# Distribution and Activity of Red Deer (*Cervus elaphus* L.) in Relation to Vegetation and Topography

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# Abstract

Habitat use by red deer was examined during winter in N. Scotland.

Observations showed that hinds and stags occupied separate areas, but also used some ground communally. Site utilisation was influenced by the type of vegetation and the availability of topographic shelter. *Calluna* was used extensively for grazing and bedding. Better quality grassland was heavily used; hinds exploited a greater area of this type of vegetation than stags. The use of topography was similar for both sexes; sites with a variety of aspects were used, but open and exposed areas were usually avoided.

Rumen and faecal samples were examined to determine the diet; they contained similar proportions of the same species. Faecal analysis revealed similarities in the diets of stags and hinds. The results do not reflect any marked superiority in the food available on the hind range, although female samples contained a greater proportion of Fescues.

Chemical analyses of *Calluna* samples, as grazed by deer, did not reveal selection to be related to nutrient or neutral detergent fibre content. However grazing was mainly restricted to the current year's growth, except when food became less available because of snow and ice. The selection of *Calluna* in relation to muirburn is discussed.

The behaviour of deer was recorded under a variety of weather conditions. Strong winds promoted shelter seeking, but low temperatures, alone, did not produce such a reaction. Strong winds together with low temperatures had most influence on shelter seeking.

A theoretical model was developed which estimates heat loss from deer. Using the model, energy expenditure under contrasting levels of activity and weather conditions was examined, and the importance of shelter demonstrated. Observed differences in the behaviour of stags and hinds are discussed in relation to energy exchange and characteristics of the home range.

It is concluded that the distribution of red deer during winter is principally governed by micro-climate in relation to food supply. Although vegetation had a strong influence on distribution, the most significant factor overall is the availability of shelter.

# PREFACE

## Nomenclature

The scientific nomenclature adopted in this account is as used in the following texts:

Mammals - Corbet, G B & Southern, H N (1977). The handbook of British mammals (2nd edn). Blackwell Scientific Publications, Oxford.

Birds - Hudson, R (Ed) (1978). A species list of British and Irish birds. BTO Guide No. 13. British Trust for Ornithology, Tring.

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Lichens - Duncan, U K (1970). Introduction to British lichens. T Buncle, Arbroath.

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This thesis has been composed by myself and the research presented in it is my own.

Nigel Easterbee

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# Chapter 1 Introduction

## 1.1 General Introduction

About three quarters of the total land area of Scotland, some 5.2 million hectares, is over 300m above sea level. Much of this ground is inherently infertile, the climate is harsh and the vegetation is dominated by acid tolerant species. Since the loss of tree cover, the traditional use of these areas has been for hunting and sporting purposes, and livestock production. During the present century there have been further significant uses made of this area, notably for afforestation by the state and private sector, hydro-electric schemes and more recently for recreation.

Red deer (Cervus elaphus L.) are found over approximately 2.5 million hectares of the Scottish uplands, and the current population is probably in excess of 270,000 animals. It is an important resource in the Highlands, and contributes significantly to the incomes of many estates through stalking fees and venison sales. In 1979 the total value of venison exports and trophy shooting by foreign visitors was about £3.5 million (Mutch pers. comm.). These figures do not take account of hotel accommodation for visiting sportsmen, which is a further locally important source of income. Red deer have a high aesthetic value and embody for the visitor much of the romance associated with the wildness of the Highlands, which persists from Victorian times (see: Hart-Davis 1978).

Despite its importance and traditional place within the Highlands, the red deer may enter into conflict with other users of the uplands. Hill farming is practised throughout much of the area at the lower elevations. Although the total output from these farms may be sizeable in economic terms, the subsidies afforded are considerable and reflect the marginal viability of this form of land use. Hill sheep and deer may utilise the same areas of land, particularly during winter, and, since similar areas of vegetation may be grazed by both species, competition for grazing may be suspected, but has yet to be clearly demonstrated (see: Colquhoun 1971). However damage to cereal and root crops on agricultural land adjacent to upland areas during winter, particularly by stags, may be serious, and necessitate culling of the animals concerned.

The construction of dams for hydro-electric purposes has resulted in the flooding of substantial areas of glens, thereby depriving deer of traditional wintering grounds and routes of access. Although these operations have undoubtedly had significant effects, the major influence at present on the uplands is afforestation. The afforestation of land and the exclusion of deer results in loss of range; piecemeal planting may divorce areas of high and low ground, severely disrupting deer ranging behaviour. Loss of ground from whatever cause will result in the displacement of the deer stock to other areas, leading to overstocking and marauding on any adjacent agricultural land.

The red deer/forestry interaction is not however all one-sided, and deer can and do gain access to forest plantations. Extensive damage may be caused to trees from bark stripping and browsing. Afforestation on areas of deer range cannot therefore be reasonably attempted without deer fencing, which at a cost of about £2 per metre, represents a serious financial burden on any establishment programme. Nonetheless in view of forecasts of a world timber shortage by the year 2000, with associated price rises of up to 30%, and our timber imports currently running at 92% of demand (CAS 1980), further ground in the uplands will be afforested, some of which will inevitably be at the expense of deer range.

Further interference to deer stocks from disturbance has resulted from the recreational use made of the uplands. This pressure has increased dramatically over the last 20 to 30 years, with the greater mobility and wealth of the population. However the rapidly rising price of oil may stabilise or even reduce this form of disturbance somewhat.

Recently some interest has been shown in the possibilities of farming red deer in Scotland, in a state of semi-domestication. Although a number of farms have been set up, the economic feasibility of such enterprises has yet to be clearly established.

The red deer is thus of some considerable importance both for its value in sporting and aesthetic terms, and for the problems that arise from its interactions with other forms of land use in the uplands. A sound biological knowledge of this species and its present environment is essential to any ability to understand and resolve conflicts which exist at present, or are likely to develop in the future.

