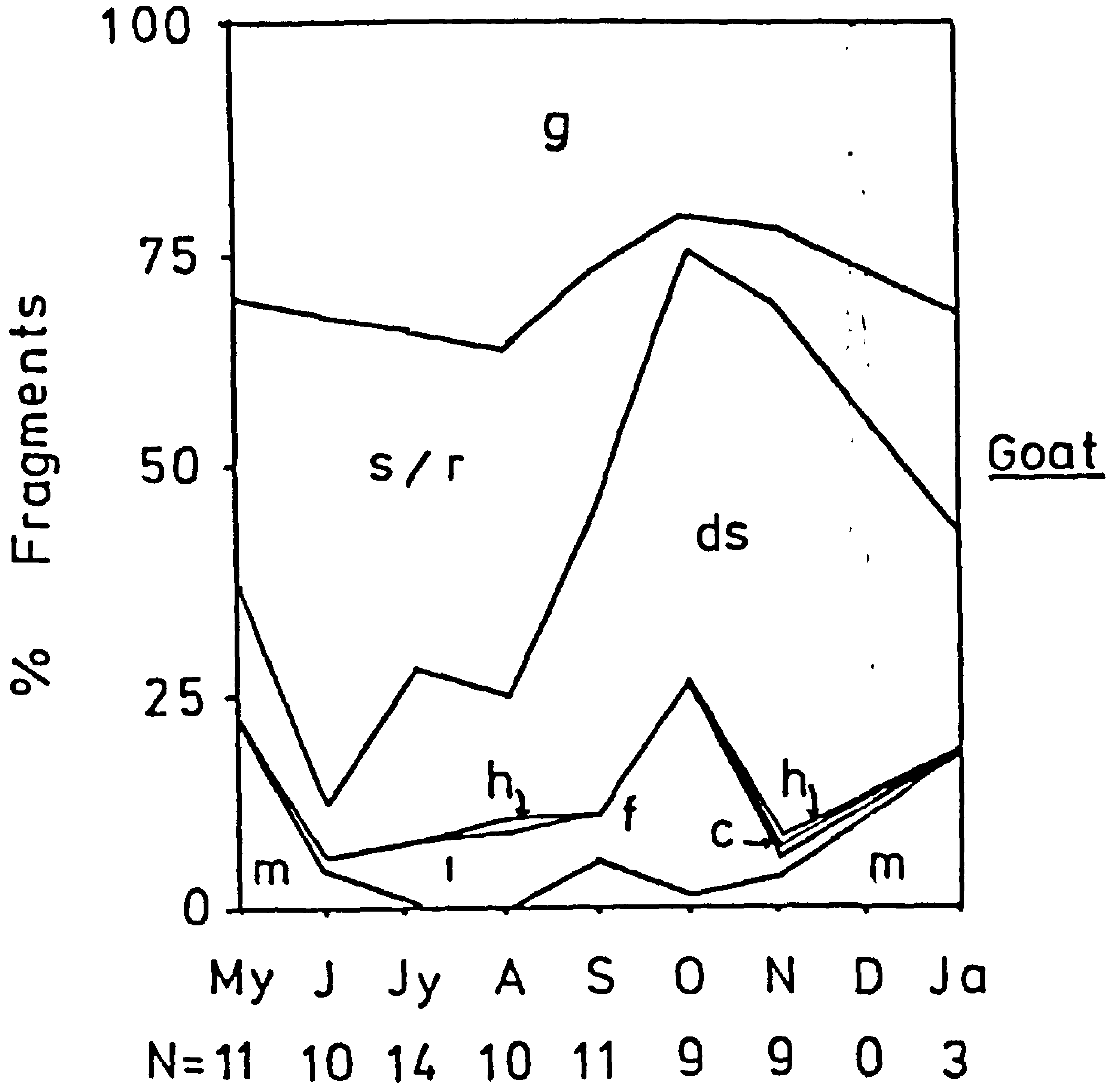
Percentages of Festuca spp. (predominantly F. ovina) were consistently higher in sheep samples than in those from goats (Figure 3.13). Both herbivores had higher proportions of Festuca spp. in their respective samples than in those from Cairnsmore of Fleet but lower than in those from Nether Hindhope.

Figure 3.14 illustrates the frequency of occurrence of plant groups in sheep and goat samples from May to October 1978 and from May 1978 to January 1979 respectively. There were marked differences in their diets, especially in the higher proportion of grasses and lower proportions of sedges/rushes and dwarf shrubs in sheep samples than in goat samples. The substantial proportion of fern (Pteridium) in the autumn diet of goats and its higher frequency in general as compared with sheep is notable. It will be shown that this difference occurred in a more dramatic form at Nether Hindhope in August and September.

Significant correlations between the diets of sheep and goats occurred only in May and September (Table 3.10). The low r_s values for

Figure 3.14

Comparison of the frequency of occurrence of plant groups in the faeces of sheep and goats from the Langholm-Newcastleton Hills between May 1978 and January 1979. g = grasses; s/r = sedges/rushes; ds = dwarf shrubs; h = herbs; f = ferns and m = mosses. N = number of pellet clusters sampled.


100
75
50
25
0
% Fragments
g
s / r
ds
h
f
c
h
m
l
m
My J Jy A S O N D Ja
N=11 10 14 10 11 9 9 0 3
Goat

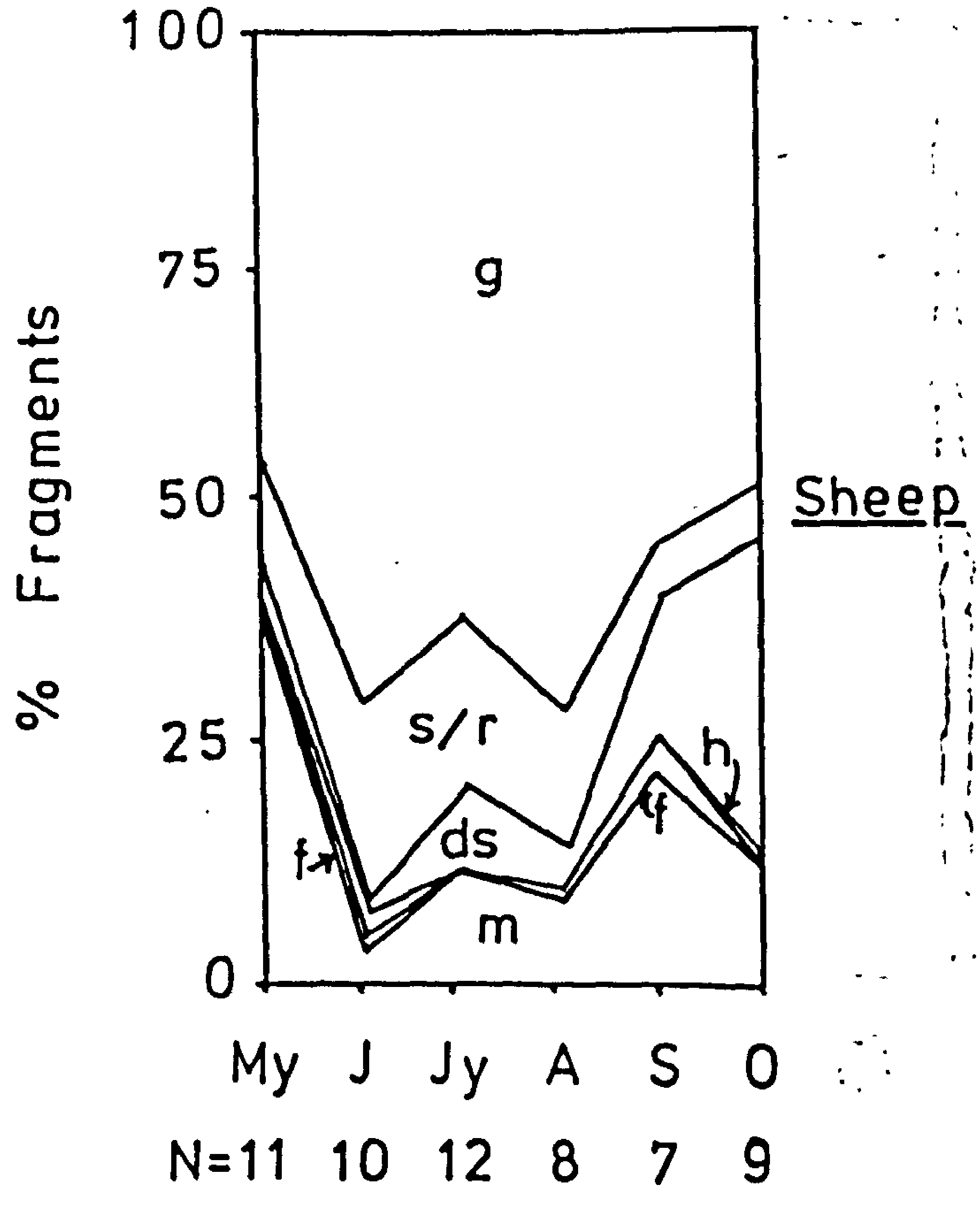

100
75
50
25
0
% Fragments
g
s / r
ds
f
f
h
m
My J Jy A S O
N=11 10 12 8 7 9
Sheep

Table 3.10

Spearman's rank correlation coefficient (r_s) and similarity indices (S.I.) for comparison of sheep and goats on the Langholm-Newcastleton Hills in 1978. $^{*}p < 0.05$, $^{**}p < 0.01$.

Month	r_s	S.I.
May	+0.47*	60.3
June	+0.24	57.1
July	+0.25	61.6
August	+0.22	59.1
September	+0.58**	57.0
October	+0.38	54.3

June, July, August and October indicate that the diets of the two herbivores differed markedly in summer and early autumn. Similarity indices for the same period (Table 3.10) were lower than those for corresponding months on Cairnsmore of Fleet (Table 3.9) but generally higher than those for Nether Hindhope.

(c) Nether Hindhope

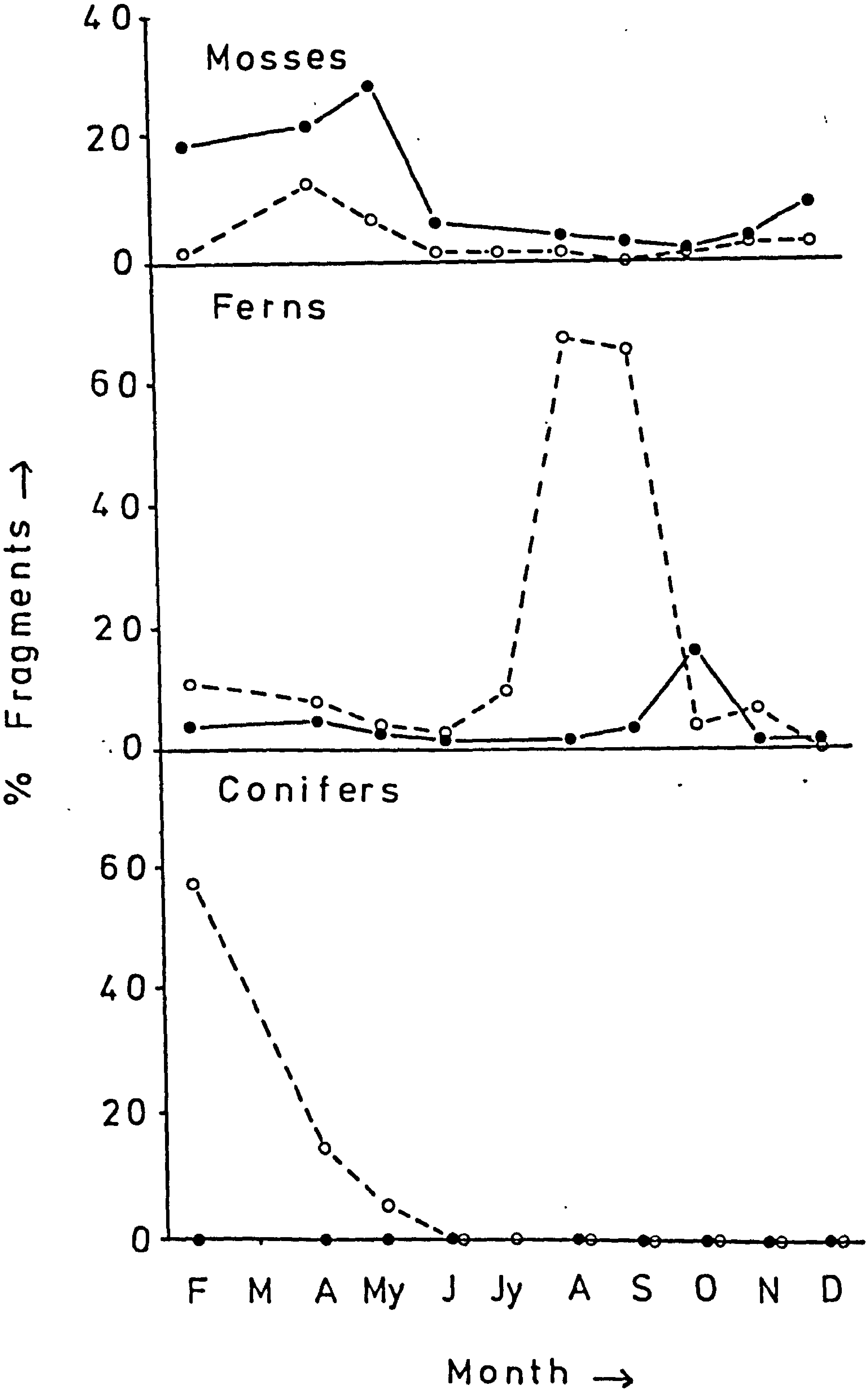
Mosses constituted a significant proportion of the sheep samples in late winter and spring. For the rest of the year, the proportions were much lower. The highest percentage of moss fragments (12% maximum) in goat samples also occurred in spring with a decline in frequency, similar to that for sheep thereafter (Figure 3.15).

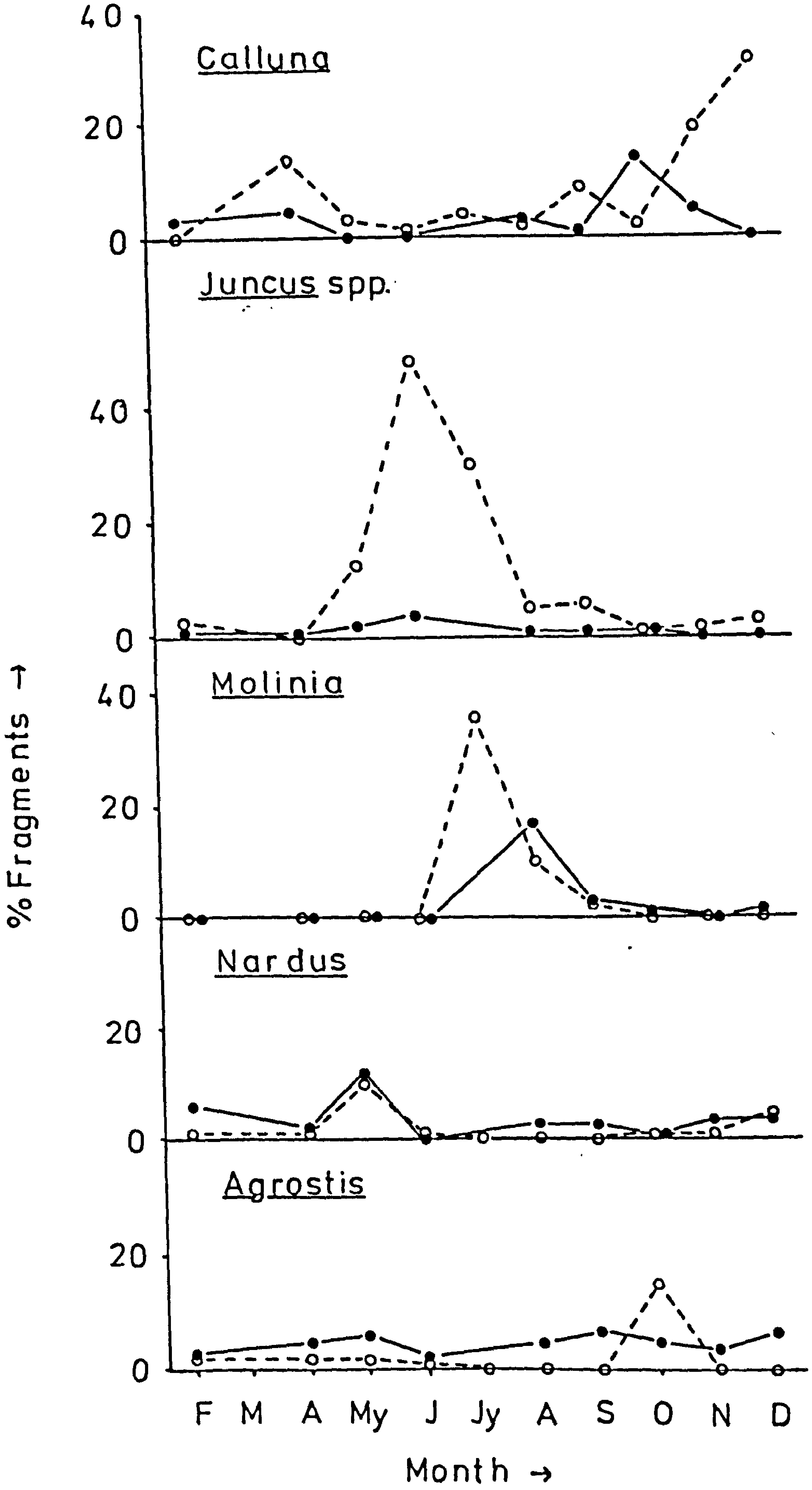
The proportion of fern (Pteridium) in both sheep and goat samples was low, at 10% or less, during winter, spring, early summer and late autumn. It was very high in goat samples from August and September when 67% and 65% of fragments respectively were fern (Pteridium). A much smaller peak in the proportion of fern was recorded for sheep samples in October (Figure 3.15).

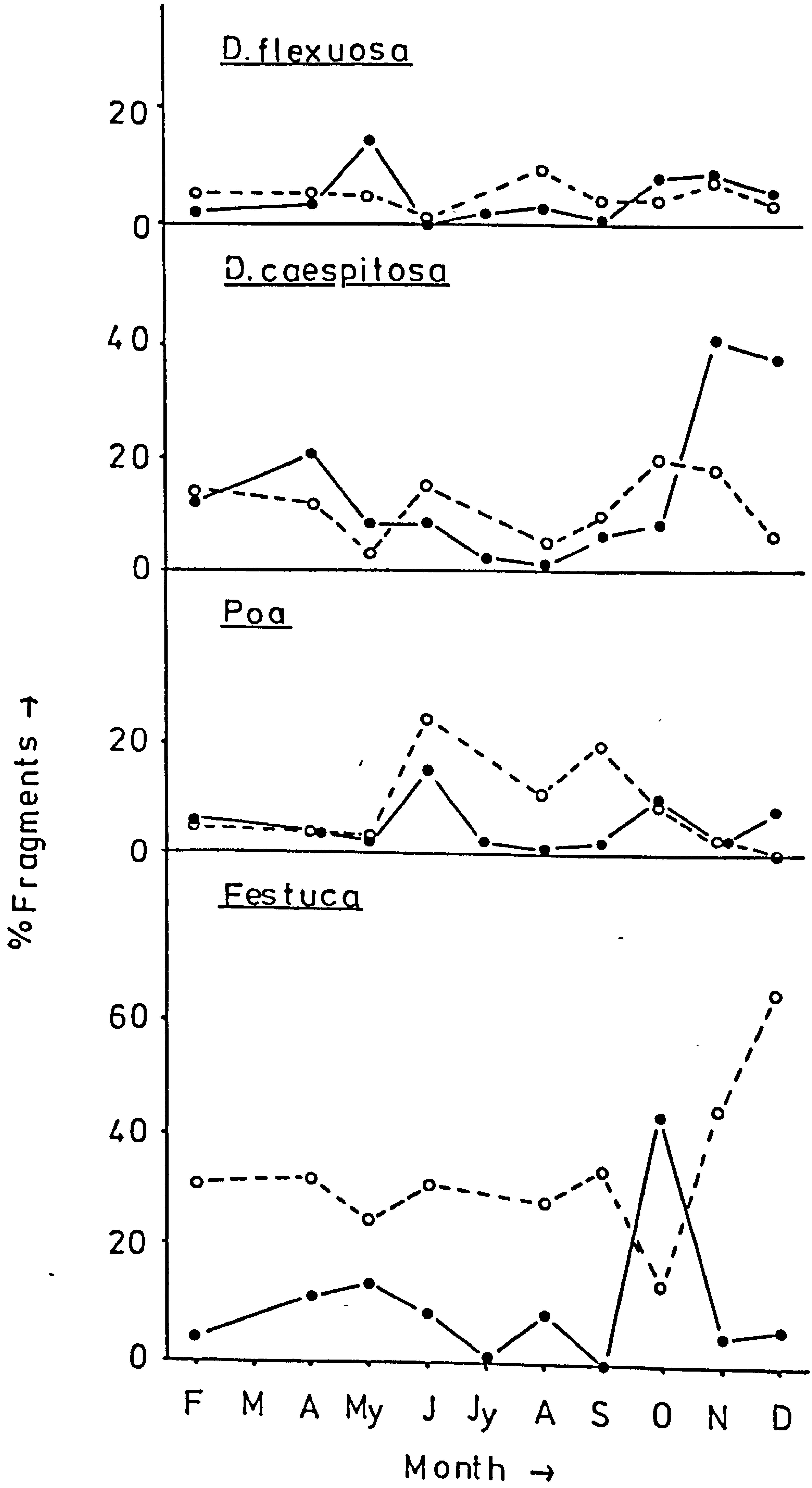
Fragments of pine (Pinus sylvestris) needles occurred only in goat samples from late winter and early spring. In February they formed 57% of the total and together with bark, were clearly an important food (Figure 3.15). The majority of the Nether Hindhope goats invaded the small conifer plantation on the hill farm at that time, as they had done in previous years (A. Crozier pers. comm.). They did so again in the winters of 1978-79 and 1979-80, some individuals remaining there throughout the season. Sheep were never observed to enter the plantation so that its trees and ground flora were food resources available solely to goats.

Figure 3.15

The frequency of occurrence of plant species/groups in the faeces of sheep (●) and goats (o) from Nether Hindhope between February and December 1978.


Mosses
Ferns
Conifers
40
20
0
60
40
20
0
60
40
20
0
% Fragments →
F
M
A
My
J
Jy
A
S
O
N
D
Month →


40
Calluna
20
0
Juncus spp.
40
20
0
Molinia
40
20
0
% Fragments →
Nardus
20
0
Agrostis
20
0
F
M
A
My
J
Jy
A
S
O
N
D
Month →


D. flexuosa
D. caespitosa
Poa
Festuca
20
0
40
20
0
20
0
60
40
20
0
% Fragments →
F
M
A
My
J
Jy
A
S
O
N
D
Month →

The only dwarf shrub of importance in the diet was Calluna. This constituted a maximum of 14% in the sheep samples from October and for the rest of the year was 5% or less (Figure 3.15). Goat samples had higher percentages of Calluna than sheep especially in the spring, autumn and winter months. The highest proportions were recorded in April, November and December; this pattern was similar to that of the frequency of occurrence of Calluna in samples from Cairnsmore of Fleet and the Langholm-Newcastleton Hills.

The only rushes or sedges that constituted a significant proportion to either sheep or goat samples were Juncus spp. (including J. effusus and J. articulatus) (Figure 3.15). However, 9% of the May and June samples for goats were of Eriophorum spp. and Luzula spp. respectively, but percentages of these genera in other months were much less. There were marked differences in the percentages of Juncus spp. in sheep and goat samples from May, June and August. Up to 48% was recorded for goats in June but the frequency of occurrence for sheep was never greater than 5% (Figure 3.15). For the rest of the year the proportion for goats was less than 10%. No data were available for sheep in July.

Grasses were an important dietary item for sheep at Nether Hindhope. Hay was provided by the shepherds in March and April 1978 and was eaten by some of the sheep and, to a much lesser extent, by goats. In the sheep samples from April, (no samples were available in March) many fragments of grass epidermes were not identified and were assumed to be from lowland meadow species. The proportion of grasses in the sheep samples from April was thus probably underestimated.

Fragments of Molinia were not recorded in the faeces of either herbivore except in the summer and early autumn (Figure 3.15). Maximum percentages were 36% in July for goats and 17% in August for sheep. For the latter no data were available in July when the percentages of Molinia fragments may have been higher.

Nardus was infrequent in samples for most of the year but constituted 10% and 12% of the sheep and goat samples respectively in April (Figure 3.15). Similarly, fragments of Agrostis spp. formed low proportions of the samples from both herbivores except in the October goat sample when 10% was recorded (Figure 3.15).

Deschampsia flexuosa constituted low proportions of the samples from both herbivores in most months. For sheep, the frequency of occurrence was never above 10% and for goats, the percentage in May was 15% but was otherwise 10% or less (Figure 3.15).

D. caespitosa was recorded in all samples for goats, the proportions varied between 1% and 40% being highest in late autumn, winter and early spring. The proportions for sheep showed less seasonal fluctuation varying between 4% and 20%, with higher values than those for goats in summer and early autumn (Figure 3.15). Since D. caespitosa occurs most frequently in the valley bottoms at Nether Hindhope where hay was given out, it is possible that goats and sheep ingested this species incidentally. If this was the case, faeces from March may have contained relatively high proportions of D. caespitosa since both herbivores tended to congregate around the haysheds in spring.

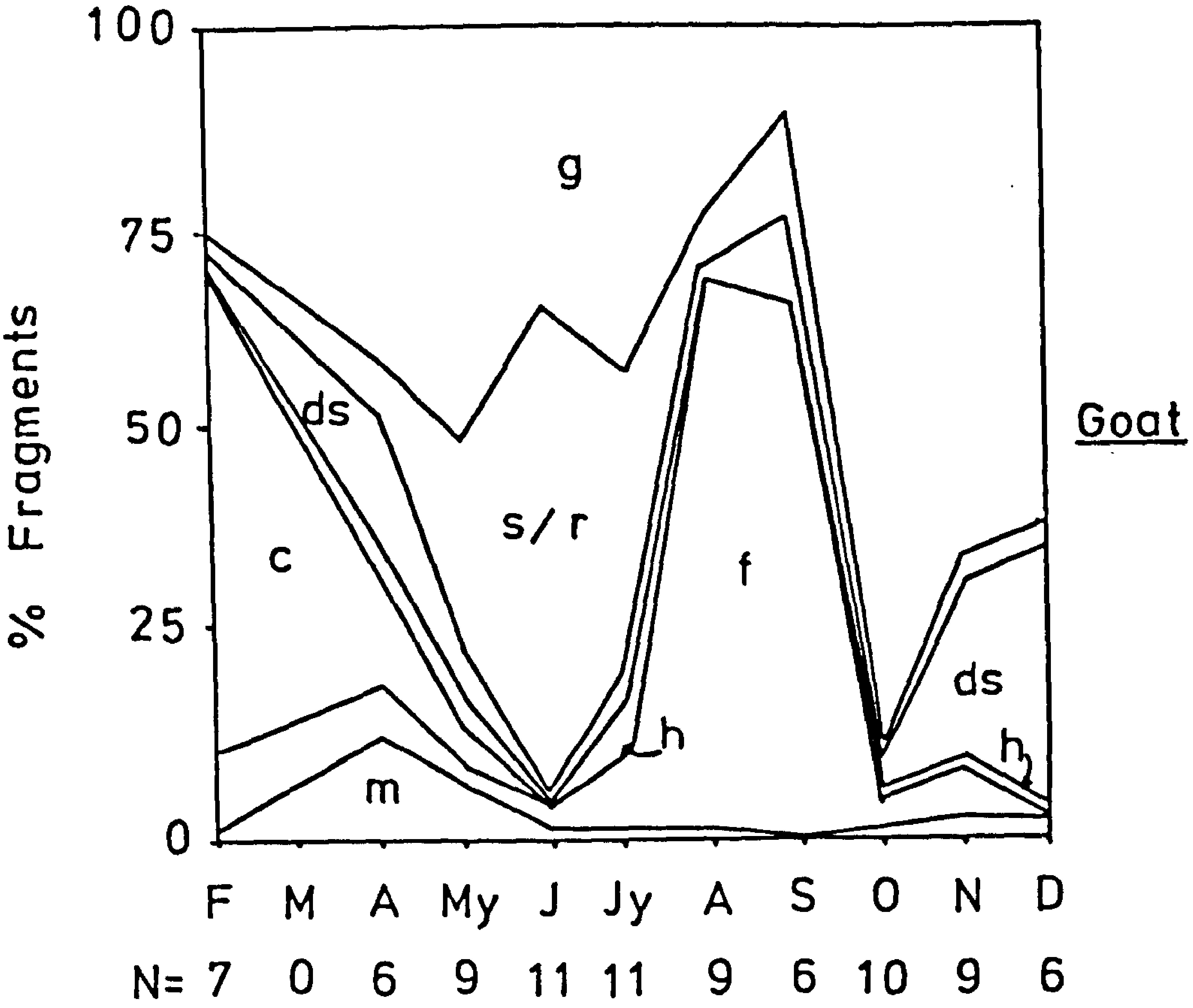
Poa spp. (including P. annua, P. pratensis, P. subcareula and P. trivialis) occurred in much higher proportions during the summer and autumn than in winter or spring. This was especially so in sheep samples, for which percentages of 24% and 19% were recorded in June and September respectively. Goat samples contained lower proportions, being greater than 10% only in June when 15% was recorded. A distinct drop in the proportion of Poa spp. occurred for goat samples thereafter until October when the value was 10% (Figure 3.15). The higher frequency of occurrence of Poa in summer than in winter is surprising considering that P. pratensis is palatable and winter green (Milner and Gywnne 1974). These authors also recorded higher percentages of Poa in faeces from Soay sheep in summer. They attributed the lower frequency of occurrence in winter to unavailability, the plants having been overgrazed during the summer.

Festuca (F. ovina with, possibly, some F. rubra) constituted up to 66% and never less than 14% of all sheep samples and was, therefore, an important food (Figure 3.15). The proportion varied little from February to September at between 25% and 34%. It dropped to 14% in October and then increased up to 66% in December. Goat samples usually contained much lower proportions of Festuca spp. Only in October was the proportion greater than that for sheep, at 44%; in the rest of the year 13% or less was recorded. Higher frequencies of occurrence of Festuca spp. in sheep, as opposed to goat samples, were also found on Cairnsmore of Fleet and Langholm-Newcastleton Hills.

Figure 3.16 illustrates the use of different plant groups by sheep and goats throughout the year. There were striking differences between the two diets; sheep samples contained mostly grasses with a large proportion of mosses in late winter and early spring. The percentages of grass in goat samples were, except in October, lower than those for sheep and also more variable. In winter and early spring goats browsed and barkstripped conifers, a resource not available to sheep, while in late spring and summer sedges/rushes contributed most to the total.

Figure 3.16

Comparison of the frequency of occurrence of plant groups in the faeces of sheep and goats from Nether Hindhope between February and December 1978. g = grasses; s/r = sedge/rushes; ds = dwarf shrubs; h = herbs; c = conifers; f = ferns and m = mosses.
N = number of pellet clusters sampled.


100
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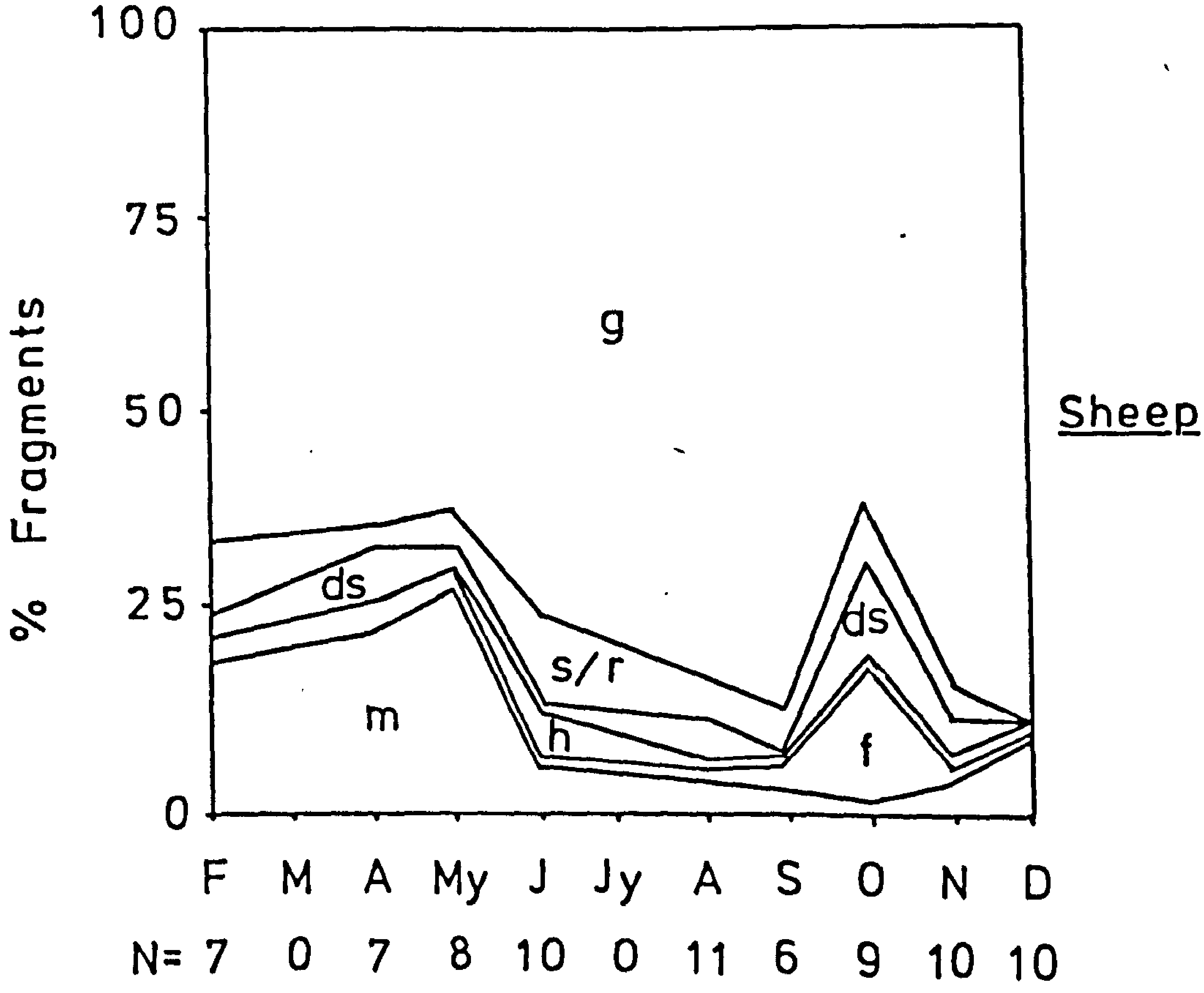
Goat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Sheep

Table 3.11

Spearman's rank correlation coefficients (r_s) and similarity indices (S.I.) for comparison of the diets of sheep and goats at Nether Hindhope during 1978. $^{*}p < 0.05$, $^{**}p < 0.01$.