The red deer evolved in the forest margins (Flerov 1952), but in the predominantly treeless environment of the Scottish uplands (excluding man-made forests) it is obliged to live in a very different habitat of exposed moors and mountains. The winter in the uplands of Scotland is severe despite the relatively low elevations of much of this ground. Attention in this study has therefore been focussed on the winter environment. It is during this period that the demands of homeothermy increase and the availability of nutritious food is severely reduced. The way in which the red deer utilises the range is thus critical to its survival, and subsequent production and ability to reproduce.

There has been little previous work devoted to this specific topic, although the diet has been investigated (see: Mitchell, Staines & Welch 1977), since many authors have supposed that inadequate nutrition is responsible for the poor performance of Scottish red deer. At the outset of this work the only studies carried out in Scotland which were concerned at least partially with such aspects of the animals' ecology are those of: Staines (1970), Colquhoun (1971) and Jackes (1974). All three studies record details of vegetation use, and both Staines (1970) and Jackes (1974) when considering the possible effects of winter weather upon red deer report that shelter is of some importance. In this study I have recorded the distribution and activity of red deer in relation to the vegetation and physiographic features of the range. Estimates of the influence of climatic parameters and the value of the natural shelter available on the open hill, on the energy budget of the deer are made. The results are considered in relation to reports from these earlier studies and other published work.

This account of the work which was carried out is arranged as follows:

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| Chapter one - | Introduction<br>Brief review of the red deer in Scotland - An outline of the history of the red deer in Scotland, which provides an insight into the current situation.<br>The study area : its location and description. |
| Chapter two - | Observations of the red deer during winter: the way in which the range is used by stags and hinds. |
| Chapter three - | Food of the deer stock, as determined by rumen and faecal analysis; evidence for any qualitative differences in diet arising from differential range use. |
| Chapter four - | The value of muirburn to deer during winter: a possible influence on ranging behaviour. |
| Chapter five - | The assessment of the relative intensity of use of different sites on the study area, in relation to site characteristics. |
| Chapter six - | The influence of the climate on the red deer during winter. |
| Chapter seven- | Final discussion and conclusions. |
| Appendix | |

During the course of this a research review of the red deer, relevant to their management in Scotland, entitled "Ecology of Red Deer", by Mitchell, Staines & Welch (1977) has been published. In view of this I have considered a comprehensive review of the literature to be unnecessary. A brief review follows and relevant literature is referred to when appropriate throughout the account as a whole.

## 1.2 The Red Deer in Scotland - A Brief Review of Specific Relevance to this Work

The species Cervus elaphus has a circumglobal distribution, and has been described by Flerov (1952) as occupying a large part of the temperate zone, chiefly the upland forest areas of Europe, Asia and N. America, between latitudes 30° and 65° north. This description of course excludes areas in the southern hemisphere where introductions were carried out in the nineteenth and early twentieth centuries. The pattern of distribution in the northern hemisphere has resulted from the colonisation of ground by the ancestors of today's deer, following the retreat of the glaciers at the end of the last Ice Age, about 7-8000 B.C. The prehistoric red deer moved westwards from eastern Europe and the Caucasus, while the wapiti (Cervus elaphus canadensis), already distinct from the red deer, moved eastwards from central Asia (Lowe 1961), colonising the North American continent, before it was severed from Asia. What is now Britain was colonised over the land-bridge which then formed a link with the European continent; this link was subsequently broken about 5000 B.C.

There are now some 16 sub-species resulting from the eastward and westward movements of these early deer. The sub-species found in Scotland is Cervus elaphus scoticus L., which is confined in its distribution to the British Isles. However the integrity of this sub-species in Scotland must now be in considerable doubt following the introductions made during the nineteenth century, particularly of continental deer (Cervus elaphus hippelaphus) and wapiti, in attempts to "improve" indigenous stock. (There may be some doubt as to the existence of subspeciation in red deer, and it may be more appropriate to consider the existence of 'races' rather than sub-species, see: Lowe & Gardiner 1974).

The contemporary range of the red deer throughout much of the northern hemisphere is confined to areas of hill and rugged terrain. Although a generalisation, the situation in Scotland is no exception. This has not always been the case, and much of the present distribution of the red deer has been the result of man's activities. Ritchie (1920) reports that before the arrival of man in Scotland, the red deer roamed the country over. The greatest number of prehistoric remains of this animal to date have come from the now-deserted lowland valleys.

A striking feature of the sub-fossil remains of the prehistoric red deer, recovered from gravel deposits and marl clays in Scotland, is the size of the animal in comparison with contemporary deer, Plate 1. Studies by a number of authors, comparing sub-fossil remains with those of contemporary red deer in western Europe, have revealed a reduction in linear dimensions of about 20% in the latter animal (see: Fraser & King 1954, Walvius 1961 and Ahlen 1965a). The reduction in body size of present-day deer follows a trend in a west and north direction, and is most marked today in Scotland, while Caucasian and East European animals have not diminished to anything like the same extent. The early Scottish remains indicate that red deer at that time were comparable in size with the largest deer found in the eastern parts of the range (Huxley 1931). Today the largest red deer, as distinct from wapiti, are those found in the Caucasus and Carpathians, weighing in excess of 300 kg liveweight (Mystkowska 1966), in contrast to those in the extreme north west of Scotland, of about 100 kg liveweight.

The explanation of this most marked decline in the size of red deer, particularly in Scotland, is believed to be the result of climatic and habitat change (see: Walvius 1961). As already mentioned, this animal evolved in the forest margin, and is confined in Scotland to a largely tree-less environment. Where red deer still occur in suitable habitat, a large body-size is still maintained, in comparison with Scottish animals. Red deer from England may be significantly larger than those in Scotland, whilst Hungarian, Yugoslavian and Bulgarian animals are approximately two to two and a half times heavier. Scottish red deer are however capable of far better performance than is realised in the upland deer forest. The descendants of Scottish red deer introduced to suitable habitat in New Zealand rapidly increased in performance and body-size, and animals in excess of 250 kg liveweight were reported as being common in parts of the South Island (Huxley 1931). Studies of the red deer at the

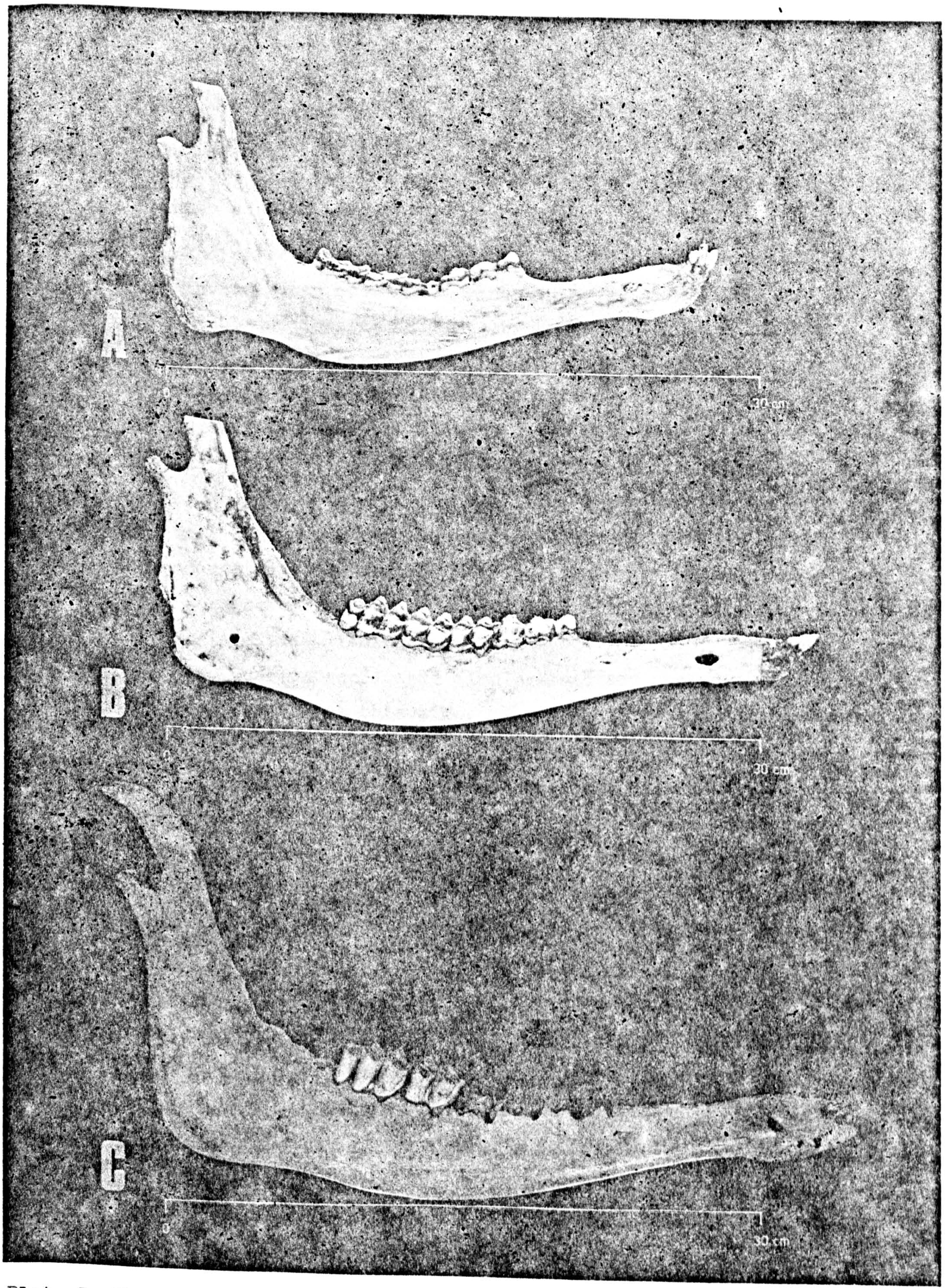


Plate 1 The comparison of red deer using jaws as an indicator of body size.

A. Contemporary Scottish hill stag from Ross-shire; 12 years of age.

B. Contemporary park stag (English origin); approximately 6 years of age.

C. Sub-fossil stag unearthed from a peat bog in E. Lothian as mentioned by Ritchie (1920).

Rowett Research Institute have also demonstrated that significant increases in growth rate and body-size can be attained in housed animals, with access to adequate supplies of nutritious food (Blaxter et al. 1974).