Month	r_s	S.I.
February	+0.34	46.3
March	n.d.	
April	+0.24	63.0
May	$+0.61^{**}$	59.4
June	+0.33	48.2
July	n.d.	
August	+0.36	32.8
September	+0.08	26.8
October	$+0.69^{**}$	56.1
November	$+0.45^{*}$	51.9
December	-0.03	31.1

Lastly, a most striking increase in the proportion of ferns occurred in the goat samples from July to August and September.

Significant, positive correlations between the diets of sheep and goats occurred in May, October and November; in other months the correlation coefficients were low and not significant (Table 3.11). Percentage overlap was low (Table 3.11) suggesting little potential food competition between sheep and goats at Nether Hindhope in any season.

The general conclusions from comparisons of the diets of sheep and goats are that firstly, dietary overlap increased from Nether Hindhope westwards to Cairnsmore of Fleet with a concomitant with decreasing range quality. Secondly, sheep tended to graze more than goats and thirdly, both herbivores used certain plant species/groups such as *Juncus*, ferns (*Pteridium*), *Molinia*, *Trichophorum* and dwarf shrubs at the same times of year.

Discussion

Few observations on the feeding style (Jarman 1974; Leuthold 1977) of feral goats were made. Such observations have been neglected in other studies but when considering the range relationships between the sexes and between goats and other herbivore species, they provide essential data. Goats, because of their agility and ability to forage whilst on their hindlegs, are able to feed in the field and low canopy layers (Elton & Miller 1954) more than sheep. Their ability to climb walls, crags and trees also enables goats to exploit a wider range of habitats than sheep. The former may not, however, be as efficient as the latter in utilising close cropped, nutritious swards. This aspect of comparative feeding ecology requires much further study.

The possession, by feral goats, of scimitar or dorcas shaped horns allows them to render spiny plant species more palatable by horning them. Horning may have other functions such as the dissemination of odours (Schaller 1977) and providing a means of expressing aggression indirectly (Geist 1971) but these additional functions do not lessen its usefulness when feeding on thistles or gorse.

The feeding activity patterns of goats and sheep appeared to be similar. In particular, the timing of the major rest period, during which most individuals were inactive or ruminated, was often synchronous. Furthermore, the mean duration of rest periods for individual goats were similar to those recorded for sheep (Arnold & Dudzinski 1979), My few observations indicated that firstly, the digestive physiologies of the two herbivores were similar and secondly, because they were active at similar times, interference competition could have occurred.

A period of minimum activity around the middle of the daylight hours has previously been observed in commercial sheep at pasture (Arnold & Dudzinski 1979; Hughes & Reid 1951) and for feral goats (Stafford-Smith 1979; Stevenson-Jones 1977). Wild caprinids show similar rest periods; Hoeffs (1974) describing the feeding activity of a Dall ram noted the constancy of the rest period around midday over an annual cycle. Himalayan tahr, markhor and some bharal watched by Schaller (1977) also showed a period of least activity around midday. The pattern is not evident from observations on hill sheep by Hunter (1954) or those by Grubb and Jewell (1974) on feral sheep. Both these studies involved instantaneous scan sampling of many social groups between which there may have been little synchrony so that any pattern was obscured.

During late spring and summer my few observations suggested that activity patterns were more variable; on some days sheep and goats showed a midday rest period, on others none was evident. It is likely that environmental and social factors influence the activity pattern more in summer than in winter, when relatively more rumination time may be necessary for the digestion of more fibrous forages.

There is no agreement in the literature as to whether sheep and other caprinids feed at night, suggesting that the extent of night time feeding varies with environmental conditions and season. Hill sheep in Colquhoun's study (1971) grazed for up to 30% of winter nights but did so for a negligible proportion of summer nights; Wallace (1884) and Hughes and Reid (1951) reported similar observations. Feral Soay sheep on St Kilda are inactive at night (Grubb & Jewell 1974); these sheep have access to cleits (stone shelters) which afford much shelter.

Hoeffs (1974) found for his Dall ram that night time feeding was restricted to the hour immediately after sunset. Other wild American sheep are, however, thought to feed much at night whereas mountain goats are predominantly inactive (Geist 1971). In the present study goats and sheep were generally active around dawn and in the evening they remained so when observations ceased at dusk. On the occasions when goats were observed before dawn and after dusk, they were predominantly inactive. However, these observations were conducted during summer; feeding may have occurred during long winter nights.

For those feral goats that frequented very steep rocky ground such as on the Moffat Hills, night time feeding (especially during the winter) may be hazardous. Sheep are not faced with such hazards since they are not found in these habitats. Goats have been observed to fall from snow and ice covered crags whilst foraging. It is possible that they camp rather than feed during dark nights when the risk of falling is relatively high.

Goats appeared to travel further during the day than ewes on similar ranges. Milner (1962) found that five hill ewes of the South Country Cheviot breed on a Cheviot Hill Farm, covered between 363 m and 852 m per day throughout the year. These are considerably shorter distances than those travelled by goats at Nether Hindhope, but are similar to those of goats on the Moffat Hills. Much greater distances are travelled by sheep and goats in semi-arid or arid environments where water and forage availability is more unpredictable in space and time (e.g. Arnold & Dudzinski 1979; Cory 1927; Lynch 1974).

The decrease in feeding activity of billies, as compared with nannies, during the autumn probably reduces the fat reserves of some individuals of the former to such an extent that they are more likely to die in the following spring. This is an important observation that has been documented for another Scottish feral goat population (Boyd 1981) and also for feral Soay sheep on St Kilda (Grubb & Jewell 1974). It is inferred from these studies that the reduced feeding time of feral male caprinids in temperate regions during the rut gives rise to their higher mortality rates compared to those of females (Chapter 4).

The strong selection of freely drained Festuca-Agrostis-type grasslands by hill sheep on Cairnsmore of Fleet has been observed elsewhere, e.g. Colquhoun (1971), Griffiths (1970) and Hunter (1962). The selection ratio decreased during the summer when an increase in Pteridium cover and heavy grazing may have made these swards less attractive. Increased use in the autumn coincided with the dieback of Pteridium; grazing probably became easier at that time than in summer when dense stands of Pteridium inhibit movement. Hunter (1962), from observations of hill sheep, noted that invasion of Pteridium caused a depression in the selection ratio for Festuca-Agrostis grasslands. Goats also selected freely drained grasslands least in summer but for both herbivores selection of soligenous mires was greatest then, implying that many individuals had moved to the latter in order to feed on the fresh growth of Molinia. The results of diet analyses support this suggestion.

In the autumn when Molinia had died down and its dead leaves were of low nutritional value, ewes avoided soligenous mires. However, nannies continued to select these communities. From diet analyses and observations it was concluded that they were browsing Myrica in soligenous mires at that time. The strong selection by goats for soligenous mire in winter 1978-79 may not have been typical because the winter was relatively severe and snowy (Chapter 1) and goats moved down to lower altitudes than they did in milder winters (W. Johnston pers. comm.) where there was a relatively greater area of these communities. Overlap between the use of vegetation types by ewes versus goats and billies versus nannies was highest in summer when competition would be expected to be least.

There were similarities in the use of vegetation types by goats on the Moffat Hills and Langholm-Newcastleton Hills. In particular, dwarf shrub communities, either dry/moist heath or wet heath/blanket mire, were selected at all seasons on each study area. Similarly, in College Valley during summer 1979, goats were seen predominatly in dwarf shrub and grassland communities (Stafford-Smith 1979).

Casual observations of sheep at these study areas suggested that they selected grasslands much more than goats at all seasons. This was particularly obvious on the Moffat Hills where sheep occupied the grasslands situated above and below the zone of dwarf shrub communities frequented by goats. Crook (1969) reported that feral goats in Snowdonia were in dwarf shrub communities (predominantly dry/moist heath) for 55% of his observations. This is similar to the comparable figure for the Moffat Hills of 53%. Clearly these communities are an important component of the niche of feral goats in Britain.

Use of freely drained grasslands by goats on the Moffat and Langholm-Newcastleton Hills was generally low although they were selected during the autumn on the latter. Avoidance by goats of the highest quality swards is possibly due to the presence of sheep which reduce the standing crop on Festuca-Agrostis grasslands to such an extent that goats can maintain a higher nutritional input in the Calluna and Molinia dominated communities. Selection of freely drained grasslands in the late summer and autumn by goats may, in part, be due to the presence of Pteridium. From diet analyses and observations they feed on this extensively rather than on the grass sward.

On the Moffat Hills and the Langholm-Newcastleton Hills, goats were most frequently observed at altitudes between 300 m and 600 m as a result of their selection of dwarf shrub communities. It is not clear why goats were selecting these communities but prominent among possible causes are reduced competition with sheep and reduced disturbance from shepherding.

On Cairnsmore of Fleet, goats were mostly observed at lower altitudes than at the previous two study areas with billies being found at lower altitudes than nannies, at least in spring. Nannies may remain at higher altitudes in order to avoid harassment by shepherds, especially during kidding; billies are less vigilant and less readily disturbed than nannies and may tolerate more disturbance than the latter. Alternatively, billies may attempt to maximise their reproductive fitness at this season by reducing their competition for food with nannies whom, according to a similar explanation for sexual segregation in bighorn sheep (Geist & Petocz 1977), they will have inseminated in the previous autumn. Another explanation is that billies in spring seek more sheltered areas than nannies in which to feed more efficiently following a winter of privation for which, because of their activity in the previous autumn's rut, they may have had lower fat reserves than nannies.

Sexual segregation in altitude did not occur on the Moffat Hills. Here, stocking density of sheep was higher and shepherding more regular than on Cairnsmore of Fleet. Furthermore, there appeared to be much less shelter at lower altitudes than within the dwarf shrub zone so that the descent of billies to lower altitudes in spring may not have increased their foraging efficiency. Sexual segregation in feral goats is discussed further in Chapter 5.

Studies of feeding ecology are not complete without data on the nutritional requirements of the animal; these vary with sex, age and season. With respect to temperate ruminants, there is a decrease in food intake which starts in autumn and continues throughout the winter (Moen 1973). All these variables can affect the accuracy of dietary analysis and particularly the indirect methods such as faecal analysis.

Milner and Gwynne (1974) considered that differential digestion of plant species and differential passage times made faecal analysis inadequate for estimating the diet of Soay sheep on St Kilda. Their results, however, were not only consistent with those of Colquhoun (1971), Grant, Lamb, Kerr & Bolton (1976) and Martin (1964) but also those of the present study. All the authors cited used faecal analysis to estimate the diets of hill sheep on mainland Scotland. The similarities, heavy use of dwarf shrubs in winter with correspondingly low summer use and the reverse situation for monocotelydons, suggested not only consistency in the reliability of the methods but also consistency in the diets.

The results of ingestal, ruminal and faecal analyses have rarely been compared. In particular, few analyses have compared the botanical composition of ingesta and ruminal contents with that of faeces. Todd & Hansen (1973) and Anthony & Smith (1974) compared the frequency of occurrence of plant species in ruminal and rectal faeces samples for culled bighorn sheep and deer (Odocoileus) respectively. Their general conclusions were that there were few differences but that woody forages were better represented in faecal than in ruminal material.

The indication in the present study that woody forages were generally present in higher proportions in faecal than ruminal samples and conversely, grasses, sedges/rushes and herbs were generally in higher proportions in faecal than in ruminal samples accord with previous observations. Martin (1955), Stewart (1967) and Vavra et al. (1978) all concluded that dry weight of plant species in ingesta is rarely similar to their frequency of occurrence in faecal samples.

Both sheep and goats in all the study areas showed higher intake of mosses in spring than at other seasons. Mosses were particularly frequent in spring samples from sheep on the Langholm-Newcastleton Hills and Nether Hindhope where sheep were predominantly grazers. Conflicting views exist as to whether mosses are accidentally or deliberately ingested (Colquhoun 1971; Martin 1964; Milner & Gwynne 1974). It is in spring, prior to the flush of new plant growth, that swards are likely to be overgrazed and accidental intake of mosses may occur, giving rise to the spring peaks. Alternatively, mosses may have been selected; this would seem unlikely in May when growth of grasses and other monocotelydons is well under way, but may be the case in April when grass swards are much poorer in available forage.

For both herbivores peak use of Molinia and Trichophorum was in summer. Goats, but not sheep, showed heavy use of Juncus spp. in spring at all three study areas. Juncus spp., (except J. squarrosus) Trichophorum and Molinia have late spring and summer growing seasons. Also, the last two species die back in the autumn and become nutritionally valueless. The changes in level of intake of these species by sheep and goats presumably reflects their availability as green forage.

Martin (1964) using faecal analysis to estimate the diets of hill sheep feeding on a similar range of plant communities described a different pattern. Juncus spp., including J. squarrosus, were most frequent in winter samples and there was no spring peak. Molinia was prevalent in faeces from January to June but Martin found that between January and March the fragments were mainly of dead material and thereafter, fresh shoots were utilized. However, Grant et al. (1976) using analyses of the sward before and after grazing and faecal analysis found that hill sheep had highest use of Molinia in summer with insignificant use at other seasons. A higher use of "long celled sedges" (Trichophorum and Eriophorum vaginatum) in summer than in winter was found and the reverse was true for the use of dwarf shrubs. These results were very similar to those of the present study.

The inferred large intake of Pteridium by goats in late summer and autumn, especially at Nether Hindhope was surprising. A predominance of ferns in the diet of ungulates has rarely been recorded. Stevenson-Jones (1977) found that the percentage of fern fragments, predominantly of

Pteridium in goat and to a lesser extent sheep faeces from College Valley, increased throughout the summer. Hjelford (1973) recorded heavy winter use of lady fern (Athyrium filixfemina) rhizomes and to some extent petioles, by mountain goats in Alaska. Three rumens contained between 60% and 91% dry weight of the fern. I observed feral goats on the Moffat Hills in summer 1979 pawing repeatedly at bare earth on a slope in order to expose Pteridium rhizomes and goats were frequently observed eating bracken fronds.

Pteridium is considered unpalatable and toxic to livestock including goats (Evans 1976; MacKenzie 1980). However, concentrations of the principle toxins, hydrogen cyanide and a thiaminase decline in the fronds to very low levels by August and September (Cooper-Driver, Finch, Swain & Bernays 1977; Evans 1976). Furthermore, the percentage dry weight of nitrogen in Pteridium is similar to that of other forages available on uplands at that time: 1.0% - 2.2% in the fronds compared to Calluna (1.4% dry weight) and Festuca-Agrostis grassland (2.1% dry weight) (Lawton 1976; Pearsall 1971). Pteridium can therefore be a nutritious and, by virtue of its stature, easily obtained forage.

Additionally, Pteridium exists as acyanogenic and cyanogenic morphs; the latter liberates free hydrogen cyanide on being bruised (Cooper-Driver & Swain 1976). Sheep can select the acyanogenic morph (Cooper-Driver et al. 1977) and presumably goats can do the same. It is possible that goats test the toxicity of Pteridium plants by horning (and therefore, bruising) them and in doing so can judge their palatability.

Information concerning the diet of British feral goats has hitherto been restricted to reports of casual observations or to studies conducted during the summer. Greig (1969) noted that the goats in the Ben Lomond area seemed to eat more Myrica and Pteridium than sheep, and Crook (1969) reported that Snowdonian feral goats fed extensively within dwarf shrub communities. McDougall (1975) used faecal analysis to estimate the diets of sheep and goats on Kielderhead Moor from late April to late June 1972. His results indicated that goats used much more Calluna than sheep, in which use decreased throughout the summer. The percentage of Trichophorum increased towards midsummer particularly for sheep, and the proportion of Festuca was always higher in sheep than in goat samples. These findings were consistent with my results from Cairnsmore of Fleet and the Langholm-Newcastleton Hills.

In College Valley during the summer of 1977, Stevenson-Jones (1977), using faecal analysis reported that goat samples generally contained twice as much browse as those from sheep and the reverse for grasses. Ulex is apparently eaten in considerable quantities by goats in College Valley although little used by sheep (Stevenson-Jones 1977; pers. obs.). Stevenson-Jones believed that faecal analysis underestimated intake of Ulex because most foraging of this shrub was of flowers, epidermal fragments of which were not detected in the faeces. During the summer, the mouths of goats in College Valley may appear wholly yellow due to feeding on Ulex flowers (Stevenson-Jones 1977; pers. obs.) indicating highly selective feeding. Ulex bushes known to be browsed by goats have a conical shape.

The preference by domestic sheep for grasses and other monocotelydons is well documented. It is not clear, however, whether goats on British uplands prefer to browse, a traditional view, or to graze. Cory (1927) in a seminal and comparative study of the feeding ecology of livestock on Texan range found that sheep and goats browsed for an average of 10% and

50% or more of the daylight hours respectively. Similarly, Wilson et al. (1975) concluded from a dietary study of sheep and goats in semi-arid woodland of New South Wales, that the latter were largely browsers, the former largely grazers. Studies of feral goat diets on tropical or subtropical islands, such as the Hawaiian Islands and the Galapagos archipelago have also indicated that browse is an important dietary item (Hamann 1979; Yocom 1967). Furthermore, goats are still used to browse and control scrub (probably one of their earliest uses) in Mediterranean maquis (Naveh 1970) and in the U.S.A. (Merrill & Taylor 1976).

All these areas have, however, had a long history of livestock utilisation, so that selection by goats of browse may be due to their inability to compete successfully with other livestock, especially sheep, for the available grazings. Goats, in the absence of sheep do graze considerably. Morriss (not seen, quoted by Coblentz 1977) for instance found that 89% of the winter diet of Hawaiian feral goats was grass. Also, Malachek & Leinweber (1972) concluded that Angora goats on Texan range were grazers for most of the year, the degree of preference for graze depending on its availability. Similarly, Coblentz (1977) has argued that goats are opportunistic generalists that tend to consume the most palatable vegetation available. He found from ruminal analyses that annual grasses were an important food of feral goats on Santa Catalina, off California, comprising between 39% and 81% of the dry weight of samples and that the remainder was largely made up of herbs rather than browse.

Feral goats in the present study utilised certain plant species/ groups (such as Myrica and Pteridium) much more heavily than sheep. The reputed unpalatability of these species is probably partly due to a bitter taste. Goats and sheep have a higher threshold for bitter tastes than do other mammals (Bell 1959; Groatcher & Church 1970) but goats are possibly better able to detoxify secondary compounds than sheep (Schaller 1977). Thus a switch by goats to apparently unpalatable and toxic forage including browse, at seasons when graze availability is low or as a result of competition with sheep, would not be surprising. Schaller (1977) reported that wild Eurasian sheep and goats prefer to eat grass when it is available, and North American sheep are predominantly grazers (Hoefs 1974; Stelfox 1976).

I suggest that goats tend towards being facultative grazers and sheep towards being obligate grazers. According to the scheme of Hoffmann (1968) as modified by Van de Veen (1979), ungulates can be divided into three main categories depending on the structure of their ruminal mucosa. These are: concentrate selectors (such as dik dik and roe deer) which feed on juicy herbage and fruits, roughage feeders - the true grazers - (such as domestic sheep and African buffalo) which always have a high proportion of monocotelydons in their diets, and the intermediate feeders (such as Thompson's gazelle and Wisent) which are all versatile feeders, adapting their diets to season and local conditions; they may either browse or graze.

A thorough comparison has yet to be made between the stomach structures of sheep and goats. It is predicted on the basis of evidence given in this chapter, that feral goats would be classified as intermediate feeders. Their ability to utilise a wide array of plant species may partly explain their successful and ecologically damaging colonisation of arid regions and oceanic islands in which sheep and other ungulates fare less well (Talbot 1960; Tomich 1969; Wilson & Orwin 1964; Dilks & Wilson 1979).

CHAPTER 4. POPULATION ECOLOGY

Introduction

The effects on animals of a varying food supply together with those of social behaviour and interspecific interactions are ultimately manifested in the dynamics of their populations. For large herbivores in temperate regions, the availability of nutritious forage varies widely with season; in summer, abundant fresh forage is available but in late winter and early spring, food quality is not sufficient for maintaining body weight (Anon 1979; Eadie 1970; Jewell *et al.* 1974; Mitchell *et al.* 1976).

These factors shape the annual cycle of events for upland herbivores so that most deaths and births occur in late winter, spring or early summer. It was expected therefore, that feral goats in the Southern Uplands would show this pattern. Initially the populations had to be located and their sizes estimated.

There have been few estimates of British and Irish feral goat populations. Whitehead (1972) summarised information on numerous populations but, at least for northern Britain, much of this requires revision. Crook (1969) and Greig (1969) listed estimates available for Wales and Scotland respectively. These surveys have been supplemented by the more recent estimates of McDougall (1975) and Stevenson-Jones (1977) in the Southern Uplands and Brown (1977) in Meirionydd. In addition, the Forestry Commission regularly census the feral goats in central Galloway and the Nature Conservancy Council, Buckland (1978) and Boyd (1981) have censused the population on Rhum. Population studies are also in progress in Eire (F. Bonham *in litt.*).

This chapter is concerned with the population ecology of feral goats in the study areas. The specific aims were firstly, to determine the sizes and structures of the populations; secondly, to estimate survival rates and the causes of mortality and thirdly, to assess the effects of factors such as weather, potential competitors and management.

Methods

I defined populations of feral goats as units of individuals that could potentially interbreed. Goats did not move between populations; they may have done so in the past but extensive hill fencing now prevents mixing.

Annual censuses were conducted of seven populations; Craigdews, Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Kielderhead Moor, Nether Hindhope and College Valley (Figure 1.1). During each census I aimed for an absolute count and classification by age and sex. Information on control, harvesting and stalking was obtained locally and in most cases, privately.

1. Age criteria

Scottish feral goats form one horn ring each winter of life, these become conspicuous from February as the horn grows (Greig 1969). Recapture of individual billies in November of three consecutive years at Nether Hindhope confirmed Greig's observations. For nannies, where the horn rings were less conspicuous and closer together, and the horns frequently well worn, 4 out of 37 examined in the second or third year of capture had horn ring counts that were more or less than expected. Since of necessity goats were examined quickly and in deteriorating light conditions, all descrepancies were attributed to human error.

Whilst the number of horn rings provided an accurate age estimate for goats examined at close range, this method was difficult to apply in the field. However assigning individuals to age classes on the basis of horn length was found to give inconsistent results; there was considerable variation in horn length between individuals of the same sex and the same age as judged by horn ring counts (see Chapter 2). Therefore, for most census data, the following broad age-sex classes were used:

Kid (0-1) yr; readily identified by small size, small horns and clean coat showing no signs of moult. Kids could first be sexed in the field at approximately four months old. Billy kids developed a conspicuous hair tuft on their foreheads, their horns had thick bases and their scrotums were frequently visible. Nanny kids had very small horns and lacked a hair tuft on the forehead.

Yearling nanny (1-2) yr; identifiable by small body size and short thin horns, which at close range showed one annual ring. Their horn length during the summer was usually less than 1½ ear lengths.

Adult nanny (2+) yr; distinguished from yearling nanny by larger body size, longer horns with two or more annual horn rings and a longer jaw.

Yearling billy (1-2) yr; identified by large thick horns with one annual ring and a conspicuous hair tuft on the forehead.

Adult billy (2+) yr; identified by having two or more annual rings on very large horns, large body size and shaggy coat. A prominent hairtuft on the forehead often remained until four years old.

Details of age and sex specific growth are given in Chapter 2. A combination of captures and close range observations were used to determine more precise estimates of structures of the College Valley, Nether Hindhope and the Moffat Hills populations.

2. Accuracy of the counts

In order to minimise the risk of counting the same individual twice, censuses were conducted as quickly as possible and the direction of flight of disturbed groups containing recognisable individuals noted. Since there was usually considerable separation between groups and I could recognise many individuals, overestimates were unlikely.

Underestimates were much more likely. All or most of the individuals in the College Valley, Nether Hindhope, Moffat Hills and Craigdews populations were individually recognisable making censuses in these study areas the most accurate. Underestimates resulted when censuses were conducted in deteriorating weather conditions and especially when visibly decreased. Even in good weather, accuracy was increased by repeating censuses. In this way I gained better knowledge of the area ranged over by goats and recognised more individuals.

The value of repeating censuses is illustrated by a comparison of those in May and August of 1978 on the Moffat Hills (Table 4.1). At least half the billies and nine nannies had been missed in May. This was probably because I neglected to search two watersheds in which, I was later informed, goats had been present. The result of counts conducted in 1979 were much more consistent; the largest difference in the totals of 11, between June and September was the result of underestimating billies (Table 4.1).

<u>Table 4.1</u>

Comparison of the results of total counts on the Moffat Hills during 1978 and 1979.

		Number			
Year	Month	Billies	Nannies	Kids	Total
1978	May	18	51	17	68
	August	34	60	18	112
1979	June	18	58	8	84
	September	13	56	4	73
	October	17	55	8	80
	December	17	57	8	82

Feral goats in the Southern Uplands usually kid between late February and early April. Several censuses were necessary to estimate accurately the number of kids that had survived the neonatal period. New born feral goat kids are 'hiders' (Lent 1974) lying out for up to several weeks after birth whilst being periodically suckled by their dams (McDougall 1972; Rudge 1970). Thus new born kids were inconspicuous and may have been underestimated during early spring censuses.

3. Estimation of production and survival rates

These were derived from censuses. The sex ratio of neonates was assumed to be unity (Greig 1969; Williams & Rudge 1969). Because of their hiding behaviour and because sacrificing nannies was undesirable, good estimates of age-specific fecundity and perinatal survival were not obtained.

Most nannies other than kids appeared to conceive in the autumn. Greig (1969) examined 53 nannies culled from Round Fell in February prior to kidding and found a conception rate of 94.3%. Similarly all 19 of the 25 nannies at Nether Hindhope in February 1978 examined by myself and an experienced shepherd were considered to be pregnant. Both samples included nannies aged almost one year. Since yearlings were rarely seen nursing kids in spring, it is believed that if nanny kids did conceive, the majority of their kids were reabsorbed as foetuses or suffered neonatal mortality.

Twinning was rarely recorded. It is possible that its incidence was underestimated due to perinatal mortality of one twin. For the purposes of analysis it was assumed that nannies conceived only singleton kids; Greig (1969) found no twin foetuses in his sample of 50 pregnant nannies.

In order to make comparison between populations, kid production was calculated as the ratio of the number of kids to the number of adult nannies. Postnatal survival rates of kids were estimated from the number of yearlings in one year to the number of kids in the previous summer. Survival rates of yearlings plus adults were estimated as the ratio of the number alive in one year excluding yearlings to the number including yearlings in the previous year.

4. Determination of the causes of death

All carcases were aged and sexed and the date of death estimated. In addition estimates of condition, weight (Chapter 2), tooth wear and the incidence of oral disease were recorded where possible. The parasitic burdens of a sample of live goats were also examined.

Bone marrow fat reserves are the last to be mobilized in large herbivores suffering from malnutrition and it has been shown that visual estimates of marrow reflect actual differences in fat levels and therefore, condition (Sinclair & Duncan 1972). A sample of tibial marrow was examined from each carcase where possible and assigned to one of three categories:

1. White or creamy and firm to touch (High fat)
2. Pink, firm and wet
3. Red or yellowish, gelatinous and translucent (Low fat).

The skulls and lower jaws were extracted from carcases, cleaned and dried and examined for pathological conditions and tooth wear. The examination of teeth was restricted to premolars and molars since incisors and canines frequently fell out of their sockets after death and were never recovered.

Parasitic burdens of goats were examined by D. Britt. In November 1979, 23 of the 29 goats in the Nether Hindhope population were examined for ectoparasites and faecal samples collected. Coccidial oocysts and helminth ovae were detected by flotations from faecal samples emulsified in saturated NaCl solution.

5. Estimates of density and biomass

These were derived from census results. Areas used in density estimations were those enclosing all sightings in the form of a polygon with no re-entrant angles. Biomass was calculated using mean total weights in autumn or early winter of each of the broad age-sex classes using data from four of the study areas (Chapter 2). For hill sheep these data were obtained from landowners and shepherds and in the case of age-specific total weights in November, the Hill Farming Research Organisation (R.H. Armstrong *in litt*.). Lambs were excluded from density and biomass estimates because they were removed from the hill in autumn or winter and thus to permit comparisons between sheep and goats, kids were also excluded.

Results

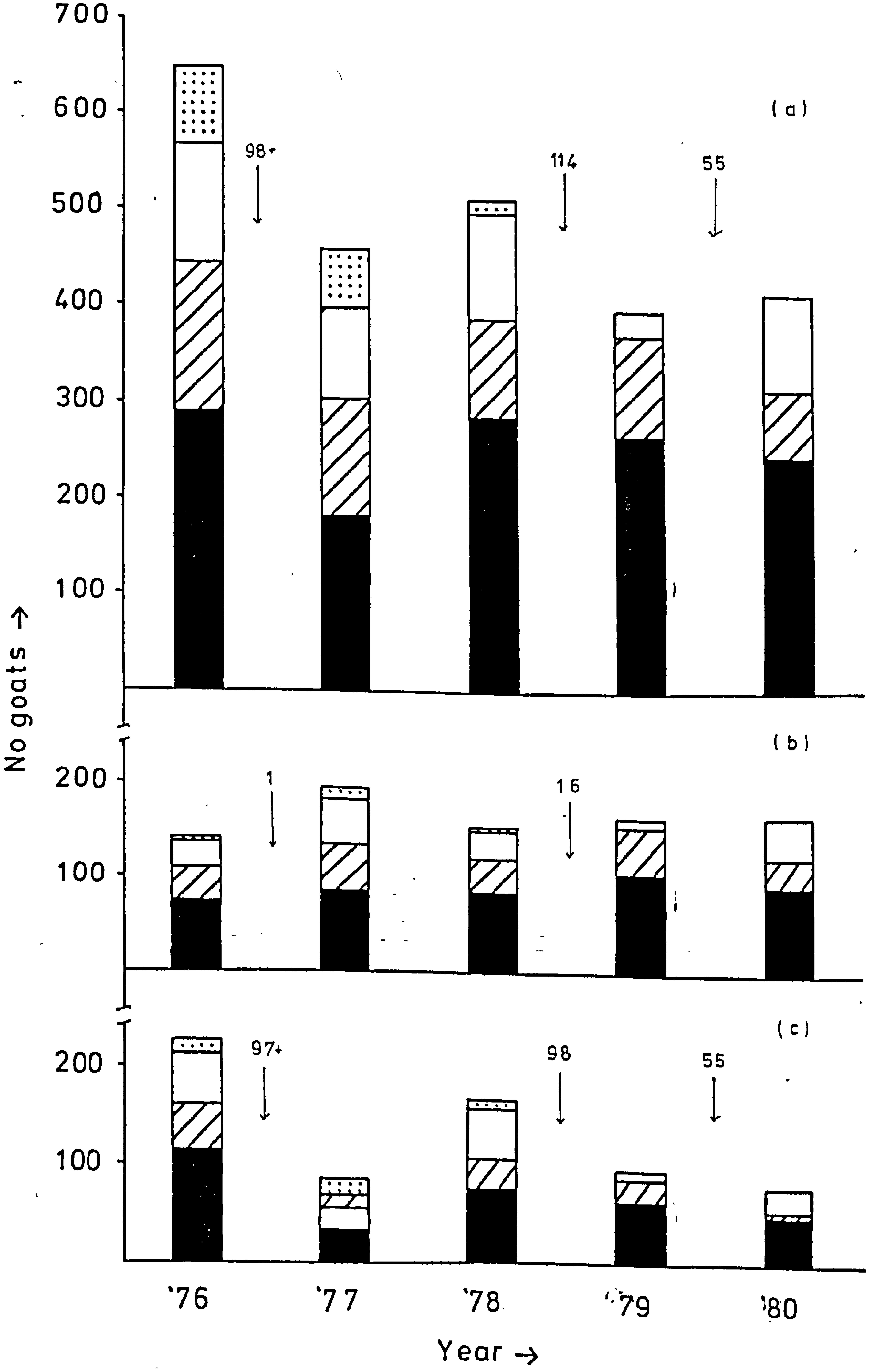
1. Population sizes and structures

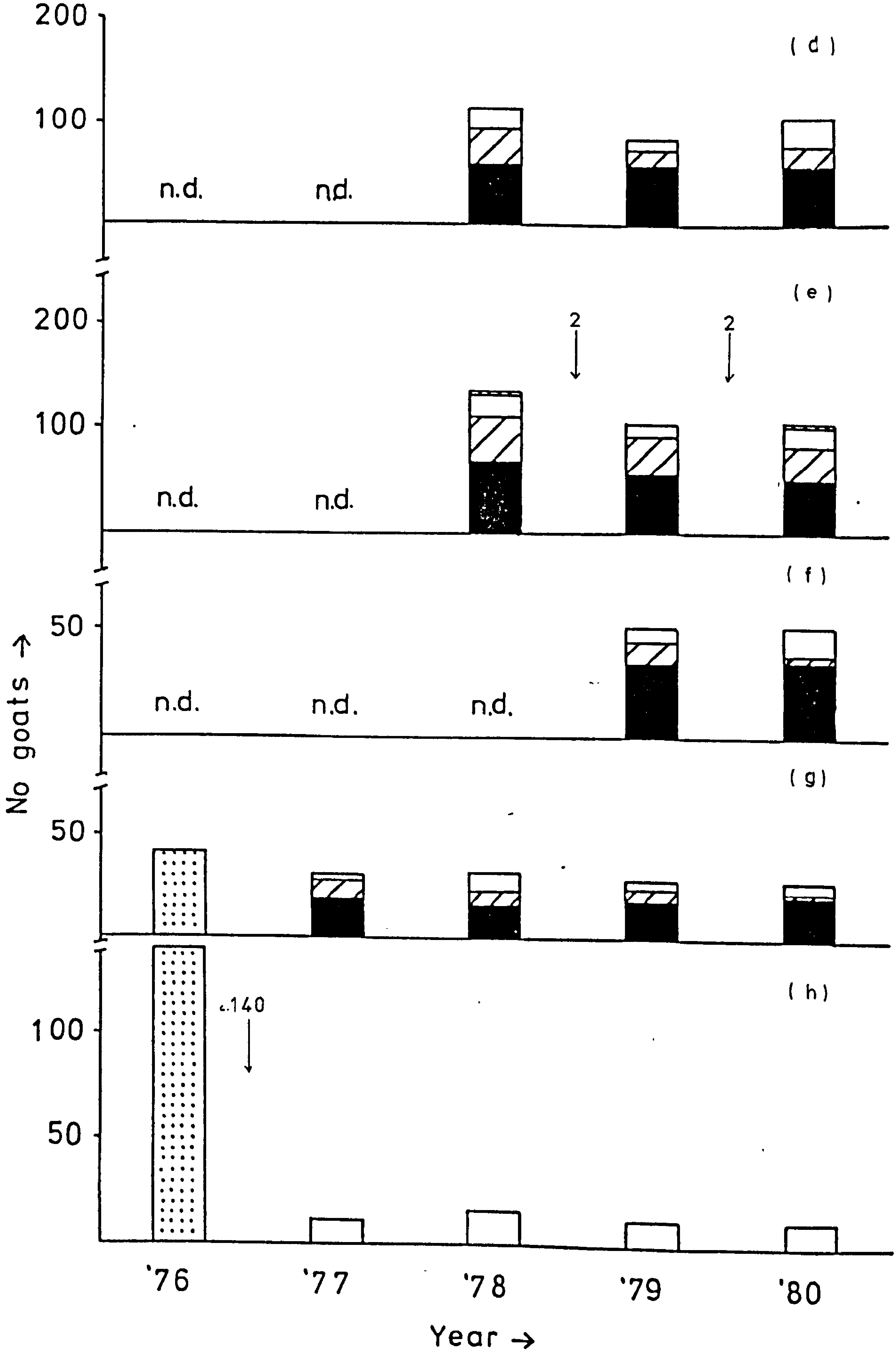
Details of all the population estimates are listed in Appendix 7. Only the maximum counts or those with the most individuals classified according to age and sex are used in the text below.