The effects of climatic change on the forest cover of Britain have been documented by Lamb (1959, 1977), and that of man in conjunction with climate by Steven & Carlisle (1959), McVean (1959) and Pennington (1969). The influence of these two main factors on the decline of the forest cover, and the consequent loss of habitat for the red deer in Scotland, may be summarised as follows: ice retreated from this country about 12,000 years ago, and from about 8000 B.C. there was a rapid improvement of the climate, which became both warmer and drier. Forest spread rapidly over northern Europe, and evidence from the pollen-record suggests that in Scotland pine (Pinus sylvestris) reached its maximum post-glacial extent at about 7000 B.C. Elm (Ulmus spp.) and oak (Quercus spp.) were also present and spreading through Scottish forests at this time. The transition from the continental conditions of the Boreal Period (7000-6000 B.C.) to the warmer and wetter, oceanic conditions of the Atlantic Period (6000-3000 B.C.) was marked by the acceleration of bog growth and the rapid increase in alder (Alnus glutinosa) over much of Scotland. Mesolithic people first arrived in Scotland about 5000 B.C., but being hunter/fishermen had little affect on the forest cover. Neolithic peoples, who were pastoralists, were the first to have an impact, albeit slight, on the forests, and are thought to have been implicated in the rapid decline in elm pollen around 3000 B.C. However it was the Bronze Age peoples with their shifting agriculture, Landnam, that brought about the beginnings of anthropogenic forest destruction. A change to a warm and dry continental climate occurred during the sub-Boreal Period (3000 to 1000-500 B.C.), favouring tree growth, but there was a decline in temperature and a return to wetter conditions after 1000-500 B.C., which lead to an extension of blanket peat over upland birch (Betula spp.) forest in Scotland. Over the course of history both the effects of man and his grazing animals and the climate continued to make greater in-roads into the forest area. Despite a further climatic change to conditions approaching those of the warmest post-glacial times, around 1200 A.D., again favouring tree growth, the clearance of forest by man continued at an ever increasing rate. By the eighteenth century the red deer, as a result of hunting pressure and loss of habitat, had been largely displaced from lowland Scotland. The destruction of most of the upland forests since the sixteenth century, for smelting, ship-building and timber, combined with the development of sheep farming in the late eighteenth and early nineteenth century, now results in Scottish red deer inhabiting a predominantly open environment, often overlying acidic and poorly drained soils of low productivity.

It is a testimony to the adaptability of this species that it has been able to survive this acute destruction of habitat together with climatic change. There are of course consequences arising from this ability to survive in the uplands of Scotland, typically the reduction in size, and also the diminished productivity, with Scottish red deer hinds first breeding later than their European counterparts, and the failure to produce a calf each year when mature ie. yeldness. Mitchell (1973) presents figures for the performance of hinds on a Scottish Deer Forest: earliest first calving was in many cases at three years of age; a calving rate of 40% was recorded, and 30 to 40% of the sexually mature hinds failed to ovulate or conceive in a given year. In contrast Phillips & Mutch (1974) give details of the performance of red deer in a number of European forests. Up to 72% of yearlings were reported to have been pregnant, and in the better forests 93% of the older hinds were pregnant. It should be noted that the management of European Deer Forests is far more intensive than that in Scotland, with effective winter feeding being carried out.

Although a range of nutrients are required in the ruminant diet, Blaxter (1962) has strongly emphasised the central and overriding importance of energy. Shortages of energy in the diet do not lead to spectacular symptoms, but to an insidious reduction of growth, reproductive and lactational performance. Blaxter (1962) points out that such insidious deteriorations are quantitatively more important sources of diminished productivity of stock than is any shortage of specific dietary essentials; the latter usually only occurring when the total dietary supply of energy is abundant. However investigations have indicated that shortages of dietary nitrogen during winter may be inhibiting the production processes of rumen micro-organisms in the red deer, and it has been suggested that increases in available nitrogen could enable more of the dietary energy to be made available to the host (see: Hobson et al. 1976).

Regardless of the ultimate factors involved, red deer experience a negative energy balance during winter which may lead to the complete depletion of fat reserves (Anderson 1978). In view of this, it is suggested that the distribution and activity of these animals, in relation to the spatial variation in food supply and micro-climate is crucial in this environment, and may represent an optimum strategy which evolved under the influence of natural selection. The work described here attempts to examine this hypothesis, and involves consideration of the movement and behaviour of deer in relation to the quality and distribution of food and the pattern of micro-climate, which is principally created by topography.

## 1.3 The Study Area

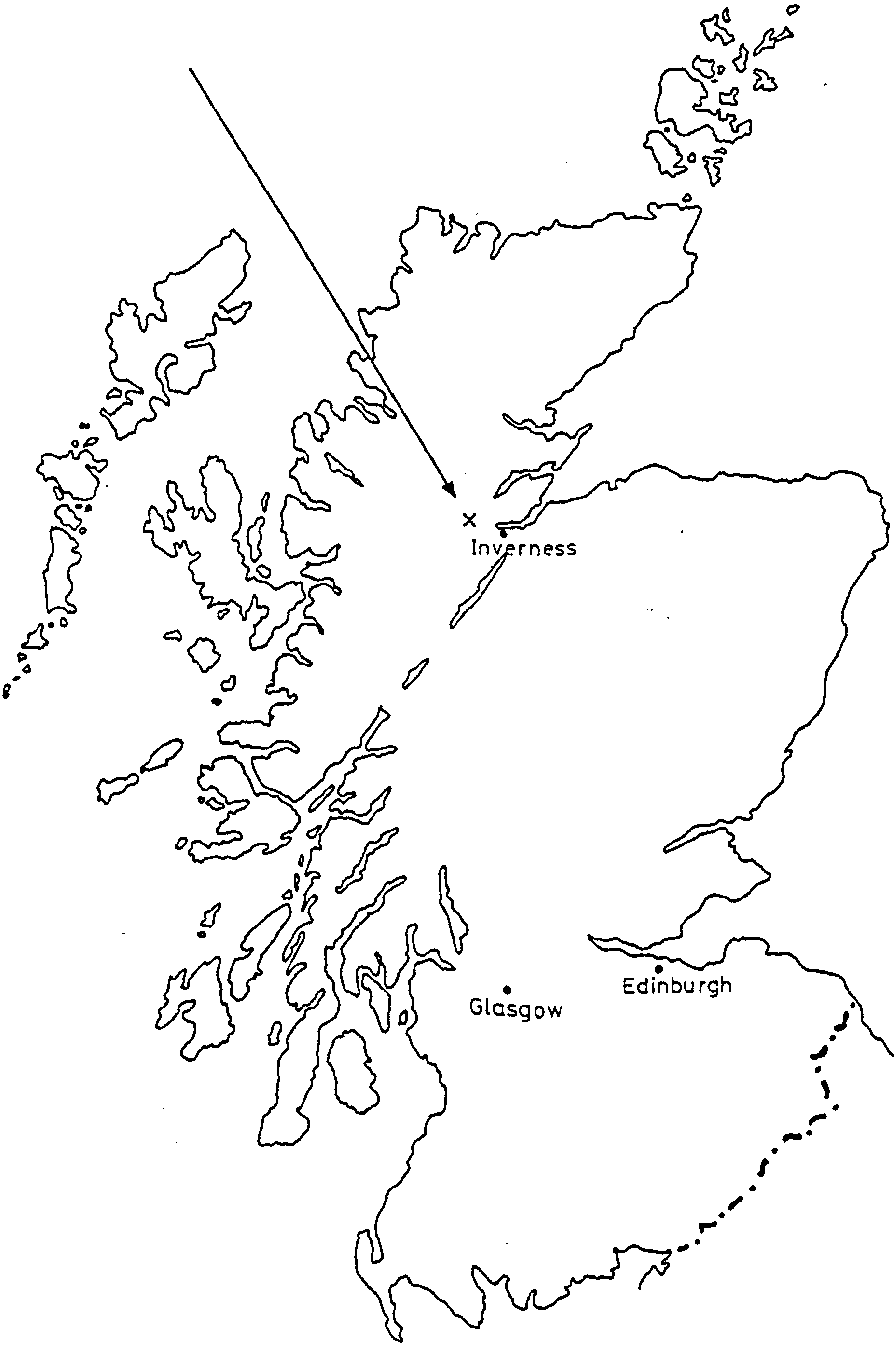
The study area covered Glen Goibhre and the eastern part of Glen Orrin. Both glens are part of the catchment of the River Conon, and lie approximately 34 km north west of Inverness (National Grid Reference NH 43 49), see Figs. 1.1 and 1.2.

The floors of the glens are approximately 210-250m above m.s.l. and rise in altitude from east to west. A central ridge, rising to 370m, separates the two glens. The land to the south rises to 580m and to the north to 450m. The ground to the west is characterised by large-scale topographical features, and forms part of the Western Highlands which exceed 1080m in height.

### 1.3.1 Geology

Most of the study area consists of rocks composed of undifferentiated schists of the Moine series. There is a small area of granite on the north side of Glen Orrin, and an area of conglomerate and old red sandstone at the east end of both glens.

Figure 1·1 The Location of the Study Area



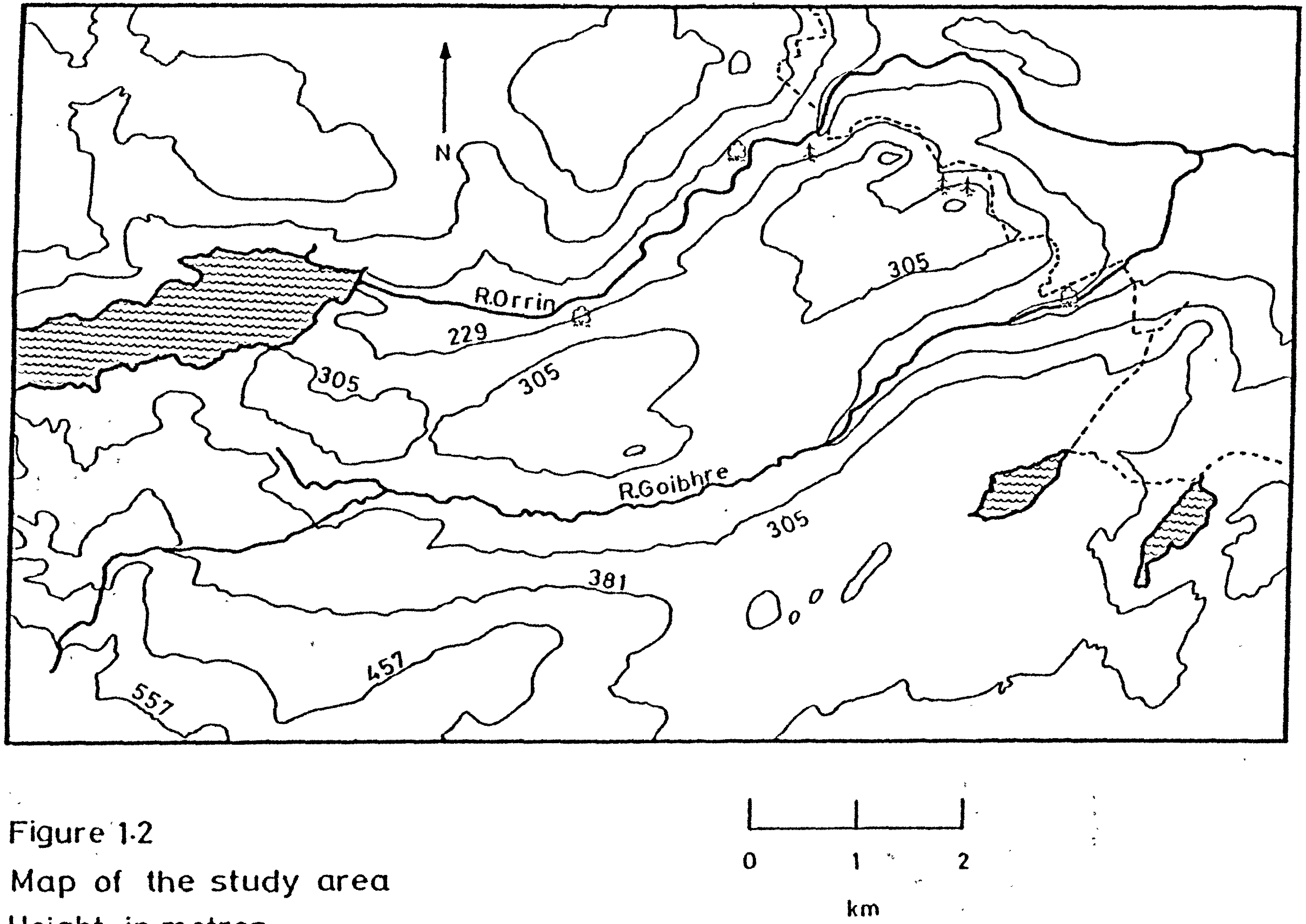


Figure 1·2
Map of the study area
Height in metres

Much of the area is overlain with peat of varying depths. In the bottom of both glens there are areas of freshwater alluvium, which are more extensive in Glen Goibhre; where the valley sides are steep there are areas of freely draining morainic drift. Boulder clay covers a fairly substantial area in the eastern part of Glen Goibhre.