The size of the populations varied markedly. From 1976 to 1980 the largest population, that on Cairnsmore of Fleet, varied between 649

Figure 4.1

Population changes on Cairnsmore of Fleet (a) whole area, (b) eastern block of N.N.R. and (c) western area; (d) Moffat Hills; (e) Langholm-Newcastleton Hills; (f) Kielderhead Moor; (g) Nether Hindhope and (h) College Valley. Histogram key: black, nannies; hatched, billies; white, kids and dotted, unclassified. The times and magnitudes of known culls are indicated.


700
600
500
400
300
200
100
No goats →
(a)
98+
114
55
(b)
200
100
1
16
(c)
200
100
97+
98
55
'76
'77
'78
'79
'80
Year →


200
100
(d)
n.d.
n.d.
(e)
200
2
2
100
n.d.
n.d.
(f)
50
n.d.
n.d.
n.d.
No goats →
(g)
50
(h)
c.140
100
50
'76
'77
'78
'79
'80
Year →

and 390 and that in College Valley between approximately 140 and 12 (Figure 4.1). Both populations declined between 1976 and 1977 because of culling. On Cairnsmore of Fleet the decline was from 649 to 456 and in College Valley from approximately 140 to 12, reductions of 30% and 91% respectively.

Inspection of the counts for the western and eastern areas of Cairnsmore of Fleet, where most of its population occurred, revealed a decline in the former area but not in the latter (Figure 4.1). Goats on the eastern area had been subject to very little culling; they occurred mostly on the N.N.R. where their number has shown relatively small fluctuations. The decrease on the western area resulted from the culling rate and natural mortality together exceeding the recruitment rate.

The populations on the Moffat Hills, the Langholm-Newcastleton Hills, Kielderhead Moor and at Nether Hindhope were fluctuating about mean values and appeared to be showing no directional trends (Figure 4.1). Culling of these populations was either nil or slight as on the Langholm-Newcastleton Hills.

The Craigdews population (Table 4.2) is regularly and heavily culled with the intention of maintaining a herd of 40 or less (R.W. Baird in litt.). During the muster of September 1979, when the goats were counted, 28 goats (10 billy kids, 2 adult billies, 3 nanny kids and 6 yearling or adult nannies) were culled leaving 31, a reduction of 48%. The population had recovered to 84% of its 1979 level by the following year when 49 were present, an indication of the high productivity of this population compared to others in the Southern Uplands.

		Number			
Year	Month	Billies	Nannies	Kids	Total
1979	September	10	28	21	59
1980	December	9	22	18	49

Table 4.2. Population changes at Craigdews between 1979 and 1980.

In all populations there were more nannies than billies (Figure 4.1). Furthermore, the numbers of the former tended to fluctuate less than those of the latter or those of kids. For instance, the numbers of billies or kids or both were relatively low in 1979 following the severe winter of 1978-79 (Chapter 1, Climate) whereas the numbers of nannies were much less affected. The result was a decline in the total size of most populations in that year, followed for some populations, by an increase in 1980.

It was amongst adults that the sex ratio (male:female) was most skewed varying between 1:1.7 and 1:8.5 depending upon the year and the population. Furthermore, the sex ratios of yearlings during the summer or autumn were also most frequently skewed in favour of nannies (Table 4.3). Given an equal sex ratio at birth, these facts suggested that billies had lower survival rates than nannies.

The survival rates of kids varied between 0% and 100%. It was usually higher for nanny kids than billy kids (Table 4.4a). These data refer to postnatal survival; I had no data on peri-natal survival but given that the majority of nannies were pregnant in February (see Methods)

Table 4.3

Comparisons of the numbers of yearling billies and yearling nannies in the populations during the spring or summer.

Cairnsmore of Fleet

	Number	
Year	Billies	Nannies
1976	25	55
1977	38	25
1978	40	45
1979	13	18
1980	12	22

Moffat Hills

	Number	
Year	Billies	Nannies
1978	7	6–9
1979	6	5–7
1980	3	4

Langholm-Newcastleton Hills

	Number	
Year	Billies	Nannies
1978	17	6
1979	6	5
1980	2	6

Kielderhead Moor

	Number	
Year	Billies	Nannies
1979	1	3
1980	1	2

Nether Hindhope

	Number	
Year	Billies	Nannies
1977	0	4
1978	1	0
1979	1	5
1980	0	5

College Valley

	Number	
Year	Billies	Nannies
1977	0	2
1978	0	3
1979	1	1
1980	0	0

Table 4.4

Survival rates, raw data followed by percentages in parentheses, of (a) kids and (b) adults plus yearlings. Kielderhead Moor and Craigdews were excluded from the analysis because of heavy culling and inaccuracies respectively. For (b), Cairnsmore of Fleet, because nannies were underestimated in the 1977 census, their survival rates were probably underestimated and overestimated for 1976-77 and 1977-78 respectively.

(a)

Cairnsmore of Fleet

Year	Survival rate Billies	 Nannies
1976-77	38/51 (75%)	25/74 (34%)
1977-78	40/49 (82%)	45/49 (92%)
1978-79	-	-
1979-80	12/26 (46%)	22/26 (85%)

Moffat Hills

Year	Survival rate Billies	 Nannies
1978-79	6/9 (67%)	5/9 (56%)
1979-80	3/3 (100%)	4/5 (80%)

Langholm-Newcastleton Hills

Year	Survival rate Billies	 Nannies
1978-79	6/11 (54%)	5/11 (45%)
1979-80	2/6 (33%)	6/6 (100%)

Nether Hindhope

	Survival rate	
Year	Billies	Nannies
1977-78	1/3 (33%)	0/0 (0%)
1978-79	1/2 (50%)	5/6 (83%)
1979-80	0/0 (0%)	5/5 (100%)

College Valley

	Survival rate	
Year	Billies	Nannies
1977-78	0/0 (0%)	3/4 (75%)
1978-79	1/2 (50%)	1/1 (100%)
1979-80	0/0 (0%)	0/1 (0%)

(b)

Cairnsmore of Fleet

	Survival rate	
Year	Billies	Nannies
1976-77	73/81 (90%)	156/290 (54%)
1977-78	62/121 (51%)	236/181 (∿100%)
1978-79	-	-
1979-80	55/104 (53%)	221/263 (84%)

Moffat Hills

Year	Survival rate	
	Billies	Nannies
1978-79	12/34 (35%)	53/60 (88%)
1979-80	16/18 (89%)	55/58 (95%)

Langholm-Newcastleton Hills

Year	Survival rate	
	Billies	Nannies
1978-79	26/42 (62%)	53/70 (76%)
1979-80	29/32 (91%)	45/58 (78%)

Nether Hindhope

Year	Survival rate	
	Billies	Nannies
1977-78	7/8 (88%)	16/20 (80%)
1978-79	4/8 (50%)	14/16 (88%)
1979-80	2/5 (40%)	17/19 (90%)

College Valley

Year	Survival rate	
	Billies	Nannies
1977-78	4/4 (100%)	6/6 (100%)
1978-79	3/4 (75%)	8/9 (89%)
1979-80	3/4 (75%)	7/9 (78%)

and that the kid:nanny ratio in summer was usually less than 0.60 this must have been low. In 1979 at Nether Hindhope and College Valley, no billy kids were alive in the summer or autumn (Table 4.1a). However, billy kids may have been born but suffered perinatal mortality.

With few exceptions, the survival rates of adult plus yearling nannies were higher than those for adult plus yearling billies (Table 4.4b). Survival rates of billies were more variable than those for nannies at between 35% and 100% compared to between 54% and 100%. For nannies 9 out of 13 'population/years', returned survival rates greater than or equal to 80%; the comparative figure for billies was five (Table 4.4b).

Detailed age structures were obtained for the populations on the Moffat Hills, at Nether Hindhope and in College Valley (Table 4.6). In addition, 75 goats from Cairnsmore of Fleet N.N.R. were caught in December 1980. There was circumstantial evidence that the age-sex structure of this catch was representative of the subpopulation in that area; comparison of the age-sex structures in May 1980, October 1980 and for the December catch revealed no consistent differences (Table 4.7). Lack of independence of the three data sets precluded statistical comparison. The very small number of billies compared to nannies in these counts suggested that proportionately more of the former than the latter were using areas outside the N.N.R. However, statistical comparisons of the numbers of adults of each sex within and outside the N.N.R. for all complete censuses revealed no significant differences (Table 4.5).

The detailed age structures (Table 4.6) showed that, for both sexes, the numbers in successively older age classes were often not successively smaller. Although kids usually formed the largest age class, the next

Table 4.5

Comparison of the percentages and numbers of billies and nannies in the eastern block of the Cairnsmore of Fleet N.N.R. (N.N.R.) and outside this area (Rest). Data from total censuses with that for September 1979 from Theaker (1979). For no census was the null hypothesis of "no difference in the proportions of nannies and billies in N.N.R. and the rest" rejected. (χ^2_1 = 0.053, 1.2490, 0.6020, 2.596, 0.4007, 0.6277, 0.6277 and 0.0258 for July 1976, August 1976, March 1977, March 1978, April 1978, June 1978, September 1979 and April 1980 respectively).

Year		1976		1977	1978			1979	1980
Sex	Area	July	August	March	March	April	June	September	April
Billy	N.N.R.	24.2	18.0	42.6	44.7	35.3	39.2	46.6	38.5
%	Rest	75.8	82.0	56.6	55.3	64.7	60.8	53.4	61.5
N		153	122	121	103	102	130	103	78
Nanny	N.N.R.	25.2	23.0	30.0	35.5	31.8	46.5	42.0	37.4
%	Rest	74.8	77.0	33.1	64.5	68.2	53.5	58.0	62.6
N		290	287	181	248	267	230	257	243

Table 4.6

Detailed age-sex structure for (a) Cairnsmore of Fleet N.N.R. December 1980 catch; (b) Moffat Hills, spring 1980; (c) Nether Hindhope, 1977 to 1980 and (d) College Valley, 1977 to 1980.

(a) Cairnsmore of Fleet N.N.R. (sample, December 1980)

Age (yr)	0	1	2	3	4	5	6	7	8	9	N
Nannies	16	5	6	8	4	4	5	5	1	7	61
Billies	8	1	5								14
											75

(b) Moffat Hills (total population, spring 1980)

Age (yr)	0	1	2	2/3	3	3/4	4	4/5	5	5/6	6	6/7	7	7/8	8	8/9	9+	N
Nannies	12	4	6	3	7	5	4	2	6	1	6	2	3	4	2	1	3	71
Billies	12	3	5	1	4		2		0		3		1		0		0	31
																		102

(c) Nether Hindhope (total population)

Nannies

	Number in each age class												
Year	0	1	2	3	4	5	6	7	8	9	10	11	N
1977	0	4	2	4	5	0	3	1	0	0	0	1	20
1978	6	0	3	2	3	5	0	2	1	0	0	0	22
1979	5	5	0	3	2	2	4	0	2	1	0	0	24
1980	2	5	5	0	3	2	2	3	0	2	0	0	24

Billies

	Number in each age class							
Year	0	1	2	3	4	5	6	N
1977	3	0	2	5	0	1	0	11
1978	2	1	0	2	4	0	1	10
1979	0	1	1	0	1	2	0	5
1980	3	0	1	1	0	0	0	5

(d) College Valley (total population)

Nannies

	Number in each age class																	
Year	0	1	2	3	3/4	4	4/5	5	5/6	6	6/7	7	7/8	8	9	10	11	N
1977	4	2	0	0		0	1	1		1		0		0	0	1	0	10
1978	1	3	2	0		0		0	1	1	1	0		0	0	0	1	10
1979	1	1	2	1		1	1	0		1	1	1		0	0	0	0	10
1980	3	0	1	2	1	0		1		0		0	1	1	0	0	0	10

Billies

	Number in each age class								
Year	0	1	2	3	4	5	6	7	N
1977	0	0	1	1	1	1	0	0	4
1978	2	0	0	1	1	1	1	0	6
1979	0	1	0	0	1	1	1	0	4
1980	0	0	1	0	0	0	0	1	3

Table 4.7

Comparison of two counts and one catch of the goats on Cairnsmore of Fleet N.N.R. during 1980. October census data are from Theaker (1980).

(a) Nannies

	% in each age class			
Date	Kids	Yearlings	Adults	N
May (census)	19.0	7.8	73.2	103
October (census)	18.3	81.7		115
December (catch	26.2	8.2	65.2	61

(b) Billies

	% in each age class			
Date	Kids	Yearlings	Adults	N
May (census)	54.9	8.5	36.6	36
October (census)	52.5	47.5		40
December (catch)	57.1	7.1	35.7	14

largest was not always the yearling class. For example, in the Cairnsmore of Fleet N.N.R. catch, there were seven nine year old nannies, but only one eight year old nanny and five yearling nannies (Table 4.6). Similar anomalies can be seen in the age structures of the other populations. Because of these anomalies and the small size of most of the populations, construction of time specific life tables was inappropriate.

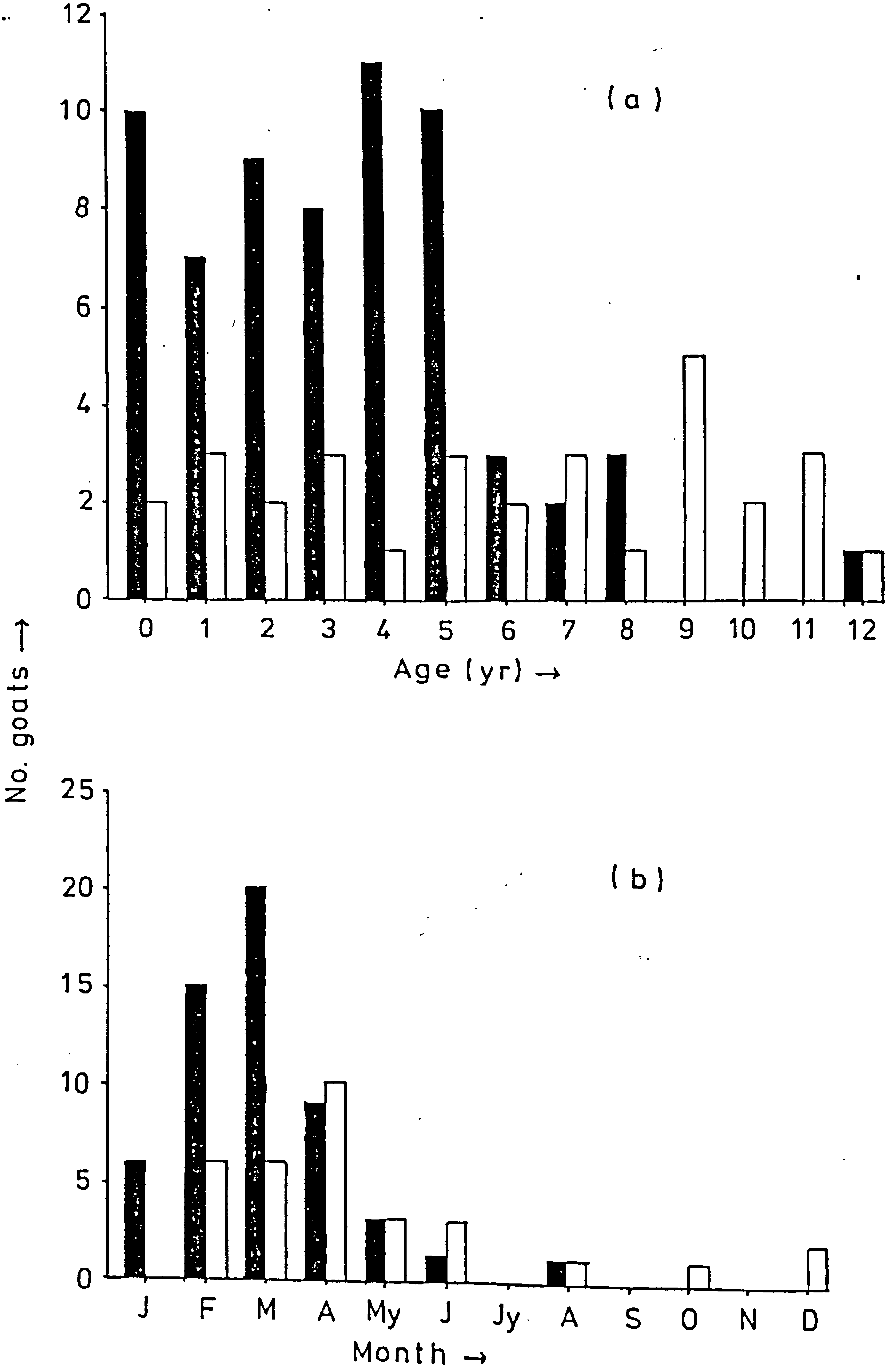
Nannies clearly had a longer average life than billies (Table 4.6). The maximum ages recorded for nannies were nine years, nine or ten years, eleven years and eleven years for the Cairnsmore of Fleet, Moffat Hills, Nether Hindhope and College Valley populations respectively. For billies on the Moffat Hills, Nether Hindhope and in College Valley the respective maximum ages were seven, six and seven years. However, older billies were observed. One, on the Langholm-Newcastleton Hills was last seen aged nine years in 1978 and another on the Moffat Hills died close to his 13th birthday in 1980; these billies were exceptionally old.

The differential survival rates found in living populations were confirmed by examination of the ages and sexes of goats found dead. Since for each sex there were no obvious differences between populations, in the distribution of ages at death and also because population samples were small, I pooled all the data in the present analysis. Totals of 64 male and 31 female carcasses were examined; the distribution of their ages at death was markedly dissimilar (Figure 4.2a).

Approximately twice as many billies as nannies were found dead and 87% of the former had died before their sixth birthday compared to 33% of the latter. Only one billy (1.6%) was older than eight years at death in the sample compared to 11 (35.5%) nannies. Median ages at death, corrected for the month of death, were 3.75 years and 6.75 years for

Figure 4.2

(a) the ages at death and (b) the months of death of billies (black histograms) and nannies (white histograms) of goats found dead. Data from all the study areas has been pooled.


(a)
No. goats →
0
2
4
6
8
10
12
0
1
2
3
4
5
6
7
8
9
10
11
12
Age (yr) →
(b)
0
5
10
15
20
25
J
F
M
A
My
J
Jy
A
S
O
N
D
Month →

billies and nannies respectively.

Kids, because their remains were more perishable and more easily dispersed by scavengers than those of adults, were probably underepresented in the pick up samples. I rarely found carcasses of kids aged less than six months old but many of these must have died. This bias has not been corrected for but its effect would be to lower the median ages at death; it does not alter the conclusion that survival rates of billies were much lower than those of nannies.

Kid production varied widely between and within populations depending on the year (Table 4.8). Relatively low kid production occurred in all populations, except that at Craigdews in 1979, when the maximum was 0.24 and the minimum 0.14 kids per adult nanny respectively. The markedly high productivity of the Craigdews population may be accounted for by the absence of sheep and the supplementation of their winter food.

The winter of 1978-79 was more severe than that of 1977-78 or 1979-80 with lower extreme temperatures and a longer period of snowlie (Chapter 1, Climate). On Cairnsmore of Fleet, where accurate census data were available from 1976 to 1980, kid production was correlated with two indices of the severity of the preceding winter. Firstly, production was negatively correlated with the number of days with snow lying at 0900 h in the preceding January, February and March ($r_s = -0.800$, $p > 0.05$) and secondly, production was positively correlated with the mean minimum temperature for the same months ($r_s = +0.775$, $p > 0.05$). Neither correlation was statistically significant, a result perhaps of the small number of years for which data were available, but their high values suggested that they were of biological importance.

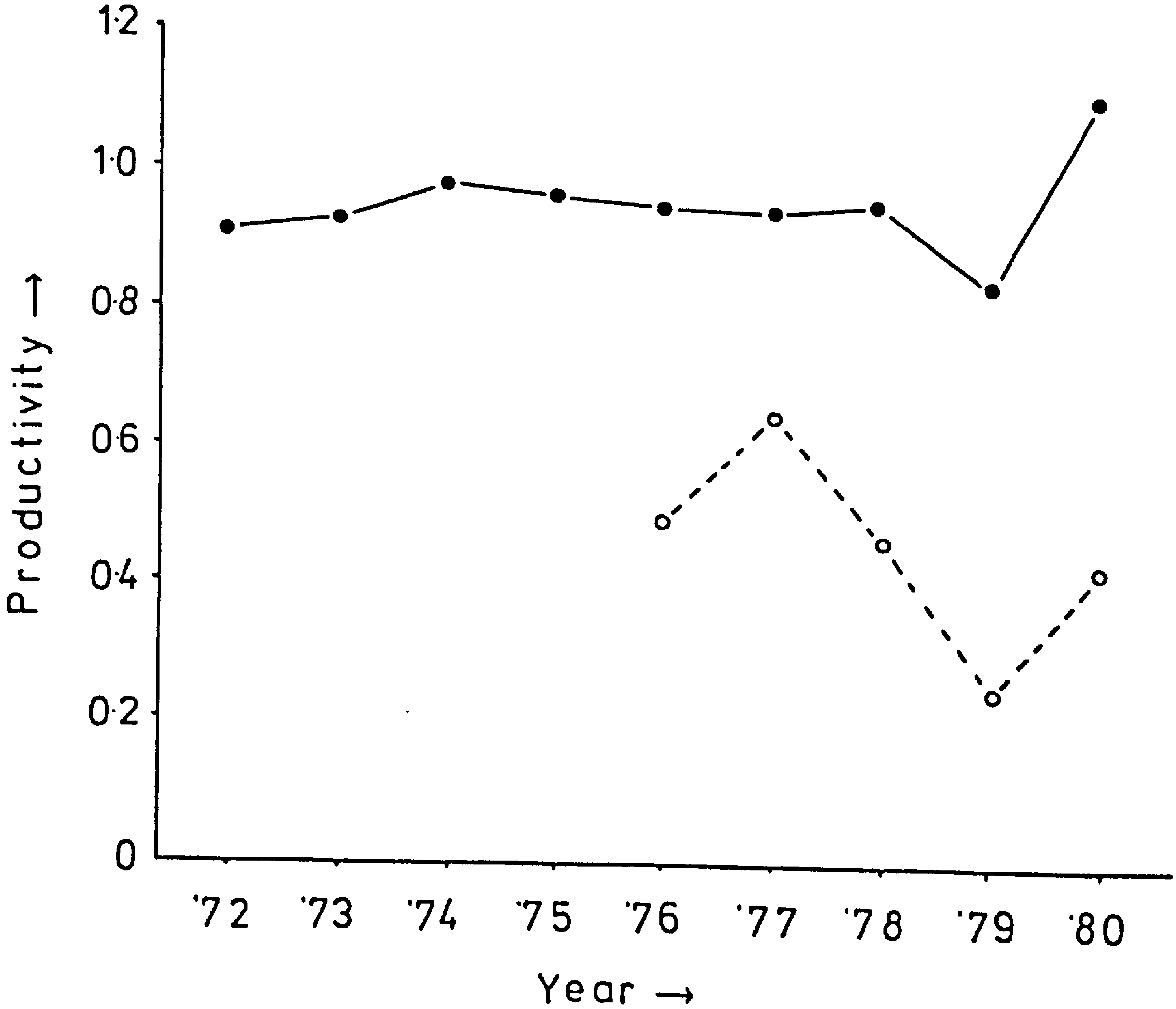
Table 4.8

Productivity (number of kids : number of adult nannies) in the study areas.

	Productivity				
Study area	1976	1977	1978	1979	1980
Craigdews	n.d.	n.d.	n.d.	0.81	0.90
Cairnsmore of Fleet	0.53	0.62	0.46	0.24	0.44
Moffat Hills	n.d.	n.d.	0.33	0.16	0.42
Langholm-Newcastleton Hills	n.d.	n.d.	0.34	0.21	0.51
Kielderhead Moor	n.d.	n.d.	n.d.	0.14	0.40
Nether Hindhope	n.d.	0.19	0.36	0.26	0.26
College Valley	n.d.	0.75	0.50	0.13	0.43

Figure 4.3

The comparative productivities (no. lambs or kids : no. of adult ewes or nannies) of sheep (●) and goats (o) on Cairnsmore of Fleet N.N.R.


1·2
1·0
0·8
0·6
0·4
0·2
0
Productivity →
'72
'73
'74
'75
'76
'77
'78
'79
'80
Year →

The relatively low kid production in 1979 was paralleled by a similar decrease in lamb production. This is illustrated by data on the productivity of sheep and goats on Cairnsmore of Fleet N.N.R. (Figure 4.3). Between 1972 and 1978, when winters were not severe, lamb production varied between the narrow limits of 0.92 and 0.99 lambs per adult (2+ yr) ewe. Production declined from 0.95 to 0.83 between 1978 and 1979. Kid production varied between 0.46 and 0.64 from 1976 to 1978 but declined to half the 1978 value (0.41) in 1979 when it was 0.24 (Figure 4.3). The productivity of sheep and goats was generally higher in 1980 following the relatively mild winter of 1979-80 (Chapter 1, Climate).

2. Determination of the causes of death

For most carcasses, the month of death was established (Figure 4.2b). Billies died predominantly (64%) in February and March whereas the mortality of nannies reached a maximum in April (30%) and exhibited a wider range of dates of death than the former. Thus most billies died at the end of winter and begining of spring prior to the onset of major plant growth on uplands. Most nannies died during or after the spring flush of plant growth and after the kidding season when some would have been lactating.

Most carcasses examined had pink or red tibial marrow that was wet and gelatinous. The number of each sex examined was small and since I could detect no sex bias, the data for the two sexes were pooled. The amount of marrow fat, which is well correlated with condition, decreases from Category 1 to Category 3 in Table 4.9. Samples were small or nil in summer and autumn. The data suggest that goats dying in January through to April were in a state of undernutrition. Goats that survive

Table 4.9

The number of goats found dead with tibial marrow in categories 1 (high fat) to 3 (low fat) throughout the year.

	Number in each category			
Month	1	2	3	N
Jan./Feb.	2	2	13	17
Mar./April	2	8	12	22
May/June	1	3	1	5
July/August	1	0	0	1
Sept./Oct.	n.d.			
Nov./Dec.	0	1	0	1

this period may, however, be in better condition; three billies and one nanny shot within a plantation in April 1979 had tibial marrow classed as Category 1, indicating that they were not suffering from malnutrition.

Natural mortality rates were, therefore, much higher for billies than nannies during the study period. Mortality was associated with poor condition, and followed an overwinter weight loss of up to 50% (Chapter 2). These facts suggested that starvation was a primary cause of death; there were, however, other possible mortality factors as described below.

Four of the nannies found dead were near to parturition and three of these had twin foetuses. The fourth, aged about 13 months died in labour of a breech birth. It is possible that in all four cases, death was primarily the result of difficulties with parturition.

Predation on neonates by foxes, ravens and crows may have occurred but was never witnessed. Goats other than neonates showed no fear of foxes. For example, a yearling nanny was observed on the Moffat Hills during the summer of 1979, charging a fox that had moved to within three metres of her whilst hunting small mammals on the same terrace. The fox retreated.

In south-west Scotland, 18.0% (N = 510) of eagle pellets collected between 1974 and 1980 contained goat hair; the proportion was higher for the Cairnsmore of Fleet area at 26.7% (N = 247) (M. Marquiss in litt.). Most of this was probably taken in the form of carrion but eagles do take live kids in the area (R. Roxburgh in litt. to S. Pickering).

The skulls and lower jaws of 45 billies and 30 nannies that had died naturally were examined for dental and periodontal pathologies and abnormalities. Skulls rarely showed pathological conditions; that of a

10 year old nanny was twisted on the antero-posterior axis and another nanny aged nine years had a broken left horn. One three year old billy had malformed occipital condyles and another aged two years had had one horn and its core broken off at the base before death. Virtually all other pathological conditions were associated with the teeth.

Up to the third birthday, neither sex showed signs of disease or heavy wear on the molariform teeth (Table 4.10). Between the ages of four and six years, about half the male and female samples respectively showed heavy wear on at least some of the molariform teeth; this in many cases was associated with abscesses, missing teeth or in one billy, an undershot jaw. Most goats aged seven years or older had some heavily worn teeth, missing teeth or periodontal disease (Table 4.10).

Abscesses and missing teeth probably make foraging painful and together with heavy tooth wear, make for inefficient grinding which may lead to malnutrition. Disease did not occur in the jaws or teeth of billies until beyond their median age of death (3.75 years) but did occur around the median age of death of nannies (6.75 years). The preliminary analysis indicated, therefore, that molariform tooth wear associated with oral disease may have been a more important mortality factor for nannies than billies.

The postcranial skeleton of some goats showed evidence of fractures, none of which were fresh and all of which had healed. Arthritis occurred in the spinal column and the bones of the feet in some specimens. It was considered, however, that bone damage amd disease were unlikely to have been a primary cause of death. Goats were occasionally observed falling from crags with, apparently, no injurious effects. Any consequences of injuries to billies sustained whilst fighting have yet

Table 4.10

The condition of the molariform teeth, in billies and nannies found dead, with age.

	Condition of molariform teeth					
	No. Billies			No. Nannies		
Age (yr)	Healthy	Heavy wear	Disease	Healthy	Heavy wear	Disease
0-3	21	0	0	8	0	0
4-6	10	7	4	4	0	4
7+	0	4	1	2	3	9

to be investigated.

Feral goats in the Southern Uplands have three main ectoparasites: the mallophagan Damilinia caprae, the ixodid tick Ixodes ricinus and the anopluran Linognathus stenopsis. Only one of these, Ixodes, is of potential pathenogenic importance since it carries the virus causing "louping ill" in sheep. Of six goats shot in the Langholm-Newcastleton Hills, four gave positive titres for antibodies of the virus (B. Mitchell, pers. comm.) but none have been observed to exhibit symptoms of the disease.

Goats at Nether Hindhope in December 1980 gave mean total helminth (cestode and nematode) ovae counts of 686, 895 and 692 per gram of faeces for the 0 (kids), (1-4) and (5+) years age classes respectively (Table 4.11). There were no consistent differences between the sexes and so that data in Table 4.11 were pooled. Sedimentation of faecal samples in water failed to reveal ovae of the fluke Fasciola hepatica.

The counts for coccidial oocysts and nematode or cestode ovae were within the range of values for healthy hill or feral sheep (Cheyne, Foster & Spence 1974). At least in November, then, loss of condition due to parasitic burden was not evident.

3. Density and biomass

The number of adult plus yearling sheep or goats per square kilometre was estimated for each study area. Year to year fluctuations in density of sheep were unknown but assumed to be negligible since their populations are managed to maintain constant density. For goats, density estimates were derived from censuses between 1978 and 1980 of each study area and

Table 4.11

The number of eggs or oocysts per gram of faeces from 23 goats in the Nether Hindhope population in November 1979. Mean values with ranges in parentheses given. + = present.

		Protozoan	Cestode	Nematode	
Age (yr)	No. goats	Coccidia	*Moniezia*	*Trichuris ovis*	other
(0-1)	7	229 (0-900)	136 (0-900)	+	550 (50-100)
(2-5)	10	50 (0-500)	95 (0-500)	+	800 (100-1200)
6+	6	150 (0-600)	58 (0-100)	+	633 (300-1200)

expressed as mean values (Figure 4.4a).