### 1.3.2 Vegetation

Because of the size of the study area, approximately 30 km$^2$, the work necessary to produce a meaningful vegetation map would have been prohibitive. In summer 1976 I carried out a reconnaissance and a vegetation survey of the area, in order to identify the most significant and widespread communities, for subsequent recognition during field work. A series of one metre square quadrats located at random was evaluated in recognisably distinct areas of vegetation, and species cover and abundance estimated by eye on the Domin Scale.

It was possible to assign the range of communities on the study area to previously defined units resulting from detailed phytosociological studies of Scottish vegetation. However, as mentioned by McVean & Ratcliffe (1962), there is frequently a lack of sharp discontinuities between communities in the Highlands, particularly where burning has occurred in the past. Vegetation in such areas forms a continuum, and so as well as those types which are recognised below, there are also intergradations between types.

Most of the units recognised were comparable with those documented by McVean & Ratcliffe (1962). The units recognised and the species recorded were as follows:

(i) *Callunetum vulgaris* - *Dry Heather Moor**

*Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Vaccinium myrtillis*, *Empetrum* spp., *Potentilla erecta*, *Trichophorum cespitosum*, *Blechnum spicant*, *Hypnum cupressiforme*, *Pleurozium schreberi*, *Hylocomium splendens*, *Polytrichum formosum*, *Cladonia impexa*, *Cladonia uncialis*, *Cladonia pyxidata*.

Widespread throughout the study area, particularly at the eastern end of the glens on both north and south-facing

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*Denotes McVean & Ratcliffe types

slopes, and on steeper south-facing slopes and hummocks in the west of the area. Estimated area covered 20%.

(ii) *Trichophoreto-Callunetum* - *Trichophorum/Calluna Bog**

*Trichophorum cespitosum*, *Calluna vulgaris*, *Erica tetralix*, *Potentilla erecta*, *Molinia caerulea*, *Narthecium ossifragum*, *Sphagnum* spp., *Cladonia uncialis*, *Cladonia impexa*, *Cladonia pyxidata*.

The most abundant type of vegetation in the study area, replacing *Callunetum vulgaris* on less steep ground and northern slopes. Much of the upper areas and western part of the study area were covered with this type. Estimated area covered 35%.

(iii) *Calluna-Eriophorum vaginatum* - *wet-heath* (Gimingham 1964)

*Calluna vulgaris*, *Eriophorum vaginatum*, *Empetrum* spp, *Eriophorum angustifolium*, *Trichophorum cespitosum*, *Hylocomium splendens*, *Polytrichum commune*, *Sphagnum* spp.

This type occurred on flatter and more gently sloping ground than the above, and was most extensive on higher ground above the two glens and was also frequently found intergraded with *Trichophoreto-Callunetum*. Estimated area of cover approximately 15%.

(iv) *Molinieto-Callunetum* - *Molinia/Calluna Bog**

*Calluna vulgaris*, *Erica tetralix*, *Molinia caerulea*, *Trichophorum cespitosum*, *Eriophorum angustifolium*, *Nardus stricta*, *Potentilla erecta*, *Narthecium ossifragum*, *Hypnum cupressiforme*, *Hylocomium splendens*, *Plagiothecium undulatum*, *Sphagnum* spp., *Cladonia uncialis*.

This type was widespread, although of a localised nature. It occurred throughout the area where there was adequate movement of drainage of water through the substrate, on slopes near flushes and at the foot of slopes. This vegetation graded into *Molinia-Myrica* nodum. Estimated area of cover, 10%.

The following types make up the remaining 20% of the most abundant vegetation found in the area.

(v) *Molinia-Myrica nodum**

*Molinia caerulea*, *Myrica gale*, *Potentilla erecta*, *Erica tetralix*, *Calluna vulgaris*, *Deschampsia flexuosa*, *Trichophorum cespitosum*, *Viola riviniana*, *Hylocomium splendens*, *Hypnum cupressiforme*.

Associated in small areas with (iv).

(vi) *Trichophoreto-Eriophoretum* typicum - *Western Blanket Bog**

*Calluna vulgaris*, *Erica tetralix*, *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Molinia caerulea*, *Myrica gale*, *Trichophorum cespitosum*, *Potentilla erecta*, *Narthecium ossifragum*, *Drosera anglica*, *Pinguicula vulgaris*, *Sphagnum* spp., *Rhacomitrium lanuginosum*, *Cladonia impexa*, *Cladonia uncialis*.

This type occurred in areas of poor drainage, particularly on the top of the central ridge between the glens, and in the western part of Glen Orrin.

(vii) *Species-poor Agrosto-Festucetum* - *Agrostis/Festuca Acidic Grassland**

*Agrostis tenuis*, *Agrostis canina*, *Festuca ovina*, *Nardus stricta*, *Galium saxatile*, *Potentilla erecta*, *Viola riviniana*, *Achillea millefolium*, *Prunella vulgaris*, *Trifolium repens*, *Hylocomium splendens*, *Rhytidiadelphus squarrosus*, *Rhytidiadelphus loreus*.