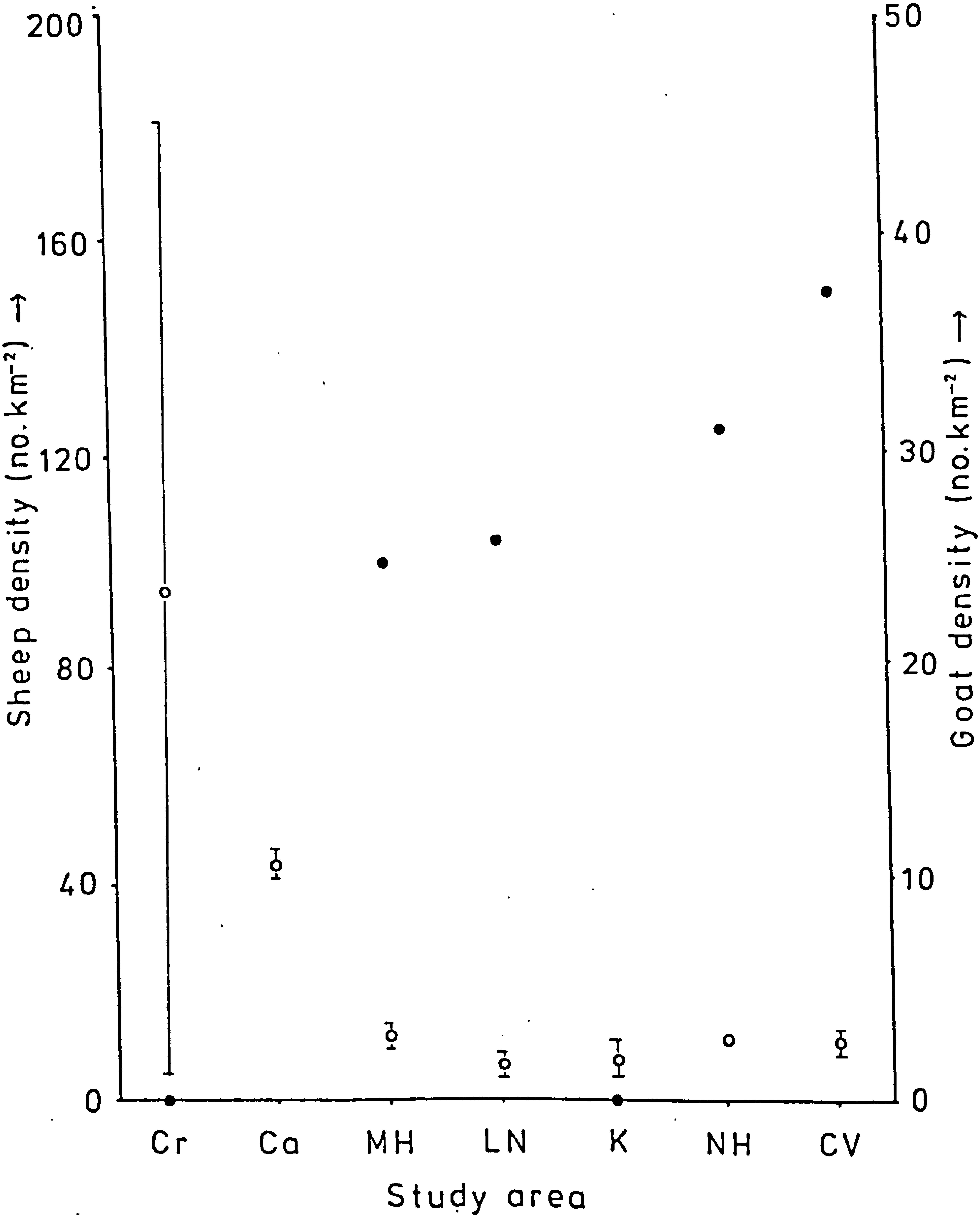
Density of sheep increased from west to east across the Southern Uplands from Craigdews and Cairnsmore of Fleet to College Valley (Figure 4.4a). The density in the latter area was more than five times that on Cairnsmore of Fleet. Goat density was highest at Craigdews, where there were no sheep, and on Cairnsmore of Fleet. At the study areas further east goat density was much lower than sheep density and relatively constant at between 1.5 km^{-2} for the Langholm-Newcastleton Hills and 2.7 km^{-2} for the Moffat Hills and for Nether Hindhope (Figure 4.4a).

The density estimations suggested an interaction between goats and sheep (or shepherds) giving rise to an inverse relationship between goat density and sheep density. Whilst sheep management was similar in the various study areas the degree of management of the goat populations was highly variable. Two, the Craigdews and College Valley populations, were heavily culled the former being artificially established and maintained.

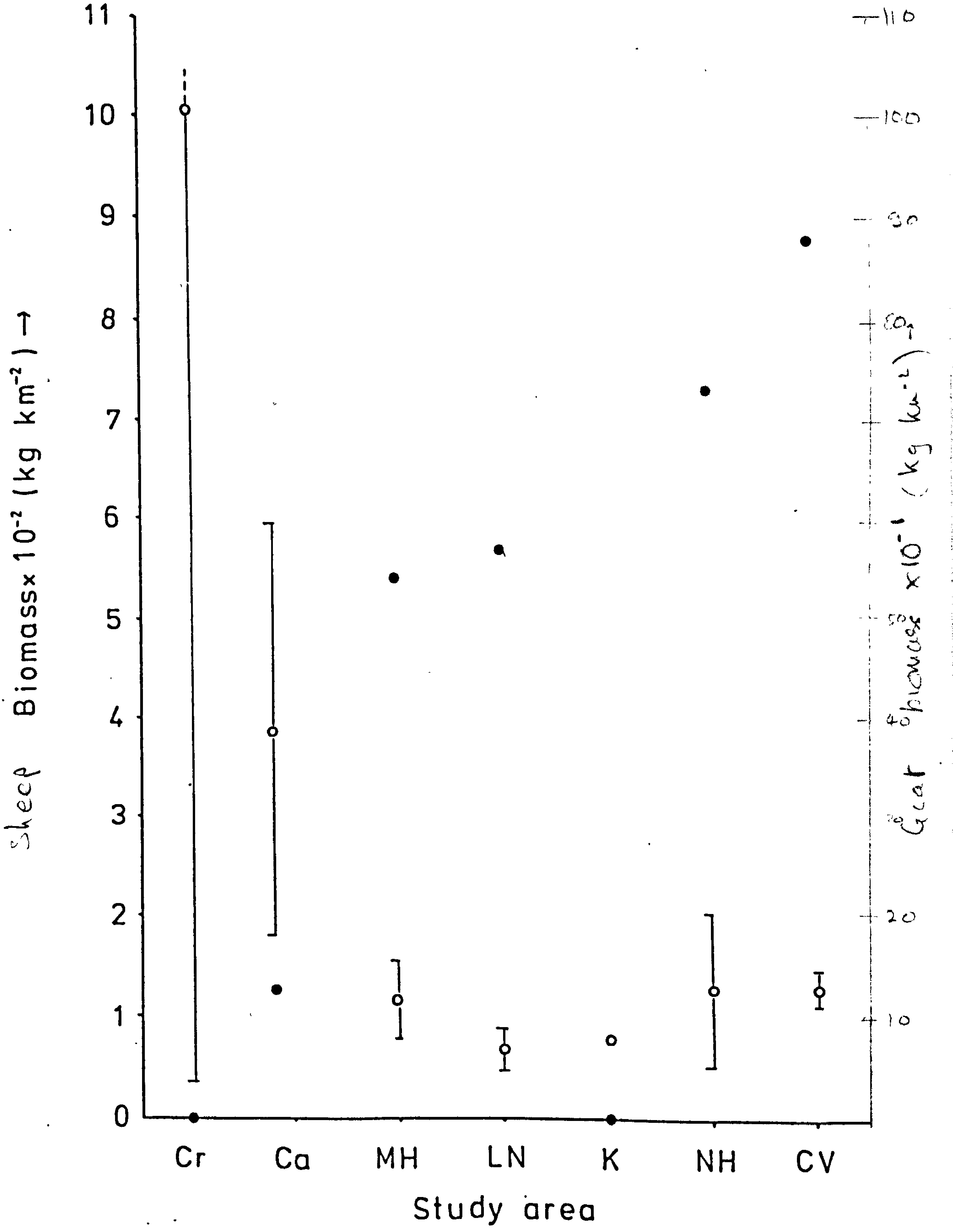
Biomass estimates for sheep population in the autumn showed the same pattern as density ranging between 1300 kg km^{-2} and 8750 kg km^{-2} for Cairnsmore of Fleet and College Valley respectively (Figure 4.4b). Goat biomass followed the same trend as goat density decreasing from a mean for 1979 and 1980 at Craigdews of 1023.5 kg km^{-2} to between 65.6 kg km^{-2} and 126.0 kg km^{-2} for the Langholm-Newcastleton Hills and College Valley respectively (Figure 4.4b). Clearly goat densities and biomasses per area were lower than those of sheep where they were sympatric.

Figure 4.4

Comparison of the density (a) and the biomass (b) of sheep (●) and goats (o) ($\bar{x}$ ± 95% C.L.) in the study areas between 1978 and 1980. Cr, Craigdews; Ca, Cairnsmore of Fleet; MH, Moffat Hills, LN, Langholm-Newcastleton Hills; K, Kielderhead Moor; NH, Nether Hindhope, CV, College Valley. The large confidence limits for Craigdews density and biomass are primarily the result of low sample size (N = 2).


200
160
120
80
40
0
Sheep density (no.km⁻²) →
50
40
30
20
10
0
Goat density (no.km⁻²) →
Cr
Ca
MH
LN
K
NH
CV
Study area

(a)


Sheep Biomass x 10^-2 (kg km^-2) →
Goat biomass x 10^-1 (kg km^-2) →
11
10
9
8
7
6
5
4
3
2
1
0
110
100
90
80
50
40
20
10
Cr
Ca
MH
LN
K
NH
CV
Study area

(b)

Discussion

In addition to the seven feral goat populations monitored in the present study one or more exist in the hills north of Craigdews, specifically between Glentrool, Merrick and the Rhinns of Kells. Goats in these areas are susceptible to control by the Forestry Commission (F.C.) and were not surveyed although counts by the latter are listed in Appendix 7. In 1977, small populations of less than 30 goats existed in the Lowther Hills and at Townhead, Ae (North in litt.) but their current status is unknown.

Several Scottish estates have now introduced feral goats for their aesthetic or sporting interest. In the Southern Uplands this has occurred at Craigoch Park Farm, near Portpatrick, and at the Ardwall Estate where in 1977 there were seven and twelve to fifteen goats respectively (North in litt.). Whitehead (1972) listed other populations in the Southern Uplands and northern England all of which are now extinct.

It was found that accurate censuses of feral goat populations could be conducted provided that exploratory work and repeated censuses had been conducted. These were particularly important for populations where sexual segregation may have occurred or where seasonal movements took place (Chapter 5). Because of the lying out behaviour of neonate feral goats (Rudge 1970a) and because births can occur as late as June (Buckland 1978), counts of kids in late summer and autumn were likely to be the most accurate.

In calculating kid production, it was assumed that the number of nannies breeding in their first year, i.e. as kids, was negligible. Although pregnant kids and nursing nannies have been observed in the Southern Uplands it appears that the survival rate of the progeny was low (Greig

1969). Grubb (1974a) noted for the feral sheep population in Hirta, St Kilda, that in some years following a year of low population density, yearling ewes made a much larger than average contribution to lamb production. Similarly for Scottish red deer populations, the proportion of pregnant yearlings in shot samples was negatively correlated with density (Mitchell et al. 1977). It is possible that a similar density dependent relationship occurs in feral goat populations but because of the error in detecting live births and because no nannies were sacrificed, this was not investigated.

Those feral goat populations in the Southern Uplands that are not subjected to heavy culling showed much less marked fluctuations in abundance than that on Rhum (Boyd 1981) and the feral sheep population of Hirta, St Kilda (Grubb 1974a). Both the Rhum and the Hirta populations exist in the absence of similarly sized herbivore species. On Rhum, the other large herbivores (cattle, ponies and red deer) do not exploit the habitats used by feral goats to any extent (Buckland 1978 and pers. observ.).

In all but one of the Southern Upland goat populations, sheep were sympatric. The considerable spatial, temporal and dietary overlap between these two herbivores in the study areas (Chapter 3) may have adversely affected the performance of the goats through competition. This in turn may have reduced population densities for goats and reduced their potential rates of increase.

In encounters, goats were usually dominant to sheep; usually this was by way of displacement but on 12 occasions (N = 40), the encounter involved aggressive behaviour (rush or butt) (Table 4.12). The two observations where sheep displaced goats were atypical in that the

Table 4.12

The outcome of 40 sheep/goat encounters. Data from several study areas.

Donor	Displacement	Rush	Butt	N
Goat	26	7	5	38
Sheep	2	0	0	2
Totals	28	7	5	40

individuals involved were a ewe with lambs and a single kid. Goats have been observed butting sheep away from forage exposed by the latter in deep snow conditions. The possession by goats of large, dangerous horns presumably confers advantages in encounters.

These observations of displacement and feeding interference (Appleby 1980) further suggested that goats and sheep were competing. Using the logic of Lack (1954) it is difficult to envisage the occurrence of such aggression unless it gives access to some limiting resource. For sheep and goats this is most likely to be food.

Preliminary analysis of the causes of death suggested that starvation was the most important factor. Ultimately, excessive tooth wear coupled with disease will cause death by starvation but most goats had died before this occurred; a similar conclusion was reached by Rudge (1970b) for feral goats in two New Zealand populations. In contrast, Murie (1944) considered that oral disease of Dall sheep on Mount McKinley, Alaska, contributed significantly to their mortality. It should be noted that hill sheep with excessive wear or missing teeth are rare in the Southern Uplands but ewes are removed from the hill in their sixth or seventh year because of their increased chance of becoming broken mouthed at and after this age.

Differential survival of nannies compared to billies was identified in all populations. Survival rates of billy kids were often lower than those of nanny kids, as occurs in other feral caprinid populations (Boyd 1981; Grubb 1974a; Williams & Rudge 1969). Extreme differences in survival rates and therefore, adult sex ratios, of caprinid species are unusual. Geist (1971), Husband (1977), Papageorgiou (1972), Schaller (1977) and Wilson (1981) all reported sex ratios of adults of wild populations in relatively undisturbed environments as much nearer unity.

One factor contributing to the lower survival rates of billies compared to nannies could be the former's reduced feeding time during the autumn rut; feral rams on St Kilda are inferred to have lower survival rates than ewes for the same reason (Jewell, Milner & Boyd 1974). Billies died mostly in late winter and early spring prior to the onset of plant growth. Furthermore, billies examined after death had healthy dentition but depleted fat reserves suggesting that they had starved. The pattern of mortality of nannies was dissimilar and deaths were not associated with late winter but later in the year when forage quality and quantity are much better and larger.

One way of assessing the importance of reproductive competition at the rut to subsequent survival rate is to determine their condition before and after this period; having determined breeding success, their survival rates in subsequent months can be monitored. This research is in progress (S. Pickering pers. comm.).

The relatively unmanaged goat populations on the Moffat Hills, the Langholm-Newcastleton Hills, Kielderhead Moor and at Nether Hindhope appeared to be fluctuating in size about mean levels and showing no long term trends. Lockie (Appendix 7) censused the Moffat Hills population between 1964 and 1967. During these years the total fluctuated between 74 and a possible minimum of 31; Lockie believed that the latter figure was an underestimate. Greig (1969) estimated that there were 60 in 1969; these figures are similar to the totals for 1978, 1979 and 1980 of 112, 84 and 101 respectively. Similarly Greig (1969) and McDougall (1975) estimated the population in the Langholm-Newcastleton Hills in 1969 and 1972 respectively to be 65 and 50. The 1978, 1979 and 1980 estimates were approximately double the earlier counts at 138, 107 and 108 respectively, but were probably more accurate.

McDougall (1975) counted goats on the eastern half of Kielderhead Moor in 1972. It is believed that many goats frequented the western half of the moor in that year and were never detected (D. Brown pers. comm.). McDougall's total of 35 was, therefore, probably an underestimate; the true total is likely to have been similar to the minimum estimates of 54 and 55 for 1979 and 1980.

The total censuses at Nether Hindhope are precise because this population is gathered each autumn and counted. Between 1976 and 1980 the population fluctuated between 29 and 42 (Appendix 7).

In terms of size, the number of kids and the number of billies were the most variable population segments; both had lower and more variable survival rates than nannies. Feral goat society is polygynous so that a change in the number of billies in all but a very small population is unlikely to reduce the conception rate of nannies. Variations in abundance were more likely to be the result of variations in kid production or kid survival.

The possibility exists that in the small population at College Valley and Nether Hindhope, all the billies may die following a particularly severe winter. This occurred in College Valley in 1948 (Brewster 1976) and at Nether Hindhope in 1963 (T. Elliot pers. comm.); furthermore, the number of billies in the latter population in 1980 was dangerously low at two (Appendix 7). Greig (1969) warned of the dangers of culling feral goat populations to such low levels that the degree of inbreeding becomes great with an associated increase in the expression of deleterious genes. Ralls, Brugger and Ballou (1979) showed that inbreeding depression occurred in small populations of normally outbreeding ungulates. Feral goats in the Southern Uplands tend not to disperse (Chapter 5) and the degree of inbreeding is likely to depend on the number of rutting seasons during which an individual billy contributes significantly to the gene pool.

Of the possible factors relevant to regulation of feral goat populations in the Southern Uplands, food supply in winter and spring was probably the most important. Food quality and quantity fluctuate widely throughout the year in seasonal environments and it was found that both feral goats and hill sheep utilise lower quality forages in winter when little else is available (Chapter 3). Food supply has been shown to be important in the regulation of several ungulate populations e.g. feral sheep on Hirta, St Kilda (Jewell *et al.* 1974), feral reindeer (Klein 1968; Leader-Williams 1981) and African buffalo (Sinclair 1977).

It is suggested that with the exception of those at Craigdews and in College Valley, the feral goat populations in the present study areas were fluctuating about levels determined by the carrying capacity of their ranges. This is similar to hill sheep populations whose densities are ultimately determined by forage quality and forage quantity in late winter and spring.

CHAPTER 5. SOCIAL AND SPATIAL ORGANISATION.

Introduction

Feral goat society consists basically of groups of nannies and their offspring with which billies associate to a variable degree (Boyd 1981; Gould 1979; McDougall 1975; Munton 1975; Riney and Caughley 1959; Rudge 1970a; Shank 1972). This is similar to the organisation of other caprinid societies (Geist 1971; Jewell et al. 1974; Schaller 1977) and many bovids (Jarman & Jarman 1979; Leuthold 1977; Wilson 1975).

Up to the present, studies on the social and spatial organisation of feral goat populations have rarely lasted for more than two consecutive seasons. However, information on the variation between seasons of social and ranging behaviour is essential for studies relating behaviour to ecological parameters and also for effective management. In these contexts, earlier studies have mostly been unsatisfactory. Caughley (1977) warned of the dangers of attempting to cull populations of social animals such as feral goats before their social organisation had been elucidated; we must be able to predict the degree to which culling will disrupt the organisation of social groups and also the effect of this disruption on the potential rate of increase.

Studies of African ungulates have shown that much of their social and spatial organisation can be correlated with ecological parameters such as the fibre content of forages, habitat stability, food dispersion and predator density (Bell 1970; Geist 1974; Jarman 1974; Jarman & Jarman 1979). It is of great interest to investigate these relationships in a feral ungulate where artificial selection by man may have altered its feeding ecology or social behaviour as has occurred in free ranging domestic sheep (Arnold and Dudzinski 1978; Schwartz and Ellis 1980).

This chapter particularly concerns variation in group size, group composition and spatial organisation since these are the basic parameters relating ecology and behaviour in ungulates (Geist 1974; Underwood 1982).

Methods

Data on group size, group composition and ranging behaviour were collected during censuses and opportunistic observations. A group was taken as consisting of all the individuals within 100 m of each other. This distance was chosen because it was believed to be the limit of effective social contact; neighbouring groups were often at much greater distances and apparently not in sensory contact. Individuals within groups were classified according to age and sex as follows: kids, nannies (including yearlings) and three classes of billies; yearlings, two and three year olds and those of four years or older. Billies were aged by counting the number of annual horn rings (Chapter 4). The following group types were recognised:

1. Billy; consisting entirely of yearling or adult billies
2. Nanny; consisting of yearling or adult nannies with or without kids
3. Mixed; consisting of yearling or adult billies and nannies with or without kids.

In order to describe group size, two preliminary comparative analyses were carried out. Firstly, the frequency distributions of group size were plotted; these were always skewed to the right (Figure 5.1). Secondly, the comparison was made between median, mean and typical

Figure 5.1

Frequency distributions of group sizes on the Moffat Hills during two years. (a) winter; (b) spring; (c) summer and (d) autumn. Data from all group types.


No= 45
No= 46
(a)
No= 76
No= 132
(b)
No= 72
No= 27
(c)
No= 85
No= 60
(d)
60
40
20
Percent →
1-3
4-6
7-9
10-12
13-15
16-18
19-21
22-24
25-27
28-30
1978
Group size →
1979

(Jarman 1974) group sizes for the same data sets (Figure 5.2). The skewed nature of the distributions meant that unless the data were transformed, medians were more meaningful in describing group size than were means. Neither, however, described the size of the groups containing, or experienced by average individuals; this, the typical group size, was adopted in the present study. Jarman (1974) described calculation of typical group size as follows:

$$\frac{n_1^2 + n_2^2 + n_3^2 + \ldots\ldots\ldots\ldots n_i^2}{N}$$

where n_1 n_2 etc. are the numbers of individuals in each group and N is the number of individuals sampled.

Ranging behaviour was studied by recording the location of individuals recognisable by natural markings or horn shape (Crook 1969; Riney & Caughley 1957) using grid references on large scale (1:10,560) maps. Many individuals were drawn and photographed. In addition, 27 goats from the Langholm-Newcastleton Hills and College Valley were ear tagged with brightly coloured, numbered 'Shire' calf tags in 1977. Between 1978 and April 1980, the majority of individuals in the College Valley, Nether Hindhope and Moffat Hills populations were recognisable individually. The last mentioned population was selected for more detailed study because of the combination of moderately large size, lack of disturbance (Chapter 4) and relatively good viewing conditions.

Preliminary observations suggested that groups of goats occupied home ranges (sensu Jewell 1966). This feature was investigated in detail for the Moffat Hills and Nether Hindhope populations using cluster analyses. Individuals within the same group were considered to be associated. The frequency of association between individuals, corrected for the number of sightings of each individual, was calculated to form association matrices. The matrices formed the basis of dendrograms, using weighted-average linkage cluster analysis (Morgan, Simpson, Hanby & Hall-Craggs 1976) and used to identify social groupings. The assumptions and procedures of the cluster analyses are detailed in Appendix 8.

On the Moffat Hills, individuals were sighted more than once per day relatively rarely; the data base, for standardisation, was therefore the first sighting of each individual per day. For Nether Hindhope, where sightings were fewer in total number but usually several per individual per day, all sightings were used.

In practice, the dendrogram defined groupings were the same as those identified during fieldwork. The conclusion that the groupings in the Moffat Hills population were natural has been corroborated by S. Pickering (pers. comm.) who had conducted a more detailed study of their spatial organisation. The groupings identified and used in the two studies contained essentially the same individuals (apart from those that had died) together with their offspring a year later.

As the number of sightings of individuals in other populations were either few or restricted to one season, the construction of association matrices was not appropriate. However, where social groupings were recognised, they have been described. In order to estimate how much of the area occupied by a group or individual had been identified, plots of cumulative area against the number of sightings were drawn (Odum & Kuenzler 1955). Areas occupied by social groups were calculated from polygons enclosing all sightings with no re-entrant angles (minimum area method - Southwood 1978); these areas were regarded as home ranges of a group of individuals with highly overlapping individual home ranges.

The groups were called hefts, the name of a similar grouping of hill sheep used by shepherds in the Southern Uplands.

The relationship between the area occupied by a heft and the biomass of the heft (the latter being an index of its energy requirements) was investigated using regression analysis.

Results

1. Group size and group composition

Data on seasonal changes in group size and group composition were obtained for the populations on Cairnsmore of Fleet, the Moffat Hills and the Langholm-Newcastleton Hills. For other populations the data were too few to warrant analysis on a seasonal basis.

Overall group size (i.e. with data pooled) for the three group types showed considerable but predictable variation throughout the year whether the statistic used was the mean, median or typical group size (Figure 5.2). Typical and median group sizes were invariably the largest and smallest for each comparison.

In general, group sizes were smallest in spring and largest in summer or autumn. The group size for Cairnsmore of Fleet in spring 1980 was unusually large for this season probably because this population was observed in mid May when group sizes were probably increasing towards their summer level.

Typical group size and maximum group size were positively and significantly correlated with population size ($r_s = +0.9226$, $p < 0.001$ and $r_s = +0.9762$, $p < 0.001$ respectively, Figure 5.3). In these correlations, data for summer would ideally, have been used throughout.

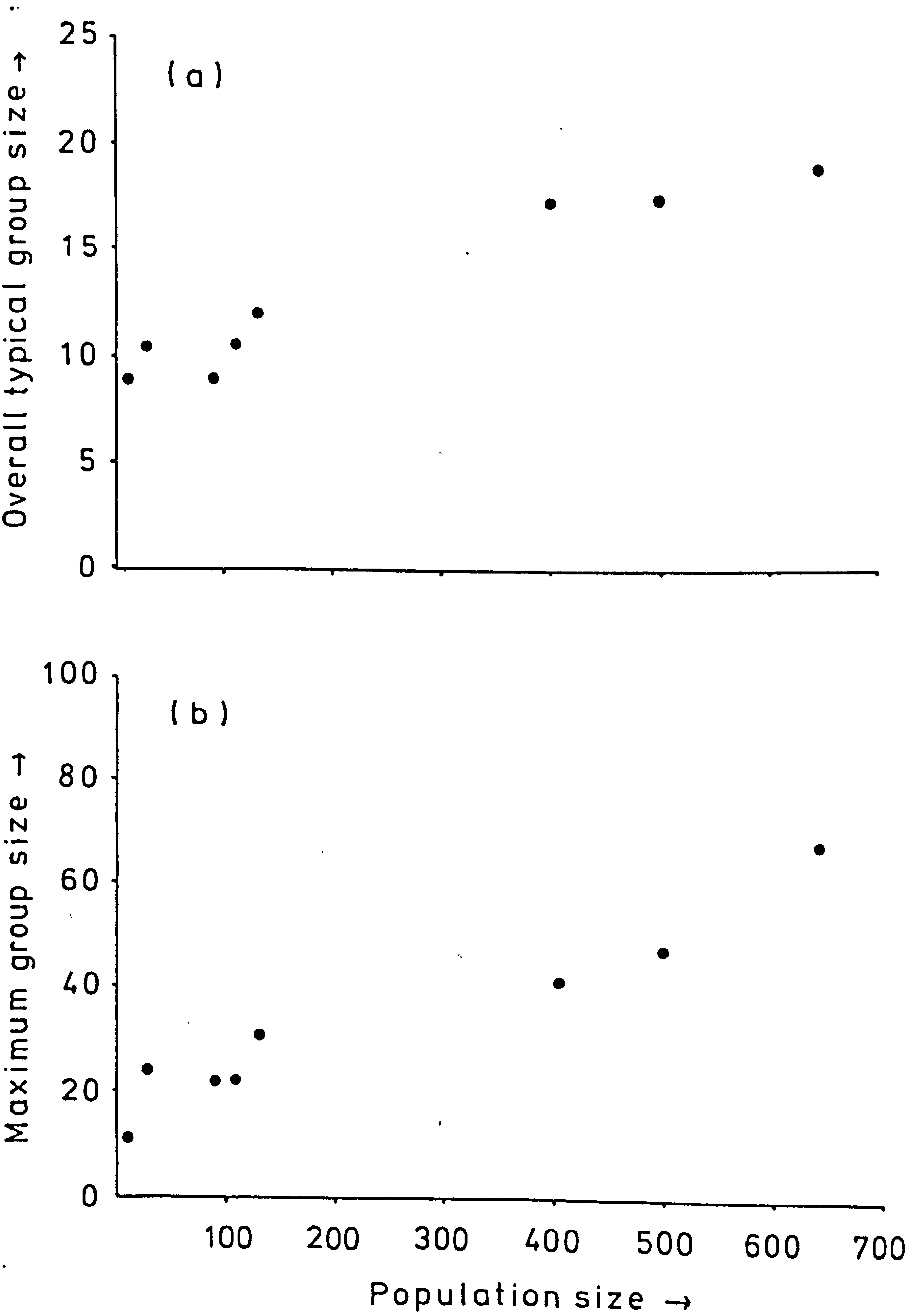
Figure 5.2

Seasonal changes in group size as expressed by the median (□), mean (o) and typical (•) group sizes. Vertical lines indicate ranges. (a) Cairnsmore of Fleet; (b) Moffat Hills; (c) Langholm-Newcastleton Hills. Data from all group types.


70
60
50
40
30
20
15
10
5
(a)
(b)
(c)
Group size →
Su
W
Sp
Su
A
W
Sp
Su
A
W
Sp
'76
'77
'78
'79
'80
Season →

Figure 5.3

The relationships between population size and (a) overall typical group size and (b) maximum group size respectively during summer. Data from Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Nether Hindhope and College Valley. For (a), $r_s = +0.9762$, $p < 0.001$; for (b), $r_s = +0.9226$, $p < 0.001$.


(a)
Overall typical group size →
0
5
10
15
20
25
(b)
Maximum group size →
0
20
40
60
80
100
100
200
300
400
500
600
700
Population size →

As these were not available for College Valley and Cairnsmore of Fleet in 1980, the autumn and May observations respectively were substituted. Furthermore, in order to increase the sample size for Nether Hindhope in summer, data from late May and the first week in September were included. The correlations suggested a causal relationship between the size of the group experienced by the average goat or the maximum group size in summer and population size.

Group sizes of 40 or more, as were recorded on Cairnsmore of Fleet, would have been unlikely or impossible in other populations. Those in College Valley and at Nether Hindhope were absolutely too small and also the spatial organisation of populations (see following section) was such that many individuals never encountered one another.

Typical group sizes of nanny and mixed groups showed similar trends to overall typical group sizes, being generally largest in summer or autumn and smallest in spring (Figure 5.4). Billy groups on the Moffat and Langholm-Newcastleton Hills usually had smaller and less variable typical sizes than those of nanny or mixed groups (Figure 5.4). Typical group size for billies on Cairnsmore of Fleet in the autumn was conspicuously larger than that for other seasons or other populations, because one group of 24 billies had been recorded. Omitting this exceptionally large group, typical group size was reduced to 6.0, that is closer to the other values.

In general, at least some billies were associated with nannies in mixed groups, throughout the year. The proportion of billies in billy and mixed groups varied not only with season but also with the age of the billy. Yearling billies associated proportionately more with nannies than with older billies during the winter, spring and summer.

Figure 5.4

Seasonal variations in the typical size of (a) billy groups; (b) nanny groups and (c) mixed groups on Cairnsmore of Fleet (o), the Moffat Hills (●) and the Langholm-Newcastleton Hills (Δ).


(a)
10
5
(b)
20
15
10
5
(c)
30
25
20
15
10
5
Typical group size →
Su
'76
Sp
'78
Su
A
W
Sp
'79
Su
A
W
Sp
'80
Season →

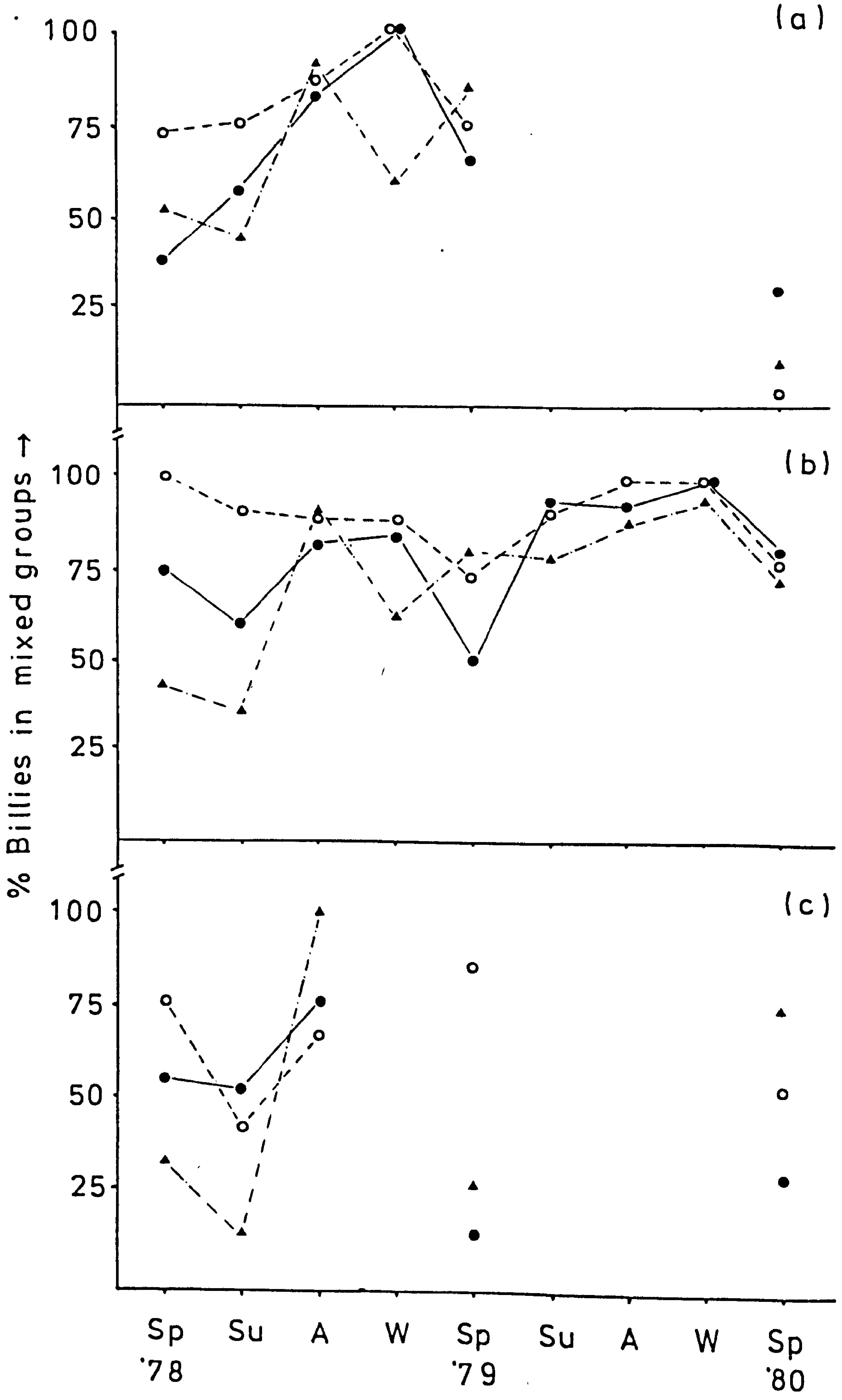
(a)
(b)
(c)
100
75
50
25
% Billies in mixed groups →
Sp '78
Su
A
W
Sp '79
Su
A
W
Sp '80

Figure 5.5

Seasonal variation in the percentage of billies (yearlings (o), two plus three year olds (•) and four years or older (Δ)) on Cairnsmore of Fleet (a), the Moffat Hills (b) and the Langholm-Newcastleton Hills (c) in mixed groups.