A localised and dispersed distribution, found in the lower eastern part of Glen Goibhre, on well-drained alluvial terraces beside the river Goibhre, and at the deserted crofts in both glens.

(viii) *Nardetum sub-Alpinum* - *Sub-Alpine Nardus Grassland**

*Nardus stricta*, *Festuca ovina*, *Agrostis tenuis*, *Agrostis canina*, *Anthoxanthum odoratum*, *Deschampsia flexuosa*, *Festuca rubra*, *Molinia caerulea*, *Calluna vulgaris*, *Juncus squarrosus*, *Potentilla erecta*, *Galium saxatile*, *Viola riviniana*, *Hylocomium splendens*, *Hypnum cupressiforme*, *Pleurozium schreberi*, *Rhytidiadelphus triquetris*, *Lophocolea bidentata*.

This was most extensively represented at the eastern end of Glen Goibhre on the north-facing slope of the glen.

#### (ix) *Juncus effusus*/Acidic Grassland, resembling the *Juncetum-Effusi* of Evans, Hill & Ward (1977)

*Juncus effusus*, *Deschampsia flexuosa*, *Festuca ovina*, *Festuca rubra*, *Anthoxanthum odoratum*, *Deschampsia caespitosa*, *Poa pratensis*, *Holcus lanatus*, *Nardus stricta*, *Potentilla erecta*, *Galium saxatile*, *Ranunculus acris*, *Polytrichum commune*, *Sphagnum* spp.

This type occurred in a number of places on the study area, in flushed areas. It was generally of very local distribution, but was most extensive on alluvial areas at the top of Glen Goibhre.

#### (x) *Molinia* Grassland

*Molinia caerulea*, *Deschampsia flexuosa*, *Calluna vulgaris*, *Erica tetralix*, *Potentilla erecta*, *Eriophorum vaginatum*, *Eriophorum angustifolium*, *Trichophorum cespitosum*, *Myrica gale*, *Sphagnum* spp.

Also of limited extent on the study area. The most extensive areas were associated with peaty sites beside the rather sluggish tributaries of the river Goibhre, in the west of the area.

There were fragments of Birch (*Betula* spp.) woodland in Glen Orrin and at the extreme easterly part of Glen Goibhre, which was also interspersed with willow scrub (*Salix* spp.). A small plantation of Scots pine (*Pinus sylvestris*) and Larch (*Larix* spp.) was open to deer at the easterly end of Glen Orrin. The remnants of a Scots pine plantation, felled during World War II, which lies above Glen Goibhre, was also open to deer; see Fig. 1.2 for the approximate location of these areas mentioned.

### 1.3.3 Land use

The study area is part of the Fairburn Estates, and is owned by Mr R W K Stirling. It is used for sporting purposes, and both red grouse (Lagopus lagopus scoticus) and red deer are shot in their respective open seasons. Muirburn for the benefit of the grouse stock was carried out on the study area, but due to labour shortages, and attempts to burn small individual areas, little suitable Calluna-dominated ground was burnt in any single season. Sheep used to be grazed on this ground, but were withdrawn in 1972.

Small areas of plantation forest were restricted to the lower ground at the eastern end of both glens, and were fenced against red deer.

### 1.3.4 Climate

There is a paucity of climatic data for the Highlands as a whole, and the study area is no exception. Reference to the 'Assessment of Climatic Conditions in Scotland' 1 and 2, by Birse & Dry (1970) and Birse & Robertson (1970), reveals that the study area falls within the zones which are described as: "cool rather wet lowland, foothill and upland region"/ "cold wet upland" and "exposed to very exposed, with rather severe winters".

Rainfall increases at the rate of approximately 40mm $km^{-1}$ within the glens, and at the Orrin dam is, on average, 1180mm $year^{-1}$. The driest month is June (70mm average) and the wettest, December (146mm average), (G Reynolds pers. comm.), see Table 1.1.

Records of temperature and wind-run were made throughout the study period, and are reported in Chapter 6.

Views of the study area are presented in Plates 1.1 - 1.3 inclusive.

Table 1.1 Mean monthly rainfall on the study area (average for the period 1941-1970), in millimetres

| Jan. | Feb. | Mar. | Apr. | May | June |
|---|---|---|---|---|---|
| 113 | 99 | 80 | 84 | 78 | 70 |
| Jul. | Aug. | Sep. | Oct. | Nov. | Dec. |
| 83 | 98 | 100 | 121 | 111 | 146 |

Mean annual rainfall - 1183mm

Data: G Reynolds (pers. comm.)

Plate 1.1 The western part of Glen Goibhre, looking east

Plate 1.2 The eastern end of Glen Goibhre, looking south

Plate 1.3 The central ridge looking westwards into Glen Orrin

# Chapter 2 Observations of Red Deer During Winter

## 2.1 Introduction

For any free-ranging homeotherm, such as the red deer, there are a number of interacting social and environmental factors which will determine the way in which these animals distribute themselves over the range. Patterns of distribution are not random, as soon becomes apparent after only casual observation.

It is impractical at present even to attempt a total evaluation of all the interacting factors influencing an animal in its natural environment. However there is good reason to expect that certain factors may be exerting major influences upon the animal, and their investigation may reveal much about the underlying causes of observed patterns of distribution and activity. It was beyond the scope of the present study to investigate the influence of sociality on behaviour and distribution, although it is recognised that in the case of an animal with a highly evolved social system, such factors may be of considerable importance.

The acquisition of food is a factor of great importance to all animals. Being a large ruminant, the red deer relies for its nutrition on the ingestion of relatively large amounts of plant material. Particularly during winter, forage is of comparatively low quality, but deer, unlike cattle, do not have a rumen of sufficient capacity to store large amounts of material for the prolonged fermentation of low quality forages (see: Short 1963 and Schoonveld, Nagy & Bailey 1974) and they need, therefore, alternating periods of resting and feeding during the day. Much of the daily activity of deer in undisturbed conditions will be tied into this cycle of feeding and resting.