Figure 5.4

Seasonal variations in the typical size of (a) billy groups; (b) nanny groups and (c) mixed groups on Cairnsmore of Fleet (o), the Moffat Hills (•) and the Langholm-Newcastleton Hills (Δ).


(a)
(b)
(c)
15
10
5
20
15
10
5
30
25
20
15
10
5
Typical group size →
Su
'76
Sp
'78
Su
A
W
Sp
'79
Su
A
W
Sp
'80
Season →

<u>Figure 5.5</u>

Seasonal variation in the percentage of billies (yearlings (o), two plus three year olds (•) and four years or older (Δ)) on Cairnsmore of Fleet (a), the Moffat Hills (b) and the Langholm-Newcastleton Hills (c) in mixed groups.

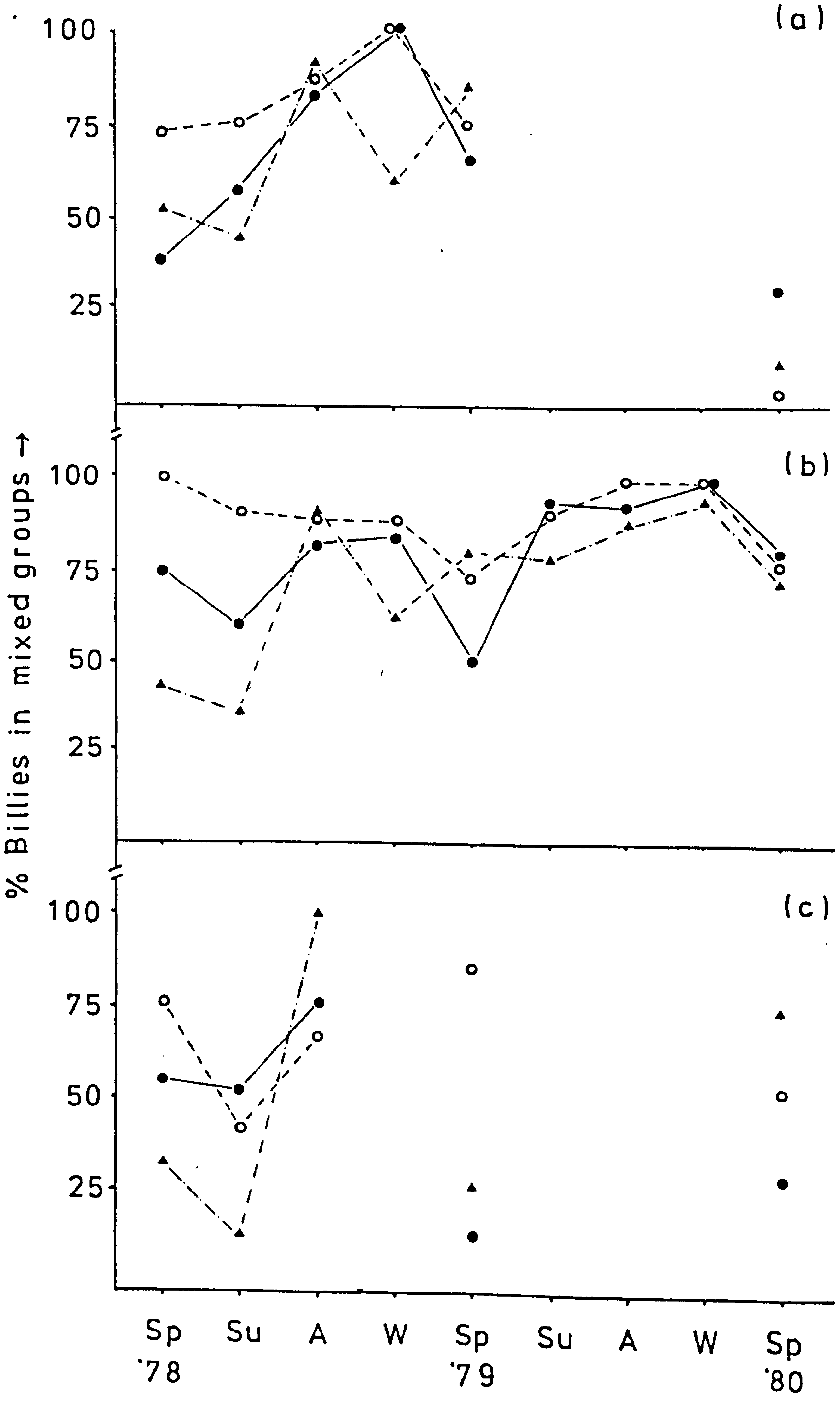
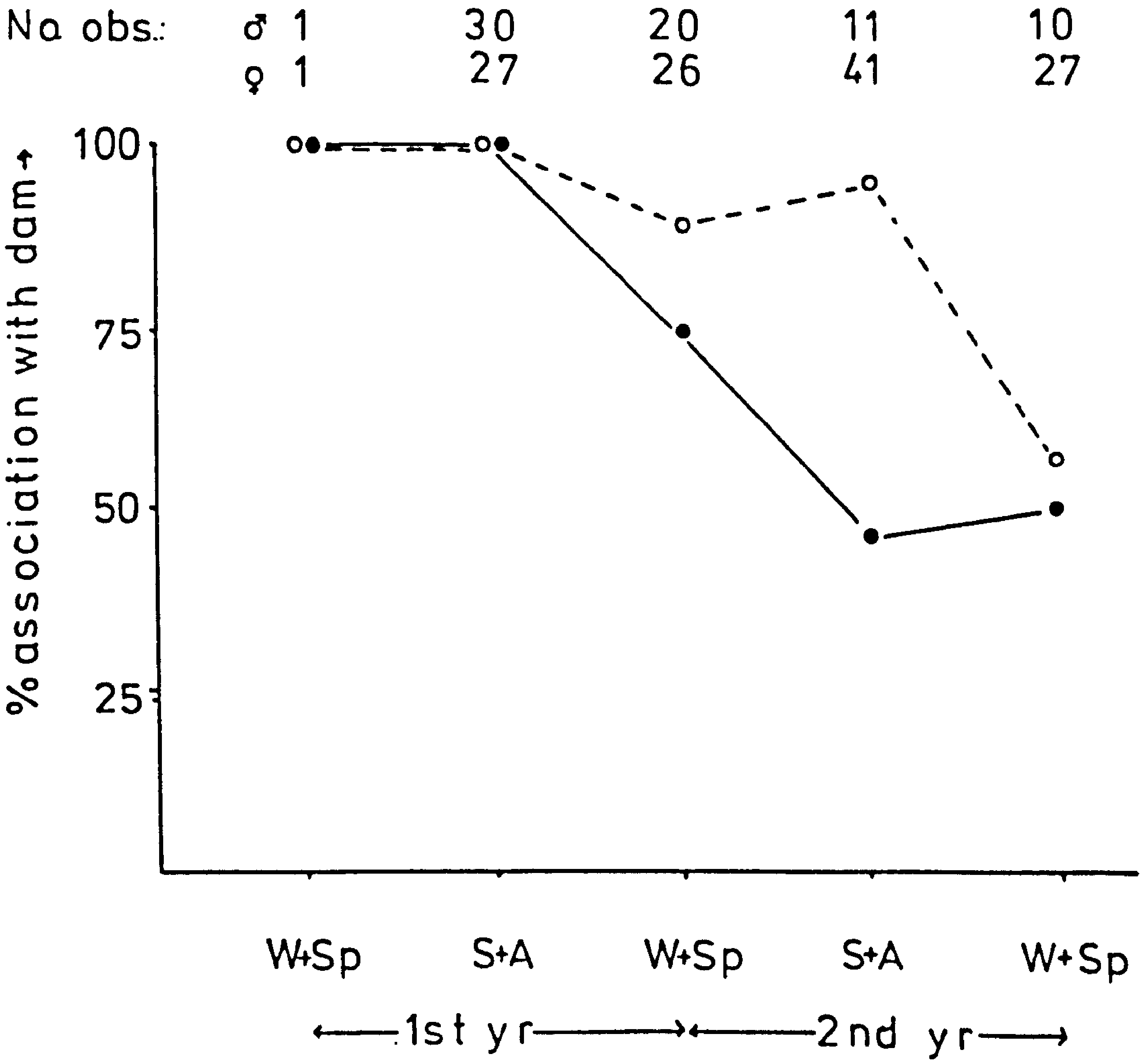

(a)
(b)
(c)
100
75
50
25
% Billies in mixed groups →
Sp '78
Su
A
W
Sp '79
Su
A
W
Sp '80

Figure 5.6

The percentage of observations of billies (●) and nannies (o) with their dams during the first two years of life. The difference between billies and nannies during summer and autumn of their second year was significant ($\chi_1^2 = 93.07$, $p < 0.001$).


No. obs.:
♂ 1 30 20 11 10
♀ 1 27 26 41 27
% association with dam →
100
75
50
25
W+Sp
S+A
W+Sp
S+A
W+Sp
← 1st yr →
← 2nd yr →

Two and three year old billies associated less with nannies and those aged four years or older associated least with nannies at these seasons but especially spring and summer (Figure 5.5).

The tendency for billies to associate less with nannies as they aged was initially the result of separation of the former from their dams. Nanny kids showed a more gradual dissociation from their dams than did billy kids; by their second birthday both sexes were associated with their dams for less than 60% of the time (Figure 5.6). Billies associated significantly less with their dams than nannies during the summer and autumn of their second year ($\chi^2_1 = 93.07$, $p < 0.001$) but not at other times ($\chi^2_1 = 0.64$ and $\chi^2_1 = 0.005$ for first winter and spring and second winter and spring respectively). Adult or yearling billies were more likely to be encountered alone than nannies. On the Moffat Hills, for instance, between spring 1978 and spring 1980, 25.1% (N = 151) of billy groups consisted of one individual compared to 6.7% (N = 743) of nanny groups.

2. Ranging behaviour

The dendrogram of the frequency of association between individual goats on the Moffat Hills, based on sightings between November 1977 and April 1980, showed five main social groupings (hefts) (Figure 5.7). The cluster on the extreme left of the dendrogram represents six individuals whose associations were not properly known and which all died during the course of the study; they have been omitted from the following descriptions. The dendrogram-defined groupings corresponded to the hefts observed in the field and consisted of between 12 and 18 individuals. Each heft, named by the watershed upon which it was centered, contained adult billies, adult nannies and kids (Table 5.1)

Figure 5.7

Dendrogram, using weighted average linkage, of the frequency of association of goats on the Moffat Hills based on sightings between November 1977 and April 1980.

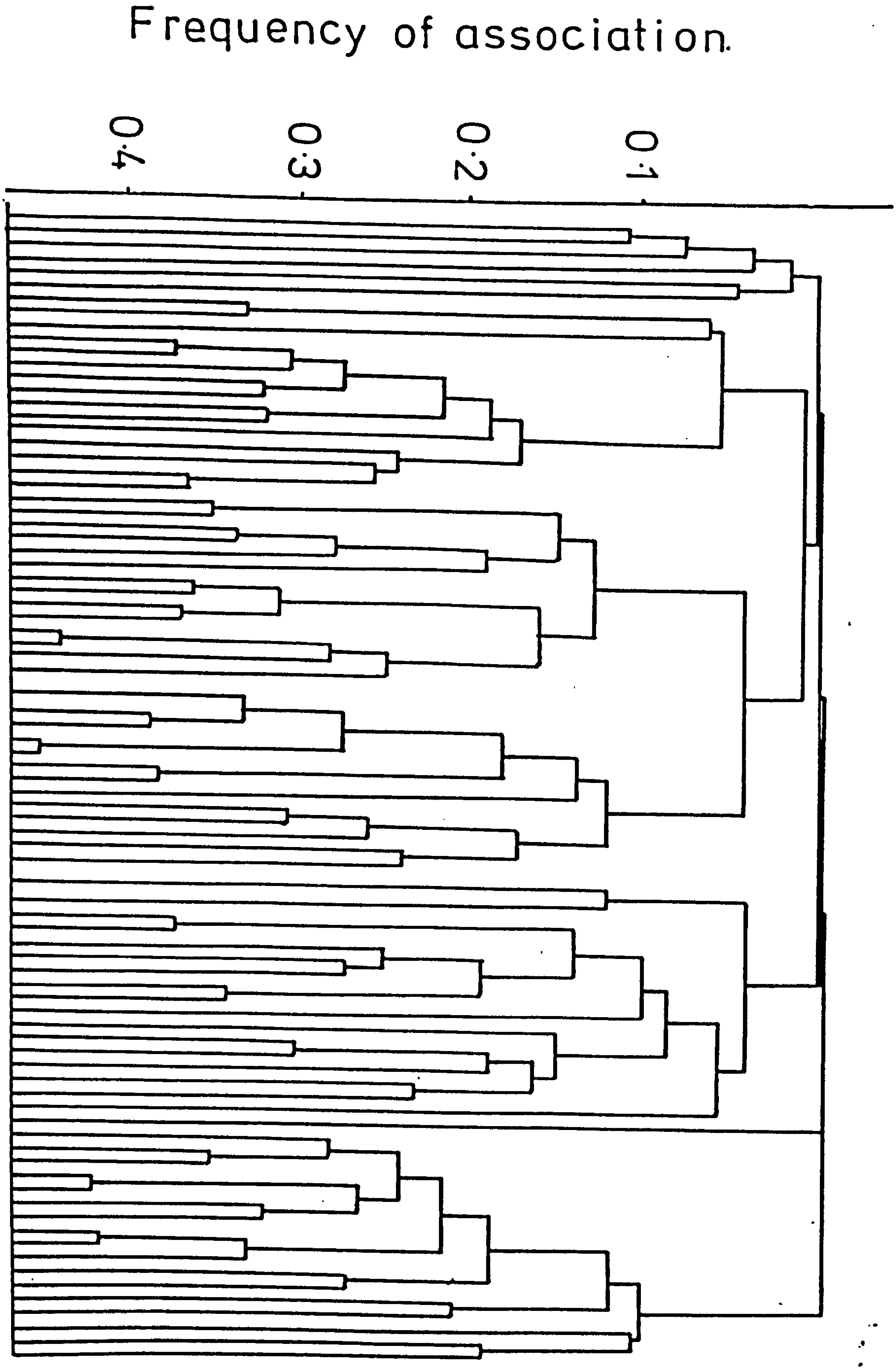
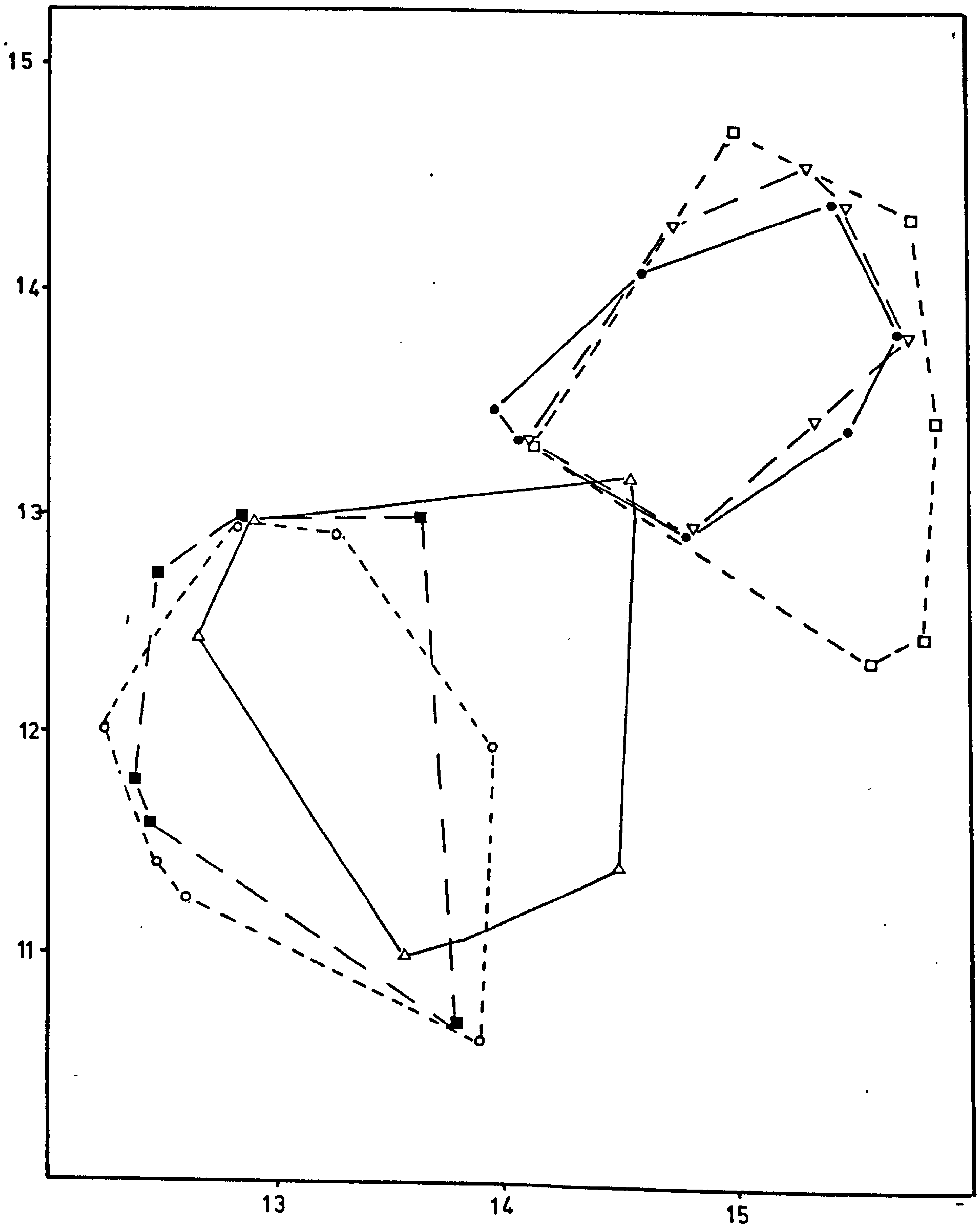

Frequency of association.
0·4
0·3
0·2
0·1

Figure 5.8

Comparison of the home range overlap between individual nannies from two neighbouring hefts, Blackhope (left) and Carrifran (right) respectively on the Moffat Hills. Sightings between May 1978 and April 1980. Only the outermost sightings for each nanny have been used. The distance between consecutive northings or eastings numbers is 1km.


15
14
13
12
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13
14
15

all of whom had highly overlapping home ranges; individuals in different hefts had home ranges that overlapped much less or not at all (Figure 5.8).

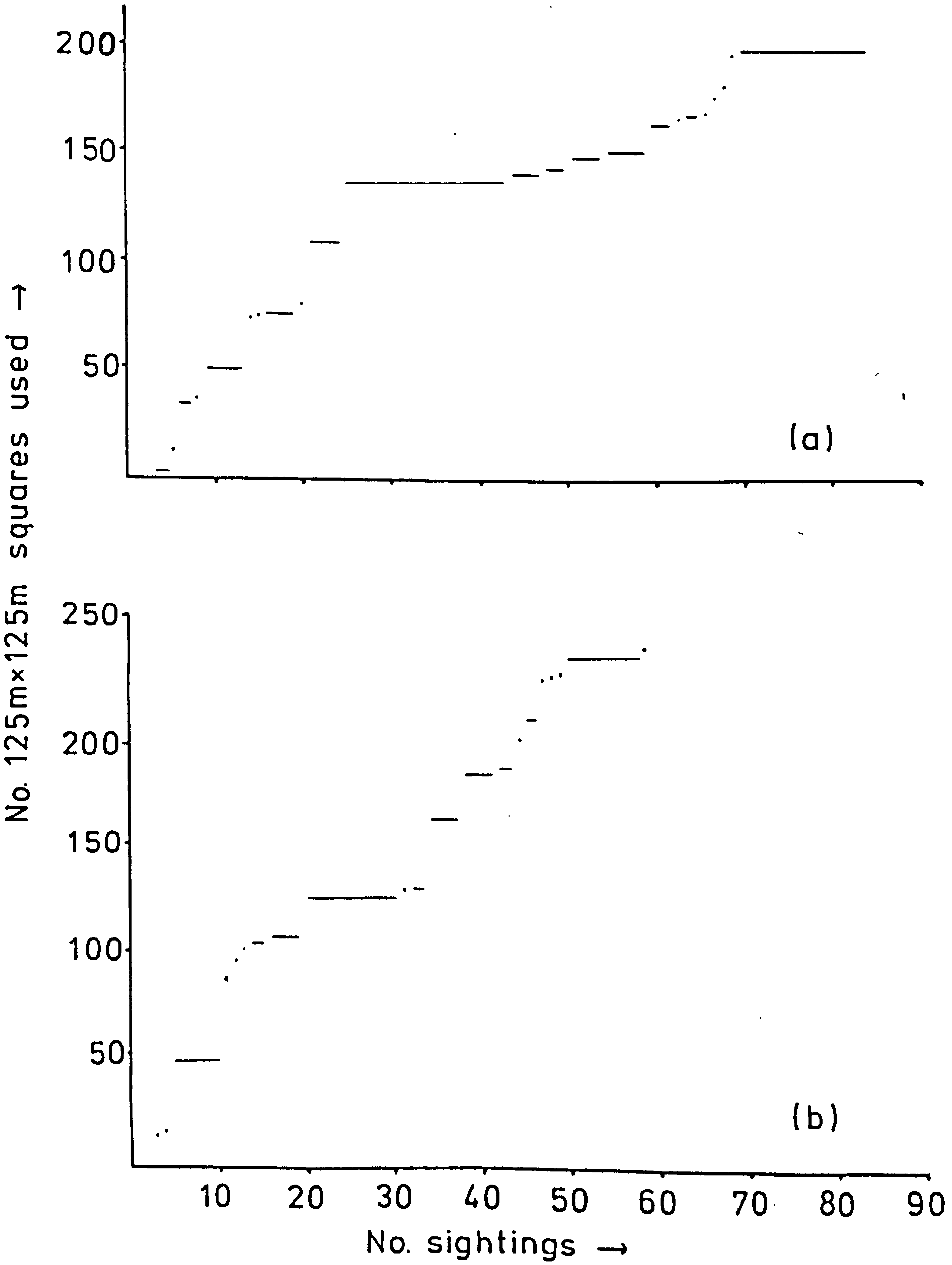
Cumulative area plots showed that, with the exception of the Carrifran and Grey Mare's Tail hefts, asymptotes were not reached indicating that the number of sightings obtained were insufficient to totally identify the areas used by the Blackhope, Capplegill and Spoon hefts (Figure 5.9 a, b, c, d & e). However, for all but the Capplegill heft the area occupied remained stable for at least one and often several seasons suggesting that shifts in home range use had taken place. For example, the Grey Mare's Tail heft used an area described by 46 sightings from the latter part of the autumn of 1978 to midsummer 1979; the area increased thereafter (Figure 5.9e).

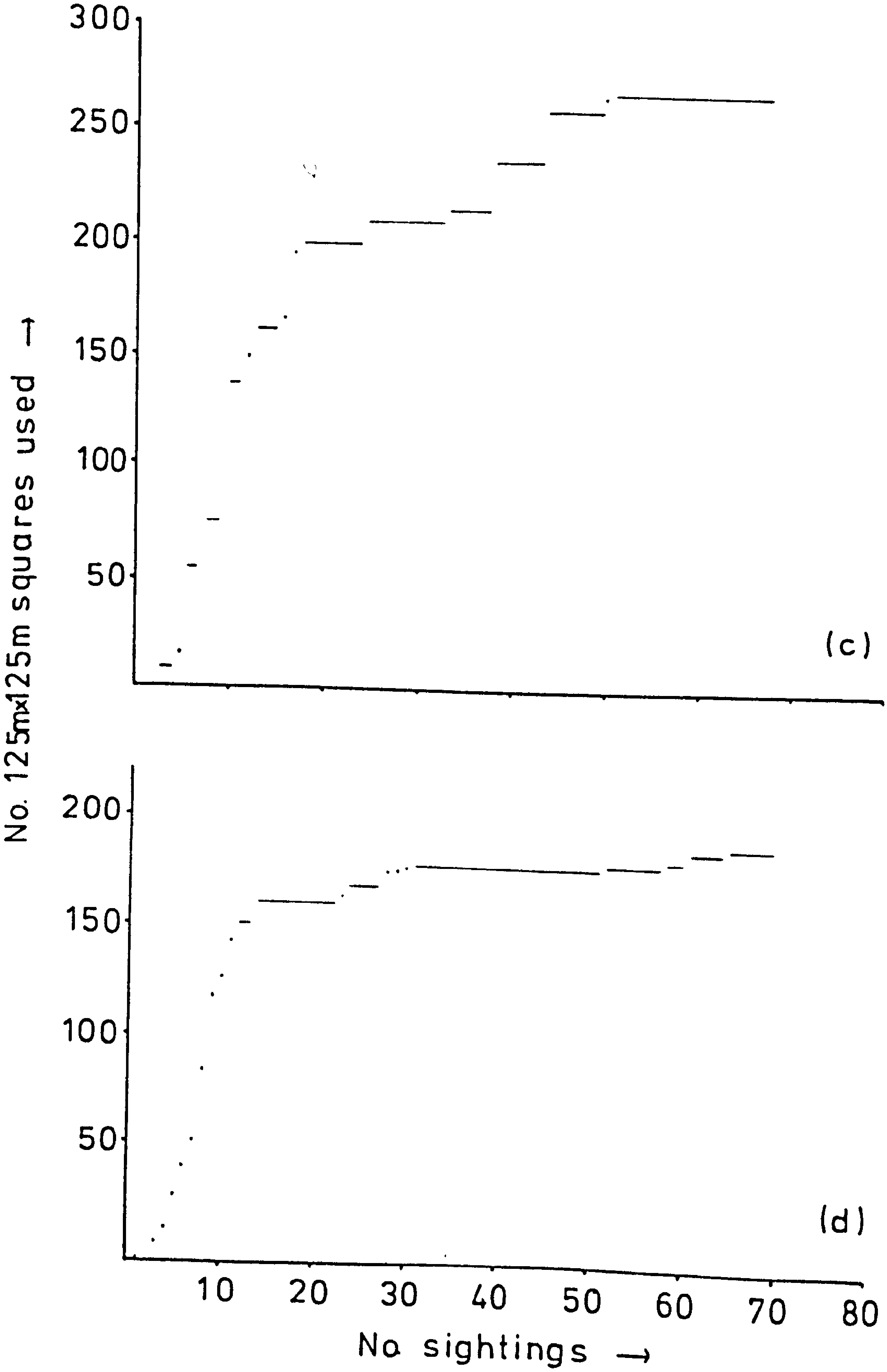
The Capplegill heft was exceptional; the goats in this heft shifted their home range during the spring and early summer into a forestry plantation within which they were undetected during most of the study period. Goats in this heft were generally more mobile than those in others as shown by their greater degree of spatial overlap with other hefts (Figure 5.10a). However, as field observations and the dendrogram showed, the frequency of association between individuals of different hefts was low.

The large home range of the Capplegill heft can be contrasted with that of the Grey Mare's Tail heft where all the individuals remained totally discrete from other goats on the Moffat Hills (Figure 5.10a); neither immigration nor emigration occurred during the study period. One old billy, ♂9, had a large home range that overlapped slightly with that of the Grey Mare's Tail heft; he was also recorded within the area of the Carrifran heft during the rut.

Figure 5.9

Cumulative area plots for goat hefts on the Moffat Hills. (a) Spoon; (b) Capplegill; (c) Blackhope; (d) Carrifran and (e) Grey Mare's Tail.


200
150
100
50
(a)
250
200
150
100
50
(b)
10
20
30
40
50
60
70
80
90
No. sightings →
No. 125m×125m squares used →

300
250
200
150
100
50
(c)
No. 125m×125m squares used →
200
150
100
50
(d)
10
20
30
40
50
60
70
80
No sightings →

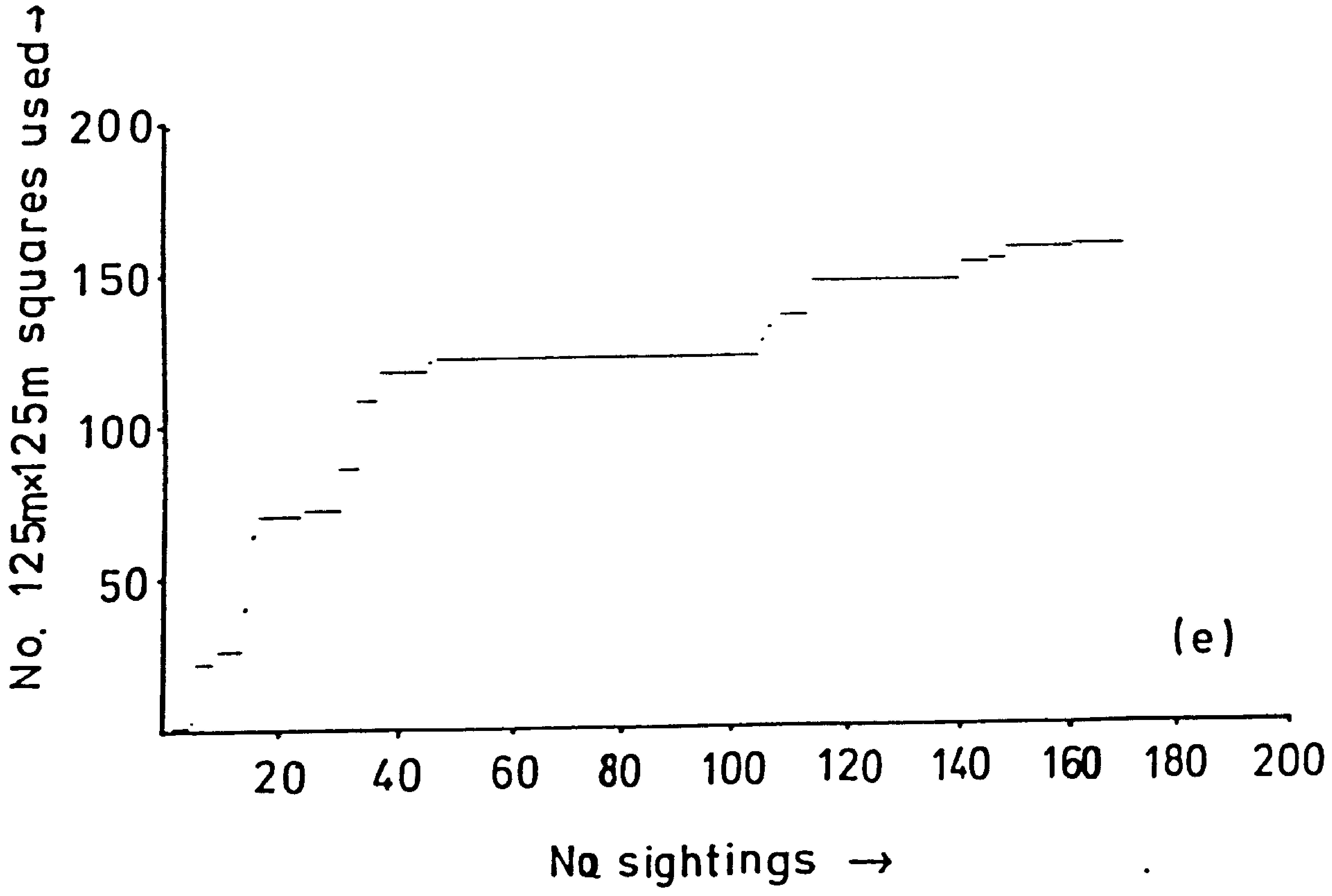

No. 125m×125m squares used →
200
150
100
50
(e)
20
40
60
80
100
120
140
160
180
200
No. sightings →

Figure 5.10

The spatial organisation of feral goats on the Moffat Hills between November 1977 and spring 1980.

(a) polygons enclosing outermost sightings detailed in (b)&(c).

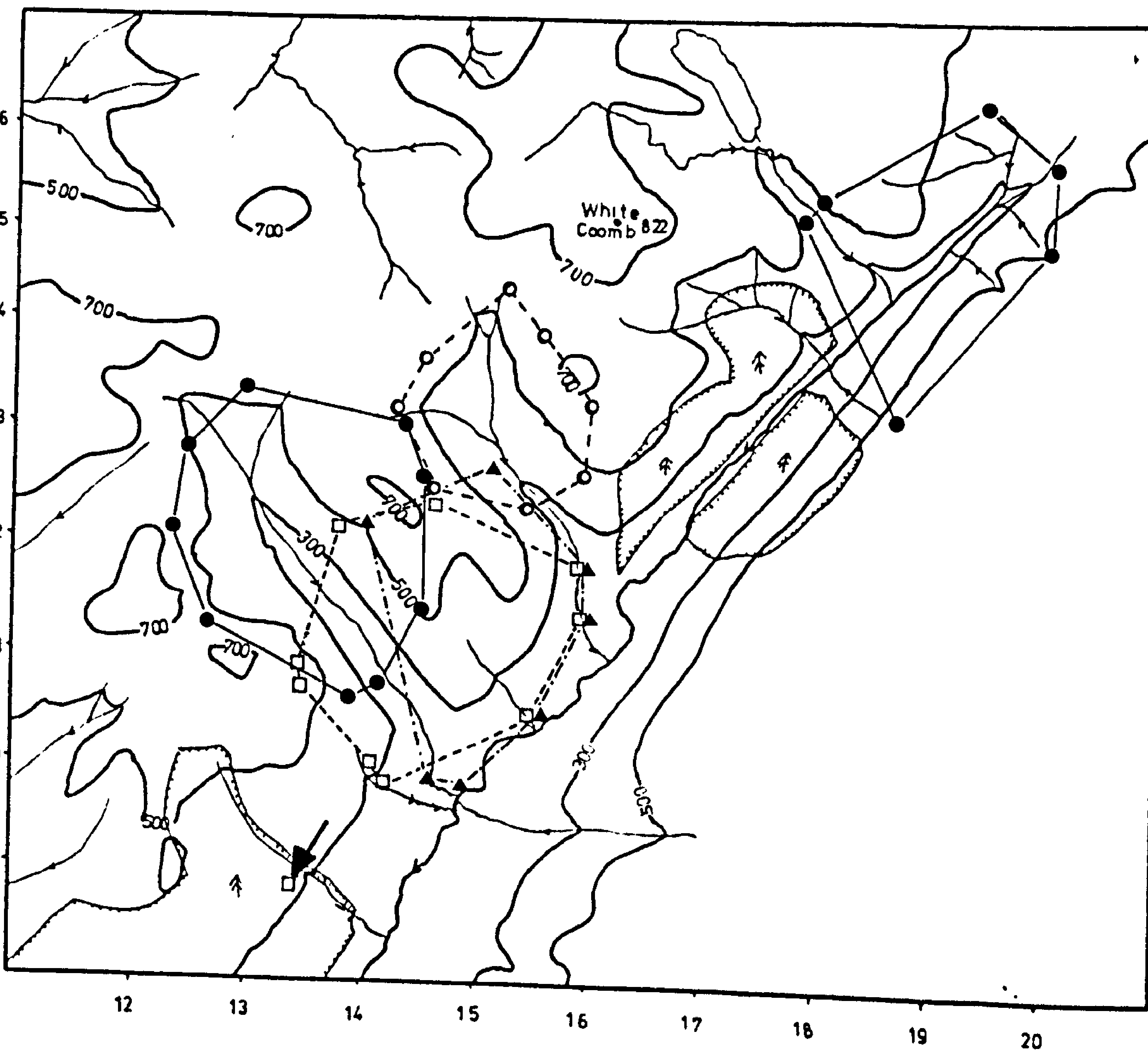
(b) range use by the Capplegill (□), Spoon (Δ), Blackhope (•) and Carrifran (o) hefts

(c) range use by the Grey Mares Tail heft (•).

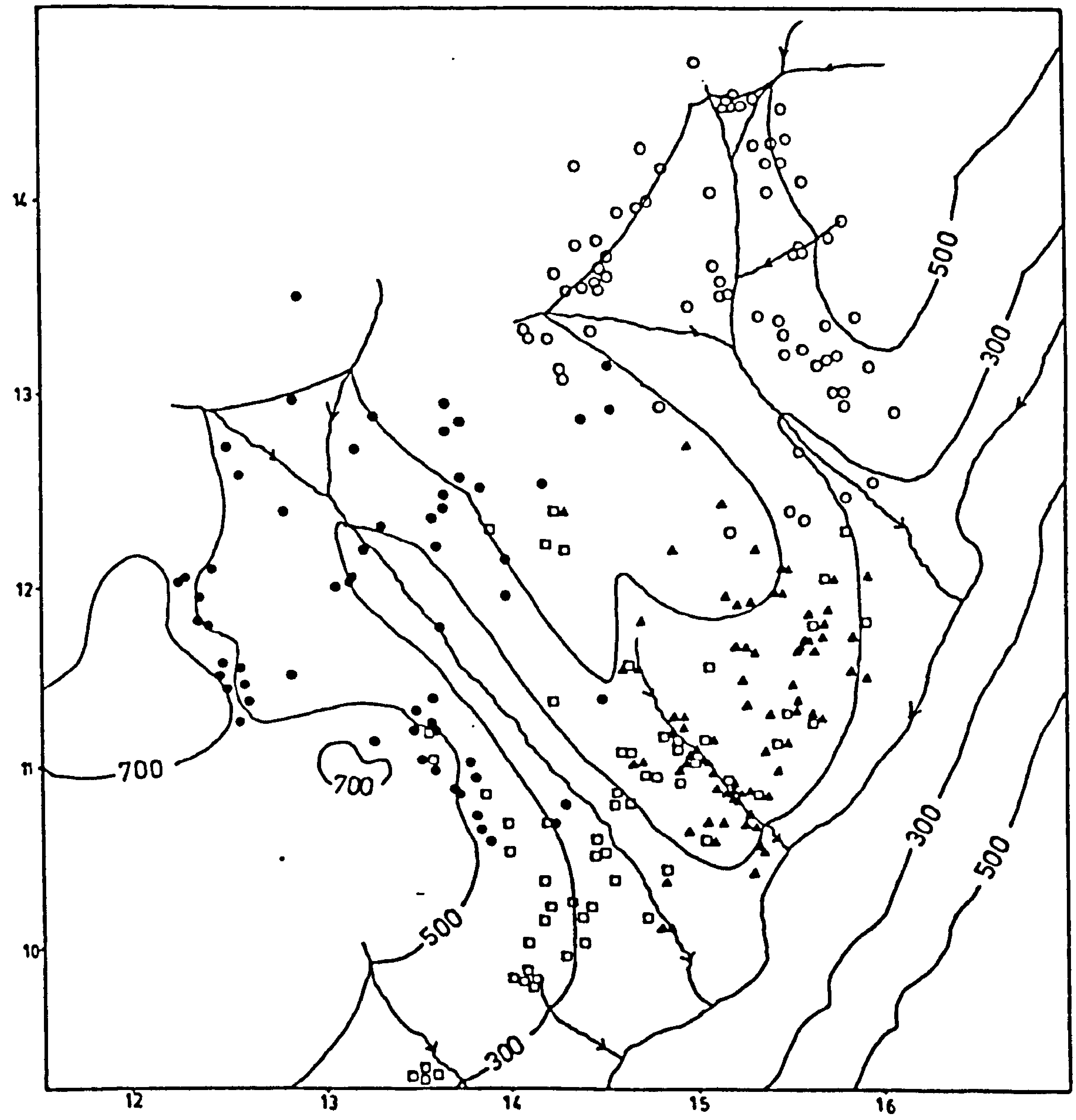
For (a),
Arrow indicates location of sightings of goats from the Capplegill heft within Forestry plantations during the spring and summer.

National Grid northings and eastings are indicated.The distance between each consecutive number is 1km.

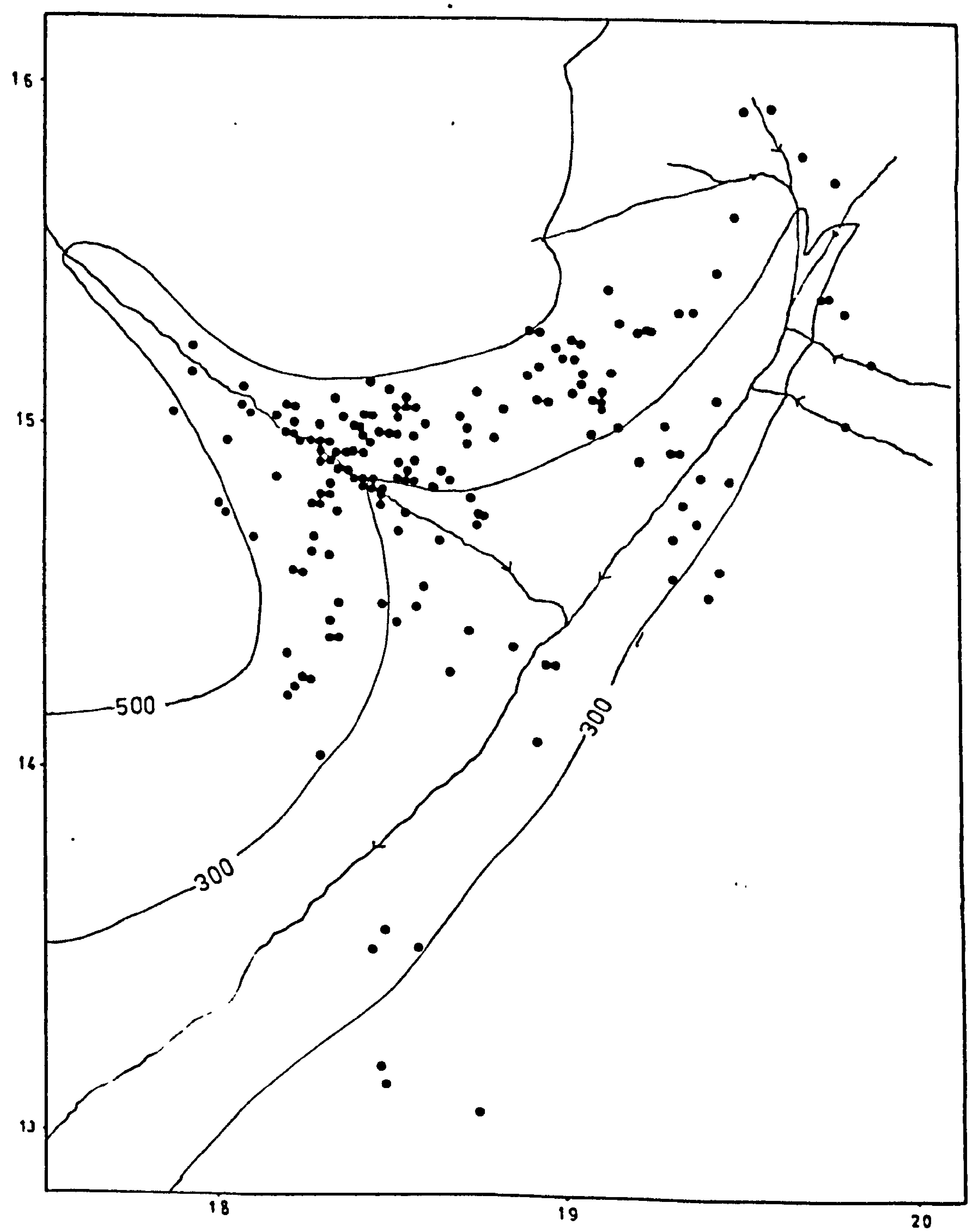
↟ indicates forestry plantations.


16
15
14
13
12
11
10
9
12
13
14
15
16
17
18
19
20
500
700
700
700
700
White Coomb 822
700
700
300
500
700
500
300
500

(a)



(b)



(c)

Within given heft home ranges were watersheds with precipitous gullies or crags. The gully of Spoon Burn was used by individuals of the Spoon and Capplegill hefts but the latter alone used the Capplegill gully (Figure 5.10b). At the Grey Mare's Tail, range use was greatest in the gully of Tail Burn (Figure 5.10c). For the Carrifran and Blackface hefts, range use was greatest on crags and gullies on hillsides above these burns (Figure 5.10b).

Billies generally remained within the heft in which they were first sighted; some movement occurred, however, and undoubtedly I did not witness all of these. Some of the home ranges of billies were relatively large and overlapped areas occupied by two or more hefts but these individuals were nevertheless primarily associated with one heft.

Goats at Nether Hindhope were not spatially organised into discrete hefts as they were on the Moffat Hills. The two social groups identified with the aid of a dendrogram (Figure 5.11) consisted of firstly, five billies and secondly nineteen nannies and two billies respectively; the ranges of these two groups overlapped considerably (Figure 5.12). Goats used virtually all the hill farm area available but have never been observed to disperse beyond the wire fence bounding the farm (T. Elliot pers. comm. and pers. observ.); goats are, however, capable of crossing such fences.

The nanny dominated social group contained several smaller social groupings; in particular, the two billies associated with this group had a small joint home range as compared with those of other goats.

Figure 5.11

Dendrogram of the frequency of association of goats at Nether Hindhope based on sightings between November 1977 and November 1978.

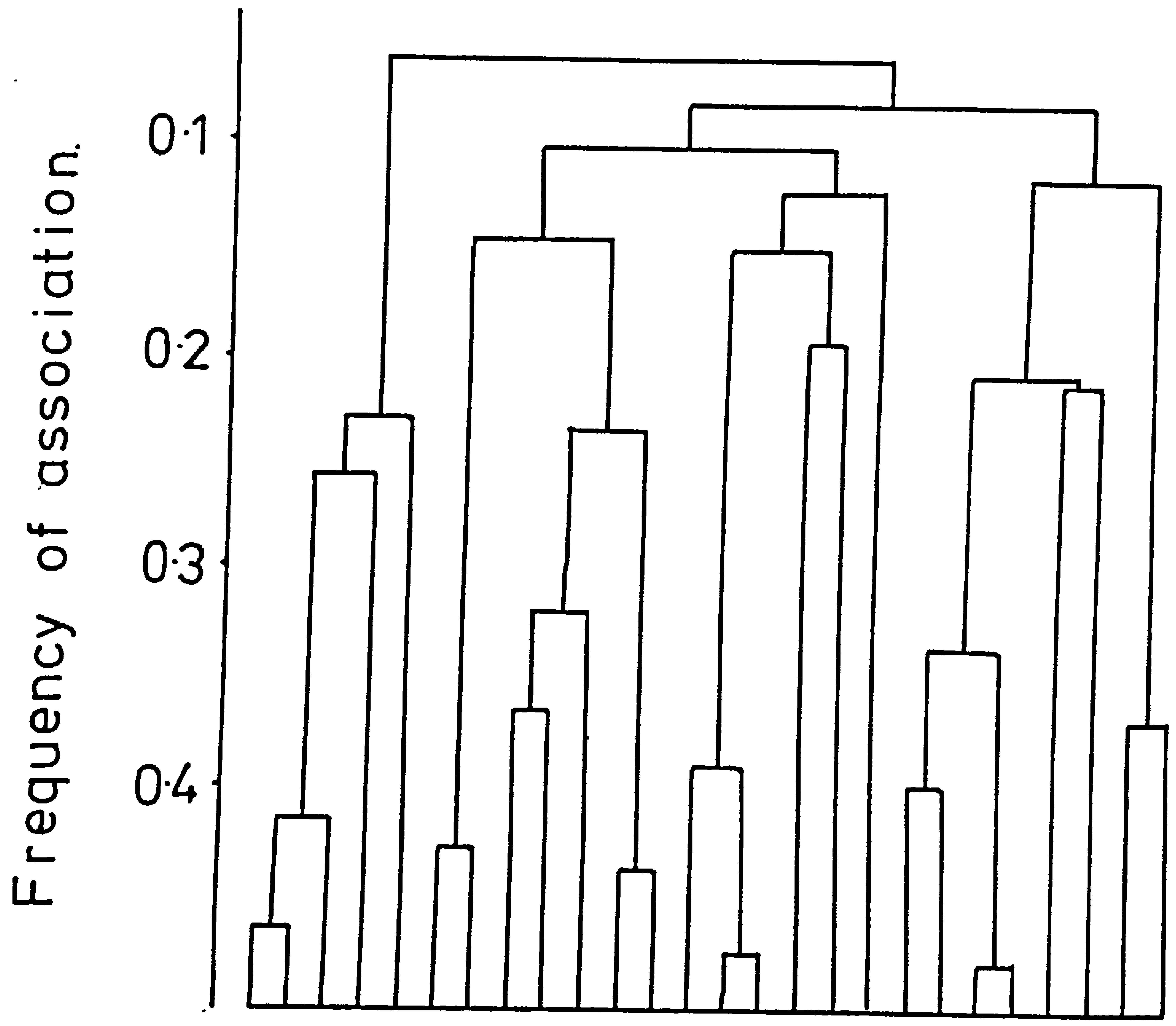
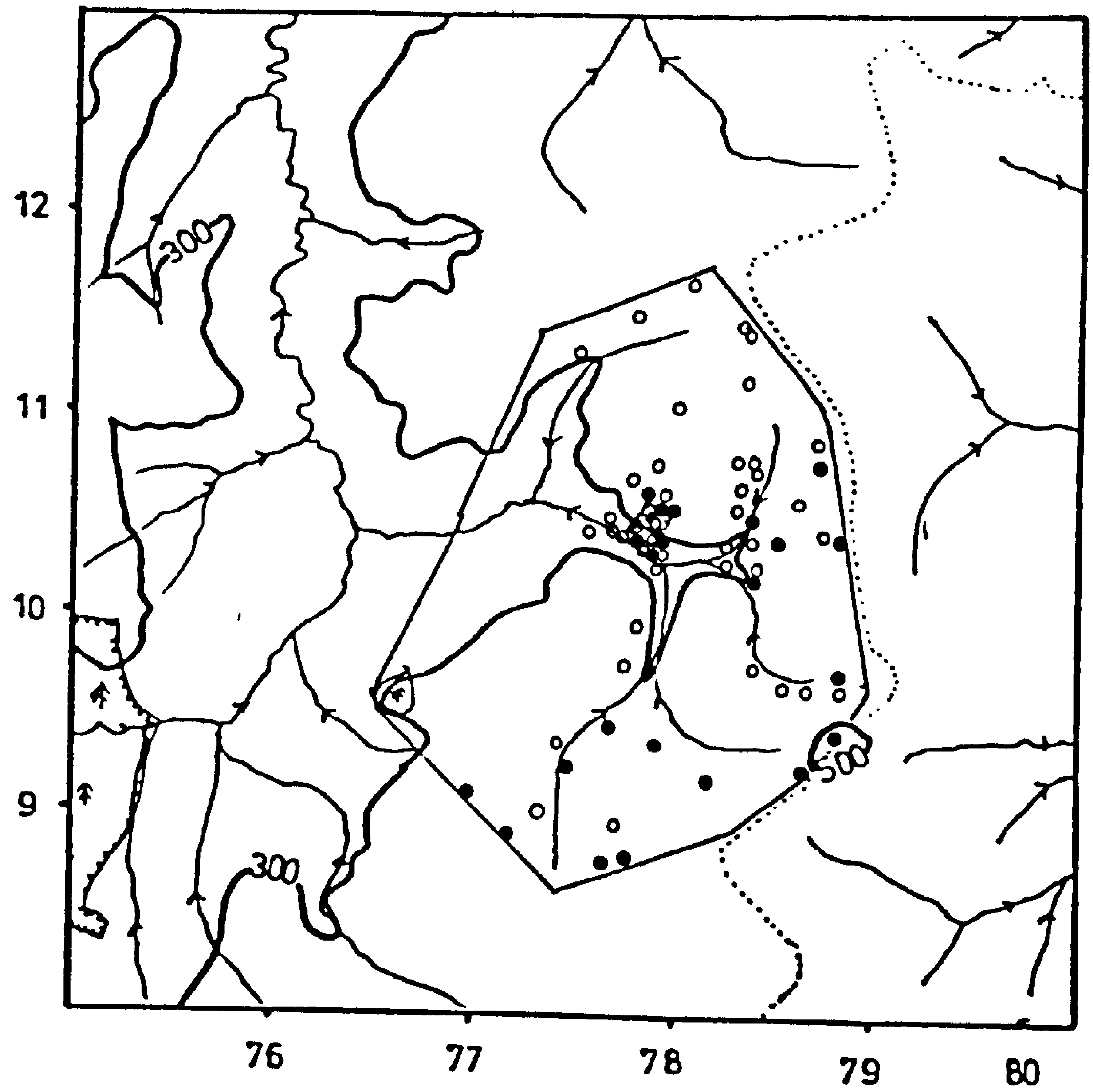

Frequency of association.
0·1
0·2
0·3
0·4

Figure 5.12

Range use at Nether Hindhope by the billy (•) and the nanny hefts (o) respectively between November 1977 and November 1978. Dotted line indicates the Scottish-English border (left-right respectively) and the line enclosing all sightings shows the position of the wire fence surrounding the farm.


12
11
10
9
76
77
78
79
80
300
300
500

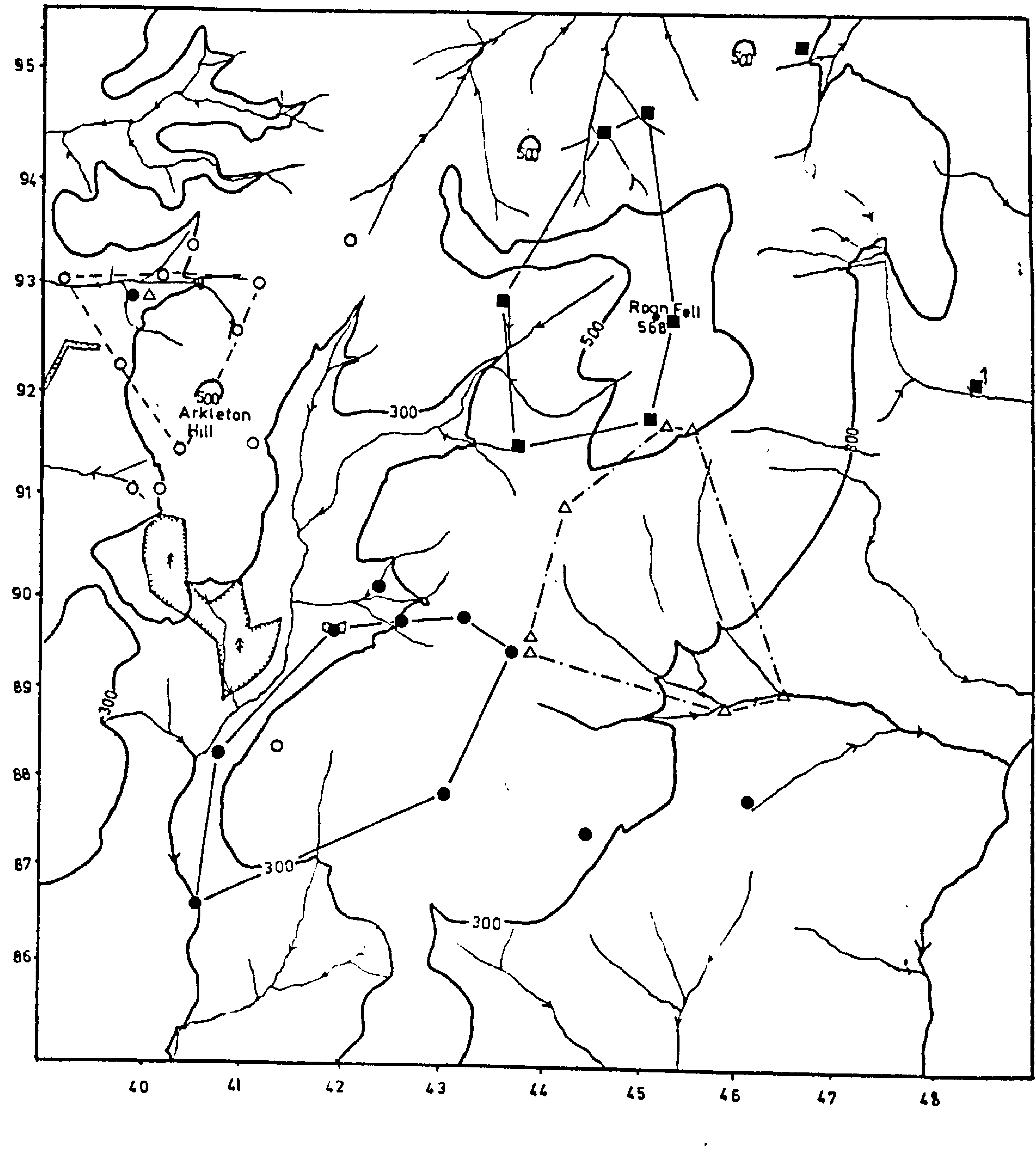
Areas used exclusively by the billy group and the nanny dominated group respectively, were the south and the north of the farm (Figure 5.12). A higher density of sightings were recorded in the middle of the hill farm where goats aggregated and invaded a conifer plantation; some goats also ate hay there in late winter and spring.

Four hefts were identified on the Langholm-Newcastleton Hills (Figure 5.13). Identification of the hefts as social groups was done subjectively but were based on the degree of overlap in the home ranges of individuals as they were for the goats on the Moffat Hills. Goats in the same heft had highly overlapping home ranges; for example, all the goats in the Arkleton heft, which in December 1977 were ear tagged with brightly coloured tags. The only movements of goats away from the heft home range were by billies once in autumn and once in spring (Figure 5.13). Another autumn movement, by nannies, billies and kids, to north of the home range was the direct result of grouse beating; the goats had returned to their home ranges within one month.

It is likely that I underestimated the movements of goats; billies were not uncommonly encountered alone or in small groups in areas outside those illustrated for hefts indicating that some sexual segregation was occurring. On Cairnsmore of Fleet N.N.R. sightings of several individuals, whilst inadequate for describing home ranges as judged by cumulative area plots, indicated a large degree of overlap between the areas occupied by nannies and billies. Significantly, even with the paucity of sightings from this population, one four year old billy was observed to move away from his previously determined home range to an area approximately one kilometre north east during the autumn of 1978 where he was observed tending a nanny. He had returned,

Figure 5.13

The spatial organisation of goats on the Langholm-Newcastleton Hills between November 1977 and April 1980. Hefts were (o) Arkleton, (■) Roan Fell, (Δ) Roan Fell Flow and (•) Taras. Symbols outside the polygons enclosing heft home ranges are of billy groups that had moved out of the hefts in which they were previously observed except [1] which included nannies and was probably winter range. Number of sightings of individuals within each heft were: Arkleton : 25; Roan Fell : 21; Roan Fell Flow : 20; Taras : 22.


95
94
93
92
91
90
89
88
87
86
40
41
42
43
44
45
46
47
48
500
500
500
500
Arkleton Hill
Roan Fell
568
300
300
300
300
300
800
1

however, to his previously recorded home range by late winter 1979 having crossed at least two fences, each one metre high, in the process.

In College Valley, two discrete hefts were identified (Figure 5.14), the histories of these are as follows: following the cull of November 1976, 14 goats remained (Chapter 4, Appendix 6) two of which were adult billies having a joint home range at Southernknowe, approximately two kilometres up the College Burn from the Newton Tors heft range. The remaining 12 goats formed a heft that ranged Yeavering Bell (Figure 5.14).

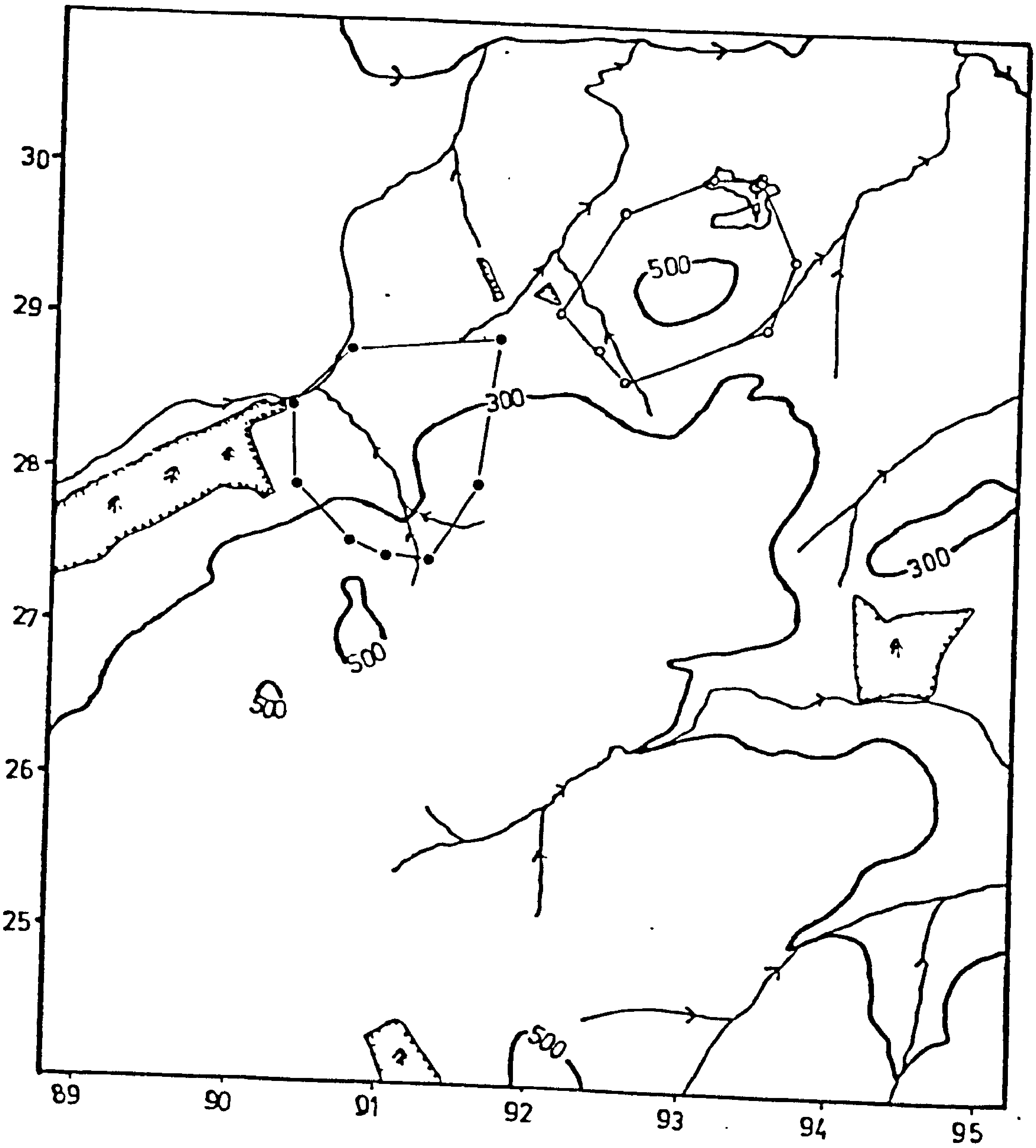
In autumn 1977, six of these goats moved to Newton Tors and formed a new heft which the two Southernknowe billies joined and never moved away from. The resultant two hefts were observed between autumn 1977 and spring 1980. It was suspected that some of the survivors from the 1976 cull, which took place at the north west base of Yeavering Bell (Figure 5.14), previously had home ranges of Newton Tors and it was these individuals that returned to the latter area in 1977.

The Yeavering Bell heft occupied the slopes of Yeavering Bell including the deciduous woodland; the Newton Tors heft used the sides of the burn (unnamed) running from these hilltops into College Water (Figure 5.14). No movements of goats outside these areas were detected between the winter of 1977 and the spring of 1980, during which time I could recognise all the adults individually. It is unlikely that the wire fences and dry stone walls between the areas occupied by these hefts prevented movements, since several movements occurred after the cull in November 1976 and before the winter of 1977.

On the basis that the areas observed to be occupied by hefts were minima, the relationship between goat biomass (independent variable, an

Figure 5.14

Spatial organisation of goats in College Valley between November 1977 and April 1980. (o) Yeavering Bell heft (number of sightings = 51) and (•) Newton Tors heft (number of sightings = 100).


30
29
28
27
26
25
89
90
91
92
93
94
95
500
300
300
500
500
500

index of energy requirements) and the heft home range size was investigated. When both variables were transformed logarithmically, they showed a close and highly significant relationship ($t_{11} = 10.4734$, $p < 0.001$, $b = 0.5149$). The data were not sufficiently detailed to permit correction for range overlap between neighbouring hefts but this appeared to be small between most of them. Potentially large errors were confined to the data for the Capplegill heft on the Moffat Hills and the two hefts at Nether Hindhope (Figure 5.15).

Discussion

From comparative studies of related herbivore species, several authors (Crook 1965; Crook & Gartlan 1966; Geist 1974; Jarman 1974) have argued that species-characteristic social organisations have adaptive significance for other aspects of the species' ecology. If social organisation is related to the abundance and distribution of resources and antipredator behaviour, we should predict flexibility in aspects of social organisation, such as group size, when environments or predation pressure vary seasonally.

In terms of dispersion, most caprinid species that have been studied are spatially organised into population units. Such units occur in wild American sheep (Geist 1971), wild Eurasian caprinids (Schaller 1977), domestic hill sheep (Hunter 1962), feral sheep (Grubb & Jewell 1966; Jewell et al. 1974), and feral goat populations (Boyd 1981; Buckland 1978; Geist 1966; McDougall 1975; Yocom 1967). Within such population units, individuals continuously join and leave groups, although the basic unit of the dam and her offspring remains.

Group sizes of feral goats were predictable on an annual basis in the present study. In spring most nannies (the most abundant age-

Table 5.1

The composition of goat hefts, the area (km^2) occupied by each heft, its density (goats km^{-2}) and biomass (kg).

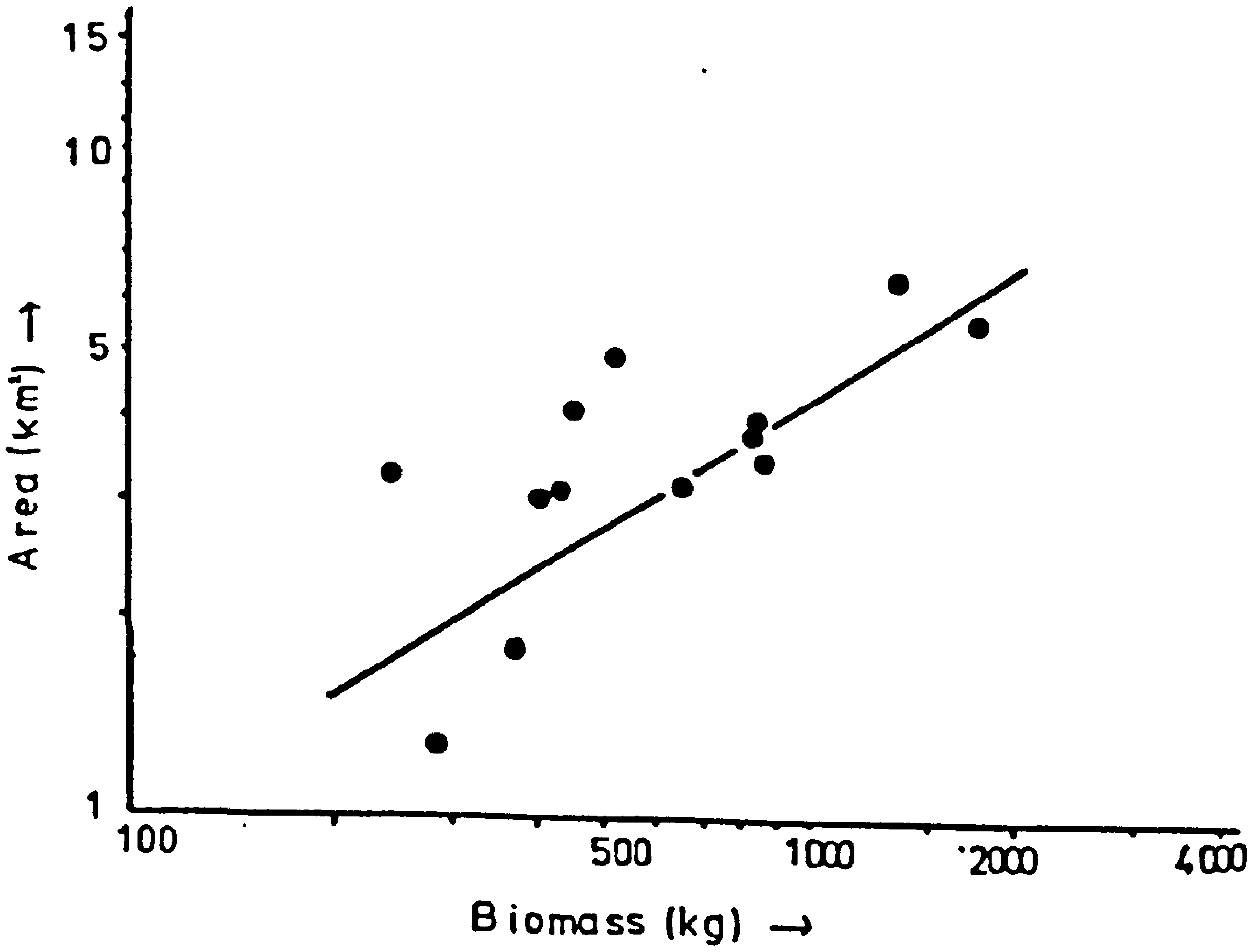
[1] Includes one castrate and two unclassified goats.

[2] Includes one castrate. [3] Biomass based on total weights in autumn/early winter.

Study area	Heft	Kids	Nannies	Ying Billies	2 + 3 yr Billies	4 + yr Billies	Total	Area (km^2)	Density (goats km^{-2})	Biomass[3] (kg)
Moffat Hills	Grey Mares Tail	2	12	1	1	1	17	3.31	5.14	657.8
	Carrifran	3	8	0	1	0	12	3.19	3.76	437.5
	Blackhope	1	9	1	1	1	13	5.00	2.60	515.6
	Capplegill	0	9	0	2	0	11	4.19	2.63	457.3
	Spoon	2	8	0	1	0	11	3.06	3.59	414.2
Langholm–Newcastleton Hills	Roan Fell	3	8	3	2	3	22[1]	3.80	5.79	825.5
	Arkleton	2	10	3	3	3[2]	21	3.50	6.00	871.0
	Taras	5	18	5	5	1	34	6.50	5.23	1313.0
	Roan Fell Flow	11	19	7	5	4	46	5.60	8.21	1858.0
Nether Hindhope	Nanny group	2	17	0	2	0	21	4.00	5.25	837.6
	Billy group	0	0	1	3	1	5	3.25	1.54	241.0
College Valley	Yeavering Bell	1	3	1	0	1	6	1.30	4.62	286.2
	Newton Tors	0	6	0	0	2	8	1.86	4.30	373.0

Figure 5.15

The relationship between the biomass of a goat heft (independent variable, kg) and the heft home range size (dependent variable, km^2). The equation is of the form $y = a + bx$ where y is area, a is y intercept, b is slope and x is biomass.


15
10
5
1
Area (km²) →
100
500
1000
2000
4000
Biomass (kg) →

sex class - Chapter 4), were in small nanny groups; this was in part the result of an increased tendency towards solitariness during kidding in March and April. At this time, the quality of forage is lowest and feral goats in common with hill sheep (Eadie 1970; Chapters 2 and 4) can be expected to be starving and losing weight. Typical group sizes would be expected to be smaller in spring because individuals in large groups would, on average, suffer greater intraspecific competition than when in small groups, especially through feeding interference (Appleby 1980). An alternative strategy would be to increase individual distance, as impala do during the dry season (Jarman & Jarman 1979). Nearest neighbour distances were not measured in the present study and the use of a fixed distance (100 m) to define groups meant that increased dispersion of large groups, if it occurred, might have led to groups of individuals acting as one unit being classified instead as several small groups.

The large groups recorded during autumn were rutting groups. Group sizes during winter were often similar to those in autumn; smaller group sizes may have been expected in the latter compared with the former season because of reduced food availability, but social factors especially rutting may have maintained the cohesion of large groups. Schaller (1967) noted that groups of chital were smaller when water and preferred forage were scarce but that fawning and rutting were also important in determining group size. Crook (1969) reported fluctuations in group size throughout the year similar to those recorded in the present study.

In all ungulate species that have been studied, either temporary or persistent detailed organisation is seen within the environmentally determined grouping. Mother-young associations create temporary detail in the organisation of all societies but they may also last for several years as in African buffalo (Sinclair 1977) and a lifetime in elephants (Douglas-Hamilton 1973). In feral goats, sheep and red deer, three species inhabiting the Scottish Uplands, the duration of association between mother and offspring depends on the sex of the latter, (Jewell et al. 1974; Guinness, Hall & Cockerill 1979). Billies, and in particular older billies, associated least with nannies during the spring. Sexual segregation of goats occurred on Kielderhead Moor (McDougall 1975), on Rhum (Boyd 1981), in Snowdonia (Crook 1969) and in New Zealand (Riney & Caughley 1959). It has also been recorded for feral sheep (Jewell et al. 1974), wild caprinids (Dunbar & Dunbar 1981; Geist 1971; Geist & Petocz 1977; Green 1978; Schaller 1977) and also in the larger cervids and bovids (Mitchell et al. 1977; Sinclair 1977). Some tropical or subtropical populations of feral goats, however, show little sexual segregation (Gould 1979; Yocom 1967).

Two arguments have been put forward to explain the adaptive significance of sexual segregation in polygynous ungulate societies. Firstly by segregation, males reduce the likelihood of attracting predators to the females (because the latter are larger and more conspicuous), and also reduce competition with females for food. It is argued that since the females have probably mated with the segregated males, this strategy maximizes reproductive success of breeding individuals (Geist & Petocz 1977).

Secondly, segregation may occur because of a sex difference in nutritional and environmental requirements. Many ungulates are strongly sexually dimorphic with males being up to several times the weight of females. The males being larger presumably require a greater absolute amount of food despite having a lower metabolic requirement per unit of body tissue. The argument, based on the observations of Bell (1970) and Jarman (1974) and called the Jarman-Bell principle by Geist (1974), predicts therefore, that large billies should feed less selectively than nannies on more abundant but less nutritious forages.

Neither the explanation based on altruism nor that based on physiological differences, has been tested for feral goats. However, as in other polygynous societies, very few of the males are likely to breed so that segregation by the majority of males would seem unnecessary if altruism were the explanation.

It is not necessary for the sexes to use geographically distinct areas to achieve sexual segregation; niche separation may occur at a much finer level as has been demonstrated for sympatric, congeneric primate species (Clutton-Brock 1974). Differences in selection of microhabitats and feeding ecology (e.g. selection of different plant parts) may occur. These require further study.

The use of home range maps to describe the spatial organisation of feral goats was an oversimplification. Range use was markedly heterogeneous and the use of polygons enclosing all sightings should be used only for making gross comparisons between home range sizes. Munton (1975) discussed the shortcomings of estimating areas occupied by feral goats and in particular stressed that the description of areas occupied by groups as opposed to individuals foreclosed important details of spatial organisation.

Fundamentally, as Jewell (1966) noted, the home range is an area having a productivity that meets the energy requirements of the individual or group in occupation. The results of several comparative studies have supported this assertion in respect of small mammals (McNab 1963), primates

(Clutton-Brock & Harvey 1978), birds (Armstrong 1965; Schoener 1968) and mammals in general (Damuth 1981; Harstad & Bunnell 1979). Despite the inaccuracies inherent in calculation of heft home range sizes and their respective biomasses in the present study, the data demonstrated a close relationship between biomass of the heft and the area it occupied in accord with previous studies.

Several authors have described the discreteness of feral goat populations (Boyd 1981; Buckland 1978; Geist 1960; McDougall 1975; Munton 1975; Stevenson-Jones 1977; Yocom 1967). The nature of this social organisation poses two important questions for studies of the behavioural ecology and management of feral goat populations. Firstly, do goats disperse (*sensu* Howard 1960) and if not, why not? Secondly, are goats territorial? Consideration of these topics is given in the final discussion.

FINAL DISCUSSION

Goats occupied a key position in the rural, upland economy until the late 18th century. From this period onwards, however, the preservation of woodlands, a new emphasis on sheep production and, in the Scottish Highlands, the clearances, all combined to eliminate goat husbandry. That the goat remains as a feral animal in upland districts is through a combination of neglect, aesthetic interests, sporting interests and also local traditions (Crook 1969; Greig 1969; Hughes et al. 1973; McNally 1979; Mackenzie 1980; Megaw 1963).

Folklore is an important factor in the conservation and management of feral goat populations in the Southern Uplands; the presence of a few goats on hill farms is believed to benefit the sheep stock. In the deeds of one farm, a clause states that the (feral) goats must never be eradicated on account of their liking for crags. Sheep, tempted by lush herbage on the terraces, would become trapped; the presence of goats was alleged to inhibit the straying of sheep into these areas (C. Tyrell pers. comm.). No attempt was made in the present study to investigate the validity of the various traditions about goats on hill farms. However, from conversations with local people it was clear that attempts to manage feral goat populations must consider their opinions.

On British uplands there is almost no plant growth during the winter or early spring; forage availability decreases over this period to a minimum in March and early April. Primary production is highest in May and June which for many plant species is the time when their dry matter digestibility is also highest. By September production and dry matter digestibility are low (Eadie 1970; Grant & Campbell 1978; Milner & Gwynne 1974; Rawes & Welch 1969). Thus for between three and five months per year, depending on the year, large herbivores may be losing weight.

The strongly seasonal nature of the upland environment shapes the annual cycle of the large herbivores including, therefore, that of feral goats. Most deaths occurred in early spring and the primary cause of death was believed to be starvation. It is generally agreed that, in the absence of predators or where the impact of predators is negligible, the quantity of available forage governs ungulate population size (e.g. Coe, Cumming & Phillipson 1976; Jewell et al. 1974; Phillipson 1975; Sinclair 1977; Taber & Dasmann 1957). The same gross regulatory mechanism was proposed for those feral goat populations described in the present study.

Whilst the quantity of forage may ultimately limit population size, its quality is more important in determining the size, survival and reproductive success of individual ungulates (e.g. Anon 1979; Appleby 1980; Guinness, Albon & Clutton-Brock 1978; Klein 1968). It was considered in the present study that variation between populations in body and horn size were primarily the result of differences in the quality of the range. If this conclusion is accepted, we should expect variations between individuals within populations as a consequence of differential access to resources. Such data were not available in the present study. Hunter (1962) reported that hill ewes in home range groups on a Cheviot hill farm varied in their performance in accordance with variation in the availability of freely drained, nutritious grasslands. He suggested, that since performance was related to the quality of the available forage within the home range, there was little value in selecting lambs as breeding stock without knowledge of their ranging behaviour. Similar logic should be used when managing feral goat populations and an effort made to gauge the relative qualities of home ranges.

Studies of red deer have indicated that an important factor in determining body size is the availability of nutritious food during the first two years of life (Mitchell et al. 1977; Suttie 1980). The faster the growth rate in these years, the larger the skeleton and hence the larger the body size and weight. In the polygynous ungulates such as red deer, sheep and goats, males are invariably larger than females. This sexual dimorphism is believed to be the result of sexual selection and it would therefore seem particularly important for males to grow as fast and as large as possible in order to be successful in reproductive competition (Jewell 1976; Gibson & Guinness 1979; Grubb 1974b). The major constraint on growth is probably food availability. It follows that variation in access to food resources in the first few years of life may profoundly affect the survival and reproductive success of a stag, ram or billy.

Amongst nannies, selection for large body size may not confer advantage. The great energy demand on female mammals of lactation (Sadleir 1969) occurs, for feral nannies, during early spring when forage quality and forage quantity are lowest. Nannies that are significantly larger than the average for a population may be at a disadvantage compared with those that are smaller since the former require a greater amount of energy in order to maintain themselves whilst lactating than the latter. Smaller than average nannies may, however, be selected against because they are less efficient than larger individuals at thermoregulating (Kleiber 1961).

Moors (1980) argued that in the small species of the Mustelidae, all of which are strongly sexually dimorphic, female body size is constrained by the need to feed herself plus her offspring. Females simply could not meet the energy requirements of maintenance and of rearing young if they were of similar size to males. Whilst small mustelids have very high surface : volume ratios compared to those of the sheep and goats, it is possible that the body size of females of the latter tribe is constrained by a similar selection pressure.

Feral goats in Britain are near the northern edge of their range. Furthermore, like red deer (Easterbee 1981; Mitchell et al. 1977) they are perhaps not as hardy as was previously thought. Not only do feral goats have little subcutaneous fat and thin, poorly insulated skins, but also relatively large, highly vascularised horns capable of causing heat loss (Taylor 1966). Goats are reluctant to feed in exposed, wet conditions and the availability of dry shelter, essential for domestic goats (Mackenzie 1980), would also appear to be necessary for feral goats (Boyd 1981; Gould in litt; pers. observ.). Indeed, Mackenzie's remark with reference to the Scottish Highlands that "the feral goat population is very much limited to the number of dry beds available on a wet night" invites scientific study.

For kids, one way of attaining a large enough body size to ensure survival over the first winter is to be born as early in the year as possible. Feral goat neonates, in exhibiting hiding or lying behaviour at a sheltered site, (Lent 1974; Rudge 1970a), minimise their energy loss at a time of year when cold, wet weather is prevalent. Those kids that survive the neonatal period have a long subsequent period in which to grow. For such a strategy to be adaptive, the survival rate of kids born early must, on average, be the same as that of kids born later in the year. Perhaps following winters of average severity this is the case. The hypothesis for feral goats remains to be tested, but has been investigated for small mammals.

Amongst deer mice populations near Vancouver, the breeding season has two peaks, one earlier in the year than the other. The early breeders have on average, a similar reproductive success to those that breed later, but with a higher variability. Fairbairn (1977) suggested that the occasional years when early breeders were highly successful were a sufficient selection pressure for the strategy to remain adaptive. If breeding relatively early in the year at a time when the environment is apparently unfavourable can be selected for, it is pertinent to ask why feral sheep on St Kilda breed approximately two months later than feral goats on the Isle of Rhum at a similar latitude (Buckland 1978; Jewell & Grubb 1974). The feral sheep, which are of similar body size to feral goats, lamb in April just prior to the onset of most plant growth. It may be unnecessary for feral lambs on St Kilda to have a long period in which to attain a large body size before the winter. The lambs are born with a fleece of high insulative value (Doney et al. 1974) and the feral sheep on Hirta minimise their heat loss in winter by sheltering at nights in cleits (drystone shelters). The shelter afforded by cleits is believed to be critical for the survival of the sheep during the winter (Cheyne et al. 1974). It is possible therefore, that owing to the possession of a fleece and the presence of shelter, the selection pressure that favours breeding as early as possible has been relaxed. Bunnell (1980, 1982) showed for wild American sheep that a delay in lambing not only shortens the time for growth but also reduces the resources available for growth.

Another possible factor affecting the breeding season of feral goats and sheep is artificial selection. Goats, as the mainstay of the upland economy, were used primarily as suppliers of milk. Man would have selected for those nannies with long lactation periods (from early spring to the autumn). Sheep, being primarily suppliers of wool and meat rather than milk, would not have been selected for breeding early in the year. Thus although the main proximate cue for caprinids to attain reproductive condition is probably decreasing photoperiod (Asdell 1964; Greig 1969) other factors such as artificial selection and a minimum overwinter body size may be important. Nutrition and population density may also affect reproductive condition (Sadleir 1969).

Domestic and feral sheep and goats can reach sexual maturity at six months of age and will attempt to breed then (Clarke 1976; Greig 1969; Grubb 1974b; Pegler 1929; Rudge 1969). This early sexual maturity is presumably a result of artificial selection by man in order to maximize milk and meat returns from the livestock. The wild ancestors of domestic sheep and goats do not usually breed in their first or second years (Bunnell 1981; Geist 1971; Schaller 1977; Valdez 1976).

Early sexual maturity for rams and billies means that they participate in the rut during their first year, although often unsuccessfully (Grubb 1974b; pers. observ.). These males are not full grown; they increase for at least three years in their body size and for longer in horn size and weight (see Chapter 2). It follows that, compared to older males and females, young males incur the energy demands of not only metabolic requirements for maintenance, increased by lack of feeding and frenetic rutting behaviour but also those of growth. These observations suggest why males have lower survival rates than females (and the origin of the skewed sex ratios) in feral caprinid populations (Boyd 1981; Grubb 1974a; Williams & Rudge 1969; this study). Amongst feral goat populations, in relatively seasonless tropical regions breeding occurs the year round (Gould 1979; Yocom 1967) and the sex ratios are much nearer unity indicating the importance of a well defined, autumnal rutting season in determining the differential survival of the sexes.

The construction of life tables was inappropriate for the population data described in the present study. However, the crude estimates of survival rates together with the few data on fecundity indicated that, generally, less than half of large foeti or neonates survive until the summer. The data also indicated that the survival rate of kids varied substantially with the severity of the winter just prior to their birth. Grubb (1974a) showed that for feral sheep, variation of the survival rates of neonate lambs was much more significant in determining population density than variations in fecundity. Similarly, variations in the survival rate of kids will probably affect the potential rate of increase of feral goat populations.

A notable feature of the spatial organisation of the feral goat populations in the Southern Uplands was the restriction of groups of individuals, (hefts), to well defined areas and the low degree of contact between individuals in neighbouring hefts. Only billies moved between hefts and then primarily at the rut when they were presumably seeking nannies in oestrus.

Several other feral goat populations have been found to be spatially organised into units, with billies wandering between units before or during the rut (Boyd 1981; Crook 1969; McDougall 1975; Munton 1975; Yocom 1967). My own observations and those reported in the literature indicate that dispersal from these populations rarely, if ever, occurs. Many of the ranges of the feral goat populations in the Southern Uplands are adjacent to tracts of forestry plantations affording food and shelter. Both roe deer and red deer have successfully colonized a large number of these plantations (Loudon 1982; Mitchell et al. 1977 & pers. comm.) but not goats. Marauding by feral goats within forestry plantations is sporadic and easily controlled compared to the sustained and much less easily prevented damage wrought by deer.

The apparent lack of an ability by goats to spread into adjacent areas may have several components. Firstly, from the earliest days of their domestication, the most intractable and exploratory individuals would have been selected against by being culled; traits for fidelity would have been proportionately increased. Secondly, feral goats may be unwilling to cross unfavourable habitat even although favourable habitat is within sight. This appears to be the reason why bighorn sheep and ibex are slow to colonise new, apparently favourable habitat (Geist 1971; Nievergelt 1966). As has been argued earlier, an important component of the niche of feral goats is shelter. The apparent lack of dispersal of feral goats could be associated with an unwillingness to occupy environments which have less topographical shelter and refuges of steep, rocky ground than that which they already occupy.

If animals live in environments where limiting resources are predictable in space and time and, in energy terms, the resources are economically defendable, we should expect natural selection to favour the evolution of territoriality (Brown 1975; Wilson 1975). Geist (1974) using this argument stated that northern ungulates, rutting in the autumn and subjected to an unpredictable food supply (the limiting resource) over the annual cycle, could not be expected to exhibit territoriality. However, as I have stressed, one important resource for large herbivores on uplands is shelter. As a resource, topographical shelter is predictable in space and time. Within the group home ranges of feral goats and feral sheep are monopolized zones (Jewell 1966) which, at least in feral sheep, may be overtly defended (Grubb & Jewell 1974). Such observations are lacking for feral goats but it is noted that the latter are behaviourally suited to exhibit territoriality. Not only are they highly vocal (Price & Thos 1980) but they frequently horn thrash vegetation leaving a potent odour on the broken plants. These two behaviours could serve in advertising monopoly of an area as occurs in other ungulates such as roe deer (Loudon 1979), black-tailed deer (Müller-Schwarze 1971) and in some rupricaprinid species such as goral and serow (Schaller 1977).

There has been a tendency to consider behavioural studies as unimportant luxuries in comparison with management-orientated ecological studies (Jarman & Jarman 1979). In no ungulate has the lack of behavioural studies and their integration with management been more acute than feral goats; even ecological studies are lacking (see Introduction) and management of their populations is often unsuccessful.

The results of the present study have indicated that movements of goats between the areas occupied by hefts, undertaken by billies, cannot be prevented by fencing. Fencing of hill ground on goat range and the subsequent planting of the fenced area, as will occur on Cairnsmore of Fleet within the next decade, can only invite marauding as it does for red deer (Mitchell et al. 1977). Furthermore, prevention of the movements of billies by culling or other means will tend to isolate hefts, effectively creating demes. This may increase inbreeding, giving rise to a decrease in the viability of kids as has been demonstrated for other small population of ungulates (Ralls et al. 1979) and baboon troops (Packer 1979) that are normally outbred.

Prior to harvesting from feral goat populations, their social organisation and range relationships with other herbivores must be considered. Since goat hefts are frequently discrete units, a few individuals should be harvested from each area rather than the removal of all from one area. Feral goat populations in the Southern Uplands are usually sympatric with those of hill sheep and the two species appear to be in a dynamic, competitive equilibrium. Total removal of goats from one area may allow sheep to increase their density and expand their range of habitats used and thus prevent recolonisation of the area by goats of neighbouring hefts. More information on the range relationships between feral goats and hill sheep is required. The Cairnsmore of Fleet National Nature Reserve is well suited for experimental manipulation of sheep and goat populations; the Nature Conservancy Council should initiate studies of range relationships between the two species with a view to their commercial exploitation.

Feral goat populations are more often controlled or eradicated than harvested. For instance, the Forestry Commission (F.C.) have eradicated 11 out of 19 populations or herds within state owned land during their planting programmes (from Whitehead 1972) in order to prevent damage to trees. The F.C. continue to cull goats when they enter plantations although there is as yet no documented evidence that goats do economic damage to trees and if they do so, that it is significant when compared with that done by deer. The current F.C. goat control policy of discrete shooting is not preventative and results in wastage of biological material that could be used to develop sound management policies. Forest rangers should be encouraged to capture goats and either harvest them for meat and skins or return them, ear tagged with age and sex noted, to the open hill. Persistent marauders, identified by ear tags, could be shot and their condition determined.

As feral goat society is polygynous, effective reduction in population size calls for reduction in the number of breeding nannies rather than billies. Yet in both areas in the Southern Uplands where heavy culling is practised, College Valley and Craigdews, billies are culled preferentially in accordance with inappropriate principles of sheep husbandry whereby 'surplus' males are removed.

Several populations of feral goats in the Southern Uplands and elsewhere are considered to be relatively pure descendants of the British breed (Greig 1969; Fowler in litt; Rudge 1982; Werner 1977). It is possible that, given the uneconomic nature of hill sheep farming these goats could become valuable for crossbreeding (Greig & Cooper 1970; Kirkton, Paterson, Hamilton & Mackereth 1976) and in mixed livestock grazing regimes. Colquhoun (1971), in reviewing the literature on competition between sympatric large herbivores concluded that mixed livestock grazing was more efficient in terms of production than single species grazing; this was believed to be because of niche separation between the herbivore species, each exploiting rather different habitats and diets.

Kiley (1974) and Cooper (1979) noted the potential for establishing mixed species communities of large herbivores on British uplands. Government backed institutions such as the Nature Conservancy Council, the Forestry Commission and the Hill Farming Research Organisation should be encouraged to experiment with and analyse the costs and benefits of grazing systems on uplands involving goats, sheep, red deer, cattle and ponies. Such systems are likely to be less damaging to their environment than single species system such as hill sheep farming (Colquhoun 1971). This is particularly important at a time when upland areas are threatened by tourism, poor grazing management and bad muirburn practice (Lance 1978; McVean & Lockie 1969).

Feral goats of the British breed are a useful source of reference material for the archaeologist. The inability of the latter to separate bones of sheep and goats and to classify individuals according to age and sex in many deposits has hampered our understanding of the significance of many discoveries. Skeletal material from feral goats has shown promise as reference material for the archaeologist (Bullock & Rackham in press; Noddle 1974), and further investigations are in progress.

There are few large wild (or feral) animals on British uplands; feral goats are with the reservations discussed, a benign addition to the fauna providing pleasure to the public and possibly benefit to the sheep farmer. It is significant that the weight of public opinion has thus far prevented the Forestry Commission and other forestry groups from eradicating goats in south-western and western Scotland. Recently, the F.C. have shown signs of a desire to manage feral goat populations constructively on or adjacent to their land. For the reasons discussed, this policy must be encouraged.

SUMMARY

1. A study of the biometrics, feeding ecology, population ecology and social and spatial organisation of feral goats in the Southern Uplands of Scotland was conducted between 1977 and 1980.

2. Goats have been feral in the south of Scotland and northern England since at least the 16th century although most populations are believed to have been established between one and two hundred years ago. The majority of the goats show characteristics of the British or Old English, (Scottish, Irish) breed which is now extinct in domestication.

3. Seven populations were surveyed. From west to east these were: Craigdews Wild Goat Park, Cairnsmore of Fleet, Moffat Hills, Langholm-Newcastleton Hills, Kielderhead Moor, Nether Hindhope and College Valley.

4. Weights and growth rates of live captured goats showed increasing sexual dimorphism with age; billies weighed up to 0.5 times more than nannies of the same age. Age and sex specific growth data for goats in seven populations are described. There were significant differences in weight, horn length and body size between some populations. In general, goats from the Cheviot Hills (eastern Southern Uplands) were significantly larger and heavier than those from the Galloway Hills (western Southern Uplands) with those from the Moffat Hills (central Southern Uplands) being intermediate in size. This variation was correlated with variation in soil fertility as judged by

the parent rock although other factors such as population density may also have been involved.

5. The feeding behaviour of billies, nannies and ewes was compared. In general, ewes fed for more of the day than nannies, and nannies more than billies. The latter fed for markedly less of the day during the autumn when they were rutting than during the remainder of the year. The feeding activity patterns of sheep and goats were similar in having a major rest period around the middle of the day and feeding bouts in the early morning and late afternoon.

6. Quantification of habitat use by sheep and goats showed that the former selected freely drained grasslands to a greater degree than the latter, while goats selected dwarf shrub communities and soligenous mires more strongly than did sheep. Goats were observed most frequently at elevations of between 300m and 600m; casual observations of sheep suggested that they were using a wider range of altitudes.

7. Using faecal analysis, the diets of sheep and goats were compared for three study areas where they were sympatric: Cairnsmore of Fleet, Langholm-Newcastleton Hills and Nether Hindhope. Both herbivores showed a similar pattern of use of plant groups at different seasons. In summer, when abundant fresh forage is available, grasses, rushes, sedges and other monocotyledons were preferred. In winter, dwarf shrubs became more important in the diet. Dietary overlap was greatest on Cairnsmore of Fleet and least at Nether Hindhope where sheep were predominantly grazers and goats utilised conifers, rushes and ferns according to the season. The ingestion of ferns by

large herbivores is discussed.

8. Estimates of age-specific fecundity, censuses and examination of carcases were used to calculate survival rates and determine the causes of death. Perinatal survival rates were estimated to be less than 50%. Survival rates of kids after the neonatal period varied with the year, population and sex of the kid. In general billy kids survived less well than nanny kids. Adult billies similarly survived less well than adult nannies, resulting cumulatively in the highly disparate sex ratios in favour of females. Median ages at death for billies and nannies that had survived their first summer were 3.25 yr and 6.25 yr respectively based on data from several populations. Most billies died in the spring and in a state of malnutrition suggesting that they had starved. Nannies tended to die later in the spring than billies. Possible reasons for the sex differential in survival are discussed.

The number of kids counted in spring varied with the population and, apparently, with the severity of the preceding winter. Kid production was always lower than lamb production on the same range and was more variable.

9. A preliminary study of the social and spatial organisation of feral goats revealed the following. Group size showed an annual fluctuation; it was smallest in the spring and largest in the summer, autumn or winter depending on the population. Group size at least in summer was also related to population size. In general, the size of mixed groups was larger than those of nanny or billy groups. There were always some billies associated with nannies and complete, geographical sexual segregation did

not occur. Older billies, however, tended to associate less with nannies than younger billies; possible reasons for this are discussed.

Goats were spatially organised into hefts in which individuals had highly overlapping home ranges. Overlap between the home ranges of individuals in neighbouring hefts was much less. Nannies rarely, if ever, moved between heft home ranges but billies did so, especially around the rut, in autumn. The biomass of a goat heft was found to increase significantly with the area that the heft occupied.

10. The ecology of feral goats was discussed in relation to studies of other Bovidae. Also, the integration of ecological studies with management of feral goat populations has been considered. It is argued that feral goats are a valuable resource but that management to date has been inappropriate and often unsuccessful. Suggestions for better management and future research are made.

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APPENDIX 1.

VERNACULAR AND SCIENTIFIC NAMES OF ANIMAL SPECIES MENTIONED IN THE TEXT.

African buffalo	*Syncerus caffer*
African elephant	*Loxodonta africana*
Baboon	*Papio anubis*
Bharal	*Pseudois nayaur*
Bighorn sheep	*Ovis canadensis*
Black-tailed (mule) deer	*Odocoileus hemionus*
Cattle (domestic)	*Bos* (domestic)
Chital	*Axis axis*
Crow	*Corvus corone*
Dall sheep	*Ovis dalli*
Deer mouse	*Peromyscus maniculatus*
Dik dik	*Madoqua kirki*
Eagle	*Aquila chrysaetos*
Fox	*Vulpes vulpes*
Goat (domestic or feral)	*Capra* (domestic)
Goral	*Nemorhaedus goral*
Ibex	*Capra ibex*
Impala	*Aepyceros melampus*
Markhor	*Capra falconeri*
Mountain goat	*Oreamnos americanus*
Pony (horse)	*Equus* (domestic)
Raven	*Corvus corax*
Reindeer	*Rangifer tarandus*
Red deer	*Cervus elaphus*
Roe deer	*Capreolus capreolus*
Red grouse	*Lagopus lagopus*
Serow	*Capricornis crispus*
Sheep (domestic or feral)	*Ovis* (domestic)
Himalayan tahr	*Hemitragus jemlahicus*
Thompson's gazelle	*Gazella thompsonii*
White-tailed deer	*Odocoileus virginianus*
Wild cat	*Felis silvestris*
Wild goat	*Capra aegragus*
Wisent	*Bison bonasus*

APPENDIX 2.

ONE WAY ANALYSIS OF VARIANCE TABLES FOR COMPARISONS WITHIN AND BETWEEN POPULATIONS OF BODY AND HORN SIZE.

1. Total weight (a) Nannies

Age (yr)

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	67.94	22.65	1.14	(NS)
SS_{WITH}	31	615.45	19.85		
SS_{TOTAL}	34	683.39			

1

S_{var}	df	SS	MS	F	
SS_{BET}	3	274.59	91.53	14.46	$p<0.01$
SS_{WITH}	15	95.02	6.33		
SS_{TOTAL}	18	369.61			

2

S_{var}	df	SS	MS	F	
SS_{BET}	2	235.93	117.97	6.24	$p<0.05$
SS_{WITH}	11	207.97	18.91		
SS_{TOTAL}	13	443.8			

3

S_{var}	df	SS	MS	F	
SS_{BET}	3	168.47	56.16	6.59	$p<0.01$
SS_{WITH}	12	102.26	8.52		
SS_{TOTAL}	15	270.73			

APPENDIX 2. (continued)

Age (yr)

4

S_{var}	df	SS	MS	F	
SS_{BET}	2	94.56	47.13	1.94	(NS)
SS_{WITH}	11	267.15	24.29		
SS_{TOTAL}	13	361.71			

5

S_{var}	df	SS	MS	F	
SS_{BET}	3	68.15	22.72	1.21	(NS)
SS_{WITH}	10	188.18	18.82		
SS_{TOTAL}	13	256.33			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	3	625.22	208.41	9.21	$p<0.01$
SS_{WITH}	36	814.27	22.62		
SS_{TOTAL}	39	1439.49			

(b) Billies

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	192.03	64.01	10.24	$p<0.01$
SS_{WITH}	31	193.87	6.25		
SS_{TOTAL}	34	385.9			

1 –

APPENDIX 2. (continued)

Age (yr)

2

S_{var}	df	SS	MS	F	
SS_{BET}	3	128.55	42.85	0.66	(NS)
SS_{WITH}	8	520.37	65.05		
SS_{TOTAL}	11	648.92			

2. Heart girth (a) Nannies

Age (yr)

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	108.43	36.14	1.18	(NS)
SS_{WITH}	26	796.77	30.65		
SS_{TOTAL}	29	905.20			

1

S_{var}	df	SS	MS	F	
SS_{BET}	3	983.11	327.7	12.13	$p<0.01$
SS_{WITH}	10	270.09	27.01		
SS_{TOTAL}	13	1253.2			

2

S_{var}	df	SS	MS	F	
SS_{BET}	2	405.93	202.97	8.05	$p<0.01$
SS_{WITH}	11	277.50	25.23		
SS_{TOTAL}	13	683.43			

APPENDIX 2. (continued)

Age (yr)

3

S_{var}	df	SS	MS	F	
SS_{BET}	2	714.55	357.27	6.52	$p<0.05$
SS_{WITH}	11	602.66	54.79		
SS_{TOTAL}	13	1317.21			

4

S_{var}	df	SS	MS	F	
SS_{BET}	2	119.41	59.71	1.06	(NS)
SS_{WITH}	8	449.50	56.19		
SS_{TOTAL}	10	568.91			

5

S_{var}	df	SS	MS	F	
SS_{BET}	3	494.75	164.92	3.79	(NS)
SS_{WITH}	9	391.25	43.47		
SS_{TOTAL}	12	886.00			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	3	550.44	183.47	4.89	$p<0.01$
SS_{WITH}	32	1201.56	37.55		
SS_{TOTAL}	35	1752.00			

(b) Billies

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	408.90	136.30	7.18	$p<0.001$
SS_{WITH}	30	569.22	18.97		
SS_{TOTAL}	33	978.18			

APPENDIX 2. (continued)

Age (yr)

1 -

2

S_{var}	df	SS	MS	F	
SS_{BET}	2	0.23	0.12	0.00	(NS)
SS_{WITH}	7	312.67	44.67		
SS_{TOTAL}	9	312.90			

3

S_{var}	df	SS	MS	F	
SS_{BET}	1	7.5	7.5	0.02	(NS)
SS_{WITH}	3	1057.9	352.63		
SS_{TOTAL}	4	1065.4			

4 -

5 -

6+

S_{var}	df	SS	MS	F	
SS_{BET}	1	42.25	42.25	13.0	(NS)
SS_{WITH}	2	6.5	3.25		
SS_{TOTAL}	3	48.75			

APPENDIX 2. (continued)

3. Body length (a) Nannies

Age (yr)

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	159.86	53.29	1.70	(NS)
SS_{WITH}	26	813.10	31.27		
SS_{TOTAL}	29	972.97			

1

S_{var}	df	SS	MS	F	
SS_{BET}	3	292.80	97.60	5.51	$p<0.05$
SS_{WITH}	10	177.20	17.72		
SS_{TOTAL}	13	470.00			

2

S_{var}	df	SS	MS	F	
SS_{BET}	2	263.93	131.96	4.13	$p<0.05$
SS_{WITH}	11	351.50	31.96		
SS_{TOTAL}	13	615.43			

3

S_{var}	df	SS	MS	F	
SS_{BET}	2	85.33	42.67	1.59	(NS)
SS_{WITH}	11	294.67	26.79		
SS_{TOTAL}	13	380.00			

4

S_{var}	df	SS	MS	F	
SS_{BET}	2	217.44	108.72	3.71	(NS)
SS_{WITH}	8	234.75	29.34		
SS_{TOTAL}	10	452.19			

APPENDIX 2. (continued)

Age (yr)

5

S_{var}	df	SS	MS	F	
SS_{BET}	3	32.69	10.90	0.29	(NS)
SS_{WITH}	9	336.55	37.39		
SS_{TOTAL}	12	369.24			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	3	937.34	312.45	7.45	$p<0.001$
SS_{WITH}	32	1342.30	41.95		
SS_{TOTAL}	35	2279.64			

(b) Billies

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	259.83	86.61	3.61	(NS)
SS_{WITH}	30	719.15	23.97		
SS_{TOTAL}	33	978.98			

1

-

2

S_{var}	df	SS	MS	F	
SS_{BET}	2	46.30	23.15	0.54	(NS)
SS_{WITH}	7	301.30	43.04		
SS_{TOTAL}	9	347.60			

APPENDIX 2. (continued)

4. Shoulder height (a) Nannies

Age (yr)

0

S_{var}	df	SS	MS	F	
SS_{BET}	3	118.74	39.58	2.31	(NS)
SS_{WITH}	46	789.28	17.16		
SS_{TOTAL}	49	908.02			

1

S_{var}	df	SS	MS	F	
SS_{BET}	4	1536.70	348.18	2.99	$p<0.05$
SS_{WITH}	18	2312.95	128.50		
SS_{TOTAL}	22	3849.65			

2

S_{var}	df	SS	MS	F	
SS_{BET}	3	216.54	72.18	4.82	$p<0.05$
SS_{WITH}	17	253.75	14.93		
SS_{TOTAL}	20	470.29			

3

S_{var}	df	SS	MS	F	
SS_{BET}	3	178.90	59.63	2.77	(NS)
SS_{WITH}	13	280.04	21.54		
SS_{TOTAL}	16	458.94			

4

S_{var}	df	SS	MS	F	
SS_{BET}	3	144.20	48.07	8.04	$p<0.01$
SS_{WITH}	13	77.80	5.98		
SS_{TOTAL}	16	222.00			

APPENDIX 2. (continued)

Age (yr)

5

S_{var}	df	SS	MS	F	
SS_{BET}	3	233.17	77.72	7.27	$p < 0.001$
SS_{WITH}	17	181.78	10.69		
SS_{TOTAL}	20	414.95			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	5	614.20	122.84	7.32	$p < 0.001$
SS_{WITH}	55	923.48	16.79		
SS_{TOTAL}	60	1537.68			

(b) Billies

0

S_{var}	df	SS	MS	F	
SS_{BET}	4	154.90	38.73	3.20	$p < 0.05$
SS_{WITH}	45	545.10	12.11		
SS_{TOTAL}	50	700.00			

1

S_{var}	df	SS	MS	F	
SS_{BET}	2	8.33	4.17	0.08	(NS)
SS_{WITH}	3	149.00	49.67		
SS_{TOTAL}	5	157.33			

2

S_{var}	df	SS	MS	F	
SS_{BET}	4	15.67	3.92	0.10	(NS)
SS_{WITH}	12	469.39	39.12		
SS_{TOTAL}	16	485.06			

APPENDIX 2. (continued)

Age (yr)

3

S_{var}	df	SS	MS	F	
SS_{BET}	3	76.83	25.61	3.92	(NS)
SS_{WITH}	6	39.17	6.53		
SS_{TOTAL}	9	115.90			

4 -

5

S_{var}	df	SS	MS	F	
SS_{BET}	2	76.00	38.00	6.52	(NS)
SS_{WITH}	3	17.50	5.83		
SS_{TOTAL}	5	93.50			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	2	64.19	32.10	1.39	(NS)
SS_{WITH}	4	92.67	23.17		
SS_{TOTAL}	6	156.86			

5. Horn length (a) Nannies

Age (yr)

0

S_{var}	df	SS	MS	F	
SS_{BET}	6	270408.04	45068.00	23.01	$p<0.001$
SS_{WITH}	53	103789.02	1958.28		
SS_{TOTAL}	59	374197.06			

APPENDIX 2. (continued)

Age (yr)

1

S_{var}	df	SS	MS	F	
SS_{BET}	5	19411.73	3882.34	10.89	$p<0.01$
SS_{WITH}	18	6414.77	356.37		
SS_{TOTAL}	23	25826.50			

2

S_{var}	df	SS	MS	F	
SS_{BET}	3	18455.56	6151.85	12.05	$p<0.01$
SS_{WITH}	18	9188.26	510.45		
SS_{TOTAL}	21	27643.2			

3

S_{var}	df	SS	MS	F	
SS_{BET}	3	6681.19	2227.06	2.91	(NS)
SS_{WITH}	12	9155.75	762.97		
SS_{TOTAL}	15	15836.94			

4

S_{var}	df	SS	MS	F	
SS_{BET}	3	12537.45	4179.15	2.07	(NS)
SS_{WITH}	13	26151.61	2011.66		
SS_{TOTAL}	16	38689.06			

5

S_{var}	df	SS	MS	F	
SS_{BET}	3	19819.28	6606.42	3.60	(NS)
SS_{WITH}	16	29353.92	1834.62		
SS_{TOTAL}	19	49173.2			

APPENDIX 2. (continued)

Age (yr)

6+

S_{var}	df	SS	MS	F	
SS_{BET}	5	122694.04	24538.80	13.24	$p<0.01$
SS_{WITH}	60	111197.06	1853.28		
SS_{TOTAL}	65	233891.1			

(b) Billies

0

S_{var}	df	SS	MS	F	
SS_{BET}	5	15080.53	3016.10	5.20	$p<0.01$
SS_{WITH}	50	28961.60	579.23		
SS_{TOTAL}	55	44042.13			

1

S_{var}	df	SS	MS	F	
SS_{BET}	3	31071.15	10357.05	7.20	$p<0.01$
SS_{WITH}	12	17252.60	1437.71		
SS_{TOTAL}	15	48323.75			

2

S_{var}	df	SS	MS	F	
SS_{BET}	5	37578.09	7515.61	2.18	(NS)
SS_{WITH}	14	48128.71	3437.76		
SS_{TOTAL}	19	85706.8			

3

S_{var}	df	SS	MS	F	
SS_{BET}	4	18796.16	4699.04	3.41	(NS)
SS_{WITH}	7	9633.84	1376.26		
SS_{TOTAL}	11	28430.00			

APPENDIX 2. (continued)

Age (yr)

4 -

5

S_{var}	df	SS	MS	F	
SS_{BET}	2	3426.34	1713.17	0.22	(NS)
SS_{WITH}	3	22837.00	7612.33		
SS_{TOTAL}	5	26263.34			

6+

S_{var}	df	SS	MS	F	
SS_{BET}	3	11954.83	3984.94	1.99	(NS)
SS_{WITH}	5	9969.17	1993.83		
SS_{TOTAL}	8	21924.00			

APPENDIX 3.

AREAS OCCUPIED BY VEGETATION TYPES IN THE STUDY AREAS.

Areas were calculated using internal squares from large scale vegetation maps prepared by the Nature Conservancy Council (1975, 1976 and 1978).

	Area (ha)		
Vegetation type	Cairnsmore of Fleet	Moffat Hills	Langholm-Newcastleton Hills
Dry/Moist heath	109	737	1098
Wet heath/Blanket mire	382	508	4146
Soligenous mire	95	0	0
Molinia grassland	0	80	1138
Nardus grassland	0	94	320
Freely drained grassland	12	998	1075
Scree/Fern	0	38	0
Totals	598	2455	7777

APPENDIX 4.

APPRAISAL OF THE USE OF FAECAL ANALYSIS TO ESTIMATE DIET.

The diet of free ranging upland herbivores can be estimated using five methods as reviewed by Van Dyne (1968) and Mitchell, Staines and Welch (1977). These are ruminal analysis, faecal analysis, direction observation, indirect observation (such as the use of spoor or feeding signs), and measurements of the loss of plant material due to feeding.

There are limitations to the use of all these methods; the results of ruminal and faecal analyses are affected principally by differential digestion of plant species and differential rates of passage of foodstuffs i.e. different retention times, indices of the times undigested food particles spend in the gut, also called throughput times (Stewart 1967). Direct observations of animals feeding amongst hill vegetation are difficult and biased towards recording the more easily recognisable species. The results of indirect observations and measurements of the loss of vegetation due to feeding are complicated by the presence of more than one herbivore species; also, indirect observations are restricted to certain weather conditions e.g. tracking in snow, and measurements of eaten vegetation may not be reliable since grazed plants perform differently to ungrazed ones (Mitchell et al. 1977).

Since there were always at least two large herbivore species on the study areas and direct observation or destructive sampling was not possible, the only appropriate method of estimating diet was by analysis of faeces (Colquohoun 1971; Vavra, Rice and Hansen 1978).

It is pertinent to ask whether the diets of sheep and goats can be validly compared using faecal analysis since the method assumes that their digestive physiologies are the same. An indication of rumen function in sheep and goats can be obtained by comparing retention times. Milne and Bagley (1976) reported mean retention times for grassin hill sheep of between 40.0 h and 47.3 h depending on the intake of Calluna. For another experiment Milne, Macrae, Spence and Wilson (1978) reported mean values of between 55.9 h and 45.1 h for hill sheep fed forage from an Agrostis-Festuca sward and between 56.2 h and 67.3 h when fed Calluna; in the same experiment, the corresponding values for red deer were 27.4 h to 32.5 h and 37.7 h to 42.4 h. The mean retention times of dyed hay particles fed to goats on a diet of hay and pellets were between 32.2 h and 44.8 h (Castle 1956).

Thus there were no consistent differences between the mean retention times of sheep and goats and although those of sheep in the second experiment of Milne et al. (1976) were higher, the digestibility of Agrostis-Festuca sward was probably lower than that of hay and would account for the longer retention time of the former. As a working hypothesis it was assumed that rumen function in sheep was at least as similar to that in goats as that of the former species and red deer, and that their diets could be validly compared using faecal analysis.

APPENDIX 5.

DETAILED METHODOLOGY OF FAECAL ANALYSIS.

Sampling methods were described in Chapter 3. For faecal, plant reference and ruminal material the same method was used.

Material was slowly dried on a hot plate and ground in a Culatti electric mill fitted with a sieve of 1 mm aperture size. Grinding reduced variation in fragment size permitting comparisons of different samples, and also made plant reference fragments of similar size to those of faecal or ruminal fragments thus aiding identification. Ground fragments were cleared of pigments and cell contents using domestic bleach (8% available chlorine content); I tested the clearing ability of several dilutions of bleach and also Hertwig's solution (500 g chloral hydrate, 300 ml water, 110 ml glycerol and 36 ml conc. HCl). In the latter experiment, fragments were steeped in the solution for 12 h at 75°C within a fume cupboard. Most fragments were clear at one sixth bleach dilution without being so transparent that identification was hindered and this dilution was adhered to throughout the analyses.

Bleached material was thoroughly washed over a fine mesh sieve (no. 120, aperture size 125µ) through which only very small unidentifiable fragments could pass and permanently mounted on slides with Hoyer's medium (200 g chloral hydrate, 30 g gum acacia (arabic), 50 ml water and 20 ml glycerol) using 22 mm x 40 mm coverslips. For each month, two pellets or the equivalent volume were subsampled from each cluster and the dried, composite sample ground. Subsampling did not alter the validity of the analyses; comparison of the botanical composition of four pairs of pellets each from the same cluster showed no significant differences and subsampling greatly reduced preparation time. For ruminal samples, between 250 ml and 500 ml (mean dry weight 27.0 g, SE = 2.4), of thoroughly mixed ruminal liquor were analysed.

Plant fragments were identified by memorising and cross checking epidermal features using the reference collection. The features used in identification have been published frequently (e.g. Hercus 1966; Martin 1955; Milner and Gwynne 1974) and detailed descriptions are not presented here. Briefly, the size and shape of the epidermal cells, the frequency and distribution of silicose bodies, suberin bodies and stomata were used. Analyses were performed at 100x magnification using a binocular microscope. A second microscope was used to check identifications. For faecal analyses, the first 25 fragments on each of six slides were recorded; for ruminal and rectal faeces analyses, the first 50 identified fragments on each of three slides were recorded making totals of about 150 fragments per sample in all analyses.

Fragments were counted in systematic sweeps across a slide using alternate rows in order to avoid duplication. Systematic sampling was less laborious than random sampling and when these methods were compared in two trials using the Poisson distribution, there were no significant differences ($\chi^2_3 = 1.8079$ and $\chi^2_2 = 0.8047$) indicating that systematic sampling was also at random.

In order to eliminate bias due to the examination of series of slides from the same composite sample, all slides were mixed and labelled with a code unknown to myself. In this way, recording of the botanical composition of a slide was not influenced by that of the previous one. Counts were transferred to checksheets for totalling, calculating frequency of occurrence and comparing months, herbivore species and study areas. I followed Stewart (1967) in his conclusions from experimental faecal analyses of large African herbivores that, given the limitations of the technique, the most satisfactory way of presenting the results is by frequency of occurrence.

APPENDIX 6.

THE FREQUENCY OF OCCURRENCE OF FRAGMENTS OF PLANT SPECIES/GROUPS IN FAECES OF FERAL GOATS AND HILL SHEEP.

1. Cairnsmore of Fleet (a) Goat

Year	1978										1979	
Month[1]	F	M	A	My	J	Jy	A	S	O	N	Ja	M
Mosses	0	1	4	7	0	1	0	0	1	2	1	6
Ferns	0	0	1	1	4	0	4	1	3	0	1	1
Herbs	1	0	2	1	4	5	1	0	0	0	1	0
Calluna	24	46	43	28	17	18	19	59	46	23	43	45
Empetrum	0	1	0	0	0	0	0	0	0	0	0	0
Erica	9	0	17	9	1	0	1	0	7	10	1	6
Vaccinium	0	0	2	1	0	0	0	0	0	0	0	0
Myrica	46	12	5	0	1	3	1	1	5	39	23	13
Juncus spp.	1	3	7	12	18	8	2	8	4	7	4	6
J. squarrosus	9	11	1	0	1	0	0	0	1	1	19	3
Narthecium	0	0	0	0	0	0	0	0	0	0	0	0
Luzula	0	0	1	1	0	0	0	0	0	0	0	0
Eriophorum	0	0	4	3	0	0	2	0	2	0	0	1
Trichophorum	0	0	0	12	21	36	53	4	6	0	0	1
Carex	5	16	3	5	4	3	1	0	4	6	3	3
Molinia	3	2	0	20	30	19	15	26	1	1	0	2
Nardus	1	3	1	2	0	1	1	0	6	5	2	6
Agrostis	0	0	1	0	0	1	1	0	4	0	0	0
Anthoxanthum	0	0	0	0	1	0	0	0	0	1	0	0
Holcus	0	0	0	0	0	0	0	0	1	0	1	0
Deschampsia flexuosa	1	1	1	0	0	1	0	0	4	1	0	0
D. caespitosa	0	1	0	0	0	0	0	0	0	0	0	0
Poa	0	2	0	0	0	1	0	1	2	1	0	1
Festuca	1	2	7	1	0	2	0	0	6	2	1	5
Lolium	0	0	0	0	0	0	0	0	0	0	0	0
No. fragments	152	148	146	153	171	152	176	155	160	175	171	158

[1] No faeces were collected in December 1978 or February 1979.

APPENDIX 6. (continued)

1. Cairnsmore of Fleet (b) Sheep

Year	1978										1979	
Month[1]	F	M	A	My	J	Jy	A	S	O	N	Ja	M
Mosses	4	2	7	6	0	1	1	2	1	3	1	8
Ferns	2	0	3	1	1	0	0	0	0	1	0	1
Herbs	2	1	1	1	0	0	0	0	0	0	1	2
Calluna	33	48	32	22	4	10	14	40	49	53	57	60
Empetrum	0	0	0	0	0	0	0	0	0	0	0	0
Erica	11	10	10	5	1	0	1	0	4	6	17	7
Vaccinium	1	1	2	1	0	0	0	0	1	0	0	0
Myrica	17	7	2	2	0	0	0	0	0	5	1	1
Juncus spp.	0	4	12	33	10	1	6	1	2	0	1	2
J. squarrosus	11	0	5	0	0	0	0	0	0	0	4	0
Narthecium	0	1	0	1	0	1	0	0	0	0	0	0
Luzula	0	0	0	0	0	1	0	0	0	0	0	0
Eriophorum	1	2	2	1	0	0	1	0	1	0	0	0
Trichophorum	0	0	2	8	20	46	16	34	12	1	2	1
Carex	2	4	8	4	5	4	2	3	2	0	1	4
Molinia	3	2	1	7	46	13	46	17	1	5	3	2
Nardus	4	9	5	1	5	0	4	1	15	7	2	5
Agrostis	2	1	1	0	1	4	1	0	3	5	2	1
Anthoxanthum	0	0	0	0	1	0	0	0	0	0	0	0
Holcus	0	1	0	0	0	1	0	0	0	0	0	0
Deschampsia flexuosa	1	1	3	1	1	2	4	1	2	1	0	0
D. caespitosa	0	1	0	0	2	1	0	0	0	1	1	0
Poa	0	1	0	0	2	4	2	0	1	1	0	0
Festuca	7	6	6	1	1	10	3	1	8	12	7	7
Lolium	1	0	0	0	0	0	0	0	0	0	0	0
No. fragments	150	160	165	166	164	156	161	158	177	167	165	167

[1] No faeces were collected in December 1978 or February 1979.

APPENDIX 6. (continued)

2. Langholm-Newcastleton Hills (a) Goat

Year	1978							1979
Month[1]	My	J	Jy	A	S	O	N	Ja
Mosses	21	4	0	0	5	1	3	17
Ferns	0	1	7	8	5	24	2	0
Conifers	0	0	0	0	0	0	1	0
Herbs	0	0	0	2	0	0	1	2
Calluna	6	5	14	11	29	47	57	20
Erica	0	1	0	1	0	0	3	0
Vaccinium	9	1	6	2	5	2	1	5
Juncus spp.	13	34	13	1	6	0	6	1
J. squarrosus	3	2	2	2	1	0	0	1
Narthecium	0	0	0	0	0	0	0	0
Luzula	1	2	0	3	0	0	3	3
Eriophorum	5	1	2	1	3	3	1	1
Trichophorum	0	3	10	11	2	0	0	0
Carex	9	10	14	19	6	1	1	8
Molinia	5	9	24	15	8	1	1	1
Nardus	6	3	0	5	0	0	1	3
Agrostis	1	1	1	2	1	7	2	3
Anthoxanthum	1	0	2	0	1	0	1	0
Holcus	0	0	0	0	0	0	0	0
Deschampsia flexuosa	5	9	3	5	9	8	1	4
D. caespitosa	5	10	2	1	2	0	3	6
Cynosurus	0	0	0	1	0	0	0	1
Poa	0	0	0	0	3	0	3	1
Festuca	8	1	3	8	4	6	11	14
No. fragments	153	146	132	146	154	149	160	156

[1] No faeces collected in December 1978.

APPENDIX 6. (continued)

2. Langholm-Newcastleton Hills (b) Sheep

Year	1978					
Month	My	J	Jy	A	S	O
Mosses	37	3	11	8	21	12
Ferns	0	1	0	1	4	0
Conifers	0	0	0	0	0	0
Herbs	2	1	0	0	0	1
Calluna	2	1	9	4	13	28
Erica	0	0	0	0	0	0
Vaccinium	2	0	0	1	2	5
Juncus spp.	3	3	5	1	3	1
J. squarrosus	0	1	0	2	1	1
Narthecium	0	0	0	0	1	0
Luzula	2	3	0	1	0	1
Eriophorum	0	0	0	1	0	0
Trichophorum	0	0	1	1	1	0
Carex	5	17	10	9	1	3
Molinia	1	9	17	13	3	0
Nardus	5	5	1	9	1	1
Agrostis	2	7	5	5	9	7
Anthoxanthum	4	2	4	0	2	3
Holcus	1	0	0	0	0	1
Deschampsia flexuosa	11	13	9	11	11	5
D. caespitosa	5	16	5	5	6	1
Cynosurus	0	0	0	0	0	0
Poa	0	0	0	1	4	5
Festuca	17	19	21	28	18	25
No. fragments	160	148	152	158	158	149

APPENDIX 6. (continued)

3. Nether Hindhope (a) Goat

Year	1978									
Month[1]	F	A	My	J	Jy	A	S	O	N	D
Mosses	1	12	6	1	1	1	0	1	2	2
Ferns	10	7	3	2	9	67	65	3	6	0
Conifers	57	14	5	0	0	0	0	0	0	0
Herbs	2	3	2	1	7	0	0	2	2	2
Calluna	0	14	3	1	4	2	9	2	19	31
Erica	0	1	0	0	0	0	0	0	0	0
Vaccinium	1	1	3	0	0	0	2	2	2	0
Juncus spp.	3	0	13	48	30	5	6	1	2	3
J. squarrosus	0	0	0	0	0	0	1	0	1	0
Luzula	0	0	0	9	0	0	0	0	0	0
Eriophorum	0	5	9	0	0	0	2	0	1	0
Trichophorum	0	0	1	0	4	0	1	0	0	2
Carex	1	4	2	5	3	2	2	1	1	0
Molinia	0	0	0	0	36	10	2	0	0	0
Nardus	1	1	10	1	0	0	0	1	1	5
Agrostis	2	2	2	1	0	0	0	15	1	0
Anthoxanthum	0	0	1	1	0	0	0	1	5	0
Holcus	0	0	0	0	0	0	0	0	0	0
Deschampsia flexuosa	2	3	15	0	2	3	1	9	10	6
D. caespitosa	11	20	8	8	2	1	6	8	40	37
Briza	0	0	0	0	0	0	0	0	0	0
Poa	6	4	2	15	2	1	2	10	3	8
Festuca	4	11	13	8	1	8	0	44	5	6
Lolium	0	0	0	1	0	0	0	0	0	0
No. fragments	162	168	166	164	171	183	161	154	174	165

[1] No faeces were collected in March.

APPENDIX 6. (continued)

3. Nether Hindhope (b) Sheep

Year	1978								
Month[1]	F	A	My	J	A	S	O	N	D
Mosses	19	22	28	6	4	3	2	4	9
Ferns	3	4	2	1	1	3	16	1	1
Conifers	0	0	0	0	0	0	0	0	0
Herbs	0	0	0	6	1	1	2	1	1
Calluna	3	4	0	0	3	1	14	5	0
Erica	0	0	0	0	0	0	0	0	0
Vaccinium	0	3	0	0	1	1	4	2	1
Juncus spp.	1	1	2	4	1	1	1	0	0
J. squarrosus	0	0	1	0	0	0	0	0	0
Luzula	2	2	0	4	1	1	3	3	0
Eriophorum	1	0	0	0	0	0	1	0	0
Trichophorum	0	0	0	0	0	0	1	0	0
Carex	5	0	2	3	3	4	2	1	0
Molinia	0	0	0	0	17	3	1	0	1
Nardus	6	2	12	0	3	3	1	4	4
Agrostis	3	5	6	2	5	7	5	4	7
Anthoxanthum	1	1	5	2	3	3	1	0	1
Holcus	0	1	2	0	1	1	1	1	0
Deschampsia flexuosa	6	6	5	1	10	5	5	9	4
D. caespitosa	14	12	4	15	5	10	20	18	6
Briza	0	0	0	0	0	1	0	0	0
Poa	5	4	3	24	11	19	9	3	0
Festuca	31	32	25	31	28	34	14	45	66
Lolium	0	1	0	1	0	1	0	1	1
No. fragments	173	170	170	163	165	155	169	160	169

[1] No faeces were collected in March or July.

APPENDIX 7.

POPULATION ESTIMATES OF FERAL GOATS IN THE SOUTHERN UPLANDS.

All population estimates of feral goats in the Southern Uplands up to 1980 are presented.

1. Craigdews Wild Goat Park

		Number				
Year	Month	Billies	Nannies	Kids	Total	Source
1979	September	10	28	21[1]	59	This study
1980	December	9	22	18[2]	49	" "

Following the 1979 count, 10 billy kids, two adult billies, three nanny kids and five other nannies were culled. [1] comprised of 12 billy and nine nanny kids respectively. [2] comprised of 12 billy and six nanny kids respectively.

2. Central Galloway

These counts, by the Forestry Commission, include Cairnsmore of Fleet and north of this massif but excluding Craigdews.

Year	Season	Total
1971	Autumn	737
1972	"	759
1973	"	794
1974	"	787
1975	"	717
1976	"	734
1977	"	538
1978	"	468
1980	Spring	311

APPENDIX 7. (continued)

3. Cairnsmore of Fleet (a) Whole area

		Number					
Year	Month/Season	Billies	Nannies	Kids	Unclassified	Total	Source
1971	Autumn	203	213	63	74	553	F.C.
1972	Autumn	-	-	-	663	663	F.C.
1976	July	153	290	125	81	649	Bullock et al. 1976
	August	122	287	123	118	650	"
	Autumn	104	334	184	0	622	F.C.
1977	March	121	181	97	57	456	Bullock et al. 1977
	Autumn	87	192	124	0	403	F.C.
1978	March	66	199	114[1]	16	395	This study
	April	102	281	108	17	508	"
	June	130	230	131	0	491	"
	Autumn	69	159	91	0	319	F.C.
1979	September	104	263	23	0	390	Theaker 1979
1980	May	67	243	98	0	408	This study
	Spring/Summer	25	84	40	0	149	F.C.

[1] Kids almost one year old.

APPENDIX 7. (continued)

(b) Eastern block of the N.N.R.

		Number					
Year	Month	Billies	Nannies	Kids	Unclassified	Total	Source
1976	July	37	73	30	1	141	Bullock et al. 1976
	August	22	66	24	20	132	"
1977	March	52	86	43	18	199	Bullock et al. 1977
1978	March	28	60	46[1]	0	134	This study
	April	36	85	33	0	154	"
	June	51	107	49	0	207	"
	September	71	88	46	0	205	"
1979	April	24	92	18	0	134	"
	September	48	108	11	0	167	Theaker 1979
1980	May	30	91	44	0	165	This study
	October	20	103	45	0	168	Theaker 1980

[1] Kids almost one year old.

(c) Western area

		Number					
Year	Month	Billies	Nannies	Kids	Unclassified	Total	Source
1976	July	47	117	52	13	229	Bullock et al. 1976
	August	52	132	58	19	242	"
1977	March	21	35	13	16	85	Bullock et al. 1977
1978	March	7	64	32[1]	0	103	This study
	April	22	86	44	17	169	"
	June	30	61	51	0	143	"
1979	September	26	63	5	0	94	Theaker 1979
1980	May	5	50	24	0	79	This study

[1] Kids almost one year old.

APPENDIX 7. (continued)

6. Kielderhead Moor

		Number				
Year	Month	Billies	Nannies	Kids	Total	Source
1963	-	-	-	-	9	McDougall (1972)
1967	-	-	-	-	25	"
1969	-	-	-	-	23	Greig (1969)
1972	January	11	17	7	35	McDougall (1972)
	July	5	17	9	31	"
1979	June	10	37	7	54	This study
	October	10	12	7	51[1]	F.C.
1980	April	4	37	14	54	This study
	October	15	22	9	55[2]	F.C.

[1] Includes 22 unclassified goats, probably nannies. [2] Includes nine unclassified goats.

7. Nether Hindhope

		Number				
Year	Month	Billies	Nannies	Kids	Total	Source
1963	-	-	-	-	10	T. Elliot pers. comm.
1972	July	4	10	4	18	McDougall 1972
1976	November	-	-	-	42[1]	T. Elliot pers. comm.
1977	"	8	20	3[2]	31	This study
1978	"	8	16	8[3]	32	"
1979	"	5	19	5[4]	29	"
1980	"	2	22	5[5]	29	"

[1] One billy died during the annual muster, leaving 41. [2] All billies. [3] Two billies, six nannies. [4] All nannies. [5] Three billies, two nannies.

APPENDIX 7. (continued)

8. College Valley

			Number			
Year	Month	Billies	Nannies	Kids	Total	Source
1908	-	-	-	-	15-16	Anon 1908
1946	-	-	-	-	28	Tegner 1952
1947	-	-	-	-	14	"
1950	-	-	-	-	32	"
1951	-	-	-	-	7-9	"
late 1950s	-	-	-	-	16	"
1963	-	-	-	-	28	Stone 1963
1969	-	-	-	-	30	Greig 1969
1970	-	-	-	-	30	Whitehead 1972
1971	-	-	-	-	30	Anon 1976
1972	-	-	-	-	26+	McDougall 1972
1976	November	-	-	-	114	Anon 1976
	"	-	-	-	125	Werner 1977
	"	-	-	-	150	Stevenson-Jones 1977
	"	-	-	-	140	Brewster 1976
1977	June	4	6	4	14	Stevenson-Jones 1977
	October	4	6	4	14	This study
1978	April	4	7	3	14	"
1979	May	4	9	1	14	"
1980	April	3	7	3	13	"

APPENDIX 8.

THE USE OF CLUSTER ANALYSIS TO IDENTIFY SOCIAL GROUPINGS OF FERAL GOATS.

Introduction

Whilst social groupings of goats were in several cases readily identifiable, it was desirable to use a visual aid based on the frequency of association between individuals in order to allow a more objective assessment. Munton (1975) used a cluster analysis as an aid to describing the social organisation of feral goats on Lundy Island. A similar analysis was used in the present study for goats on the Moffat Hills and at Nether Hindhope.

Methods

Individuals within the same group (described in Chapter 5 where data collection is also described) were considered to be in association. Association matrices were constructed based on the frequencies of association between all the individuals in the populations. The frequencies of association between individuals were corrected for the variable number of times each individual was seen, using the Dice method (Morgan, Simpson, Hanby & Hall-Craggs 1976) as follows:

$$\text{Corrected frequency of association of A with B} = \frac{\text{Total no. sightings of A with B}}{(\text{Total no. sightings of A + total no. sightings of B})}$$

where A and B are individual goats. The corrected frequencies of association were used with the S.P.S.S. (Nie, Bent & Hull 1970) computer package CLUSTAN to produce weighted-average linkage dendrograms.

Morgan et al. (1976) discussed the merits of various linkage methods for clustering. For the present study, given the preliminary nature of the data, a choice between the two simplest methods, single linkage or weighted-average linkage was appropriate. The latter was chosen because it has less bias due to chaining between links than the former; in practice, there were only minor differences between the two methods.

Whether the data are presented numerically as frequencies of association or visually as a dendrogram, descriptions of the social cohesion between individuals must to some extent, be arbitary. In the present study, separation of groups of goats into hefts based on dendrograms was done at the low frequencies of association of less than 0.1 rather than a greater frequency. More detailed separation may not have had biological significance, a problem with all cluster analysis methods.