There is a danger however of attaching too much importance to food and feeding as determinants of spatial distribution, at the expense of other environmental factors. During winter a natural decrease in appetite has been found to occur in studies of captive deer, even in the presence of ad-libitum quality food (see: Thomson et al. 1973 and Blaxter et al. 1974). It has been suggested that this phenomenon has developed in response to the lowering in quality of range food species in winter.

During winter red deer in common with other Cervids of the higher latitudes rely for much of their energy requirements on stored fat reserves. The importance of these reserves in white-tailed deer (Odocoileus virginianus) has been emphasised by Mautz (1978), although this is not to imply that deer are independent of winter food sources. However, conservation of fat reserves will improve winter survival, and deer may therefore behave in such a way as to optimise the conservation of energy. It is within this context that the interaction with the physical environment is of importance.

In this chapter I have presented results arising from repeated observations made throughout winter on the deer stock of the study area, to investigate the general distribution and activity of deer in relation to habitat factors. Further complementary work involving an indirect assessment of site usage is presented in Chapter 5.

## 2.2 Method

Observations were made of deer on the study area between October 1976 and April 1977. Fieldwork encompassed the least favourable time of year, November to March, when red deer either fail to grow or lose weight and condition (Mitchell, McCowan & Nicholson 1976). Observations covered the period from dawn to dusk; although desirable it did not prove practicable to collect further information during the hours of darkness. A few casual observations were made during the night when the opportunity arose. Any techniques relying on making field observations over long distances will suffer in mist, rain or snow, or when broken patches of snow are lying. If visibility was very poor, alternative work was carried out.

Binoculars with a magnification of x8 were used to locate deer, and a x24 telescope was used for collecting detailed information, which was spoken into a tape recorder.

When walking over the study area the same route was not taken on each occasion for a number of reasons. It was important to cause a minimum of disturbance to the deer stock, which were hunted and therefore wary of man; this necessitated taking the wind direction into account when on the study area, to avoid the detection of scent. It was considered that the deer stock might become accustomed to the adoption of a regular pattern of behaviour, and would act accordingly. This could lead to the recording of patterns of distribution consequent on the presence of an observer, rather than as a result of environmental parameters.

Apart from days devoted solely to making observations of deer, such information was also collected when carrying out the necessary servicing of the weather stations and visiting sampling plots. The careful selection of the route to and from sampling sites enabled as large a part of the study area to be scanned as possible, while minimising the risk of disturbance and displacement of deer, which could lead to duplicate registrations being made later the same day. Re-recording of disturbed animals was avoided at all times, and any such observations will only comprise a very small proportion of the total. In any case care was taken to avoid any unnecessary disturbance to the deer, since this represents an influence which could mask the effect of those variables under study, quite apart from considerations of the animals' well-being.

Once located, the position of a group or an individual deer was recorded by taking the bearing with a prismatic compass in relation to well defined topographic features in the vicinity. For deer which were not on the move, either resting or grazing, a cross-bearing taken from another position, several hundred metres from the first, enabled the location to be fixed accurately for subsequent mapping. The following details were recorded for each observation:

Date
Time
Aspect - 8 cardinal compass points
Vegetation - assigned to those communities recognised in the initial reconnaissance of the study area (see: Chap. 1)
Activity - standing, walking, running, grazing, bedded
Group composition - hind, stag, yearling (female), knobber (yearling male), calf

*Weather - free windspeed, ie. away from obvious topographic influences (Beaufort Scale, Table 2.1), wind direction, rain, snow, insolation and cloud cover.

*This information is used in Chapter 6, specifically, and is dealt with in detail in that section.

Daily cumulations of data were processed for subsequent computerised manipulations. Deer locations, expressed as compass-bearings, were plotted on a large-scale map previously prepared of the area. From X and Y axes, which had been drawn on this map, a grid reference was assigned to each deer location, which then enabled computerised mapping of deer distribution to be carried out. The altitude of deer locations was read from maps of the area after the plotting had been carried out.

The intention was not to make observations over the entire study area on any one excursion, which in many cases would have proved impossible anyway. Rather, it was to observe and record what deer were present and where, over as much of the study area as could be satisfactorily surveyed from the route taken and time permitting. In addition, a survey of as much of the area as could be viewed on any one occasion was made when servicing the weather stations at six to seven day intervals. The proportion of observation time spent in different sectors of the area is presented in Fig. 2.1.

The total number of hours specifically devoted to observing the deer in each month is presented in Table 2.2. Observations commenced during the latter half of October. Access to the study area was restricted in November, as most of the hind cull took place at this time. There were more days of poor visibility in February than in the other months of fieldwork.

## 2.3 Statistical Methods

In the statistical analyses that are presented in this chapter I have taken the group of deer, rather than the individuals constituting a group, as the unit of data. Red deer are sociable animals [illegible] and the actions of one animal within such a group is certainly not independent of its fellow group members.

Table 2.1 The Beaufort Scale

| Force | Description | Equivalent Wind speed $ms^{-1}$ at 10m above ground | | Specification for use on land |
|---|---|---|---|---|
| | | Mean | Limits | |
| 0 | Calm | 0.0 | 0.0- 0.2 | Calm; smoke rises vertically. |
| 1 | Light air | 0.8 | 0.3- 1.5 | Direction of wind shown by smoke draft, but not by wind vane. |
| 2 | Light breeze | 2.4 | 1.6- 3.3 | Wind felt on face; leaves rustle; ordinary vane moved by wind. |
| 3 | Gentle breeze | 4.3 | 3.4- 5.4 | Leaves and small twigs in constant motion; wind extends light flag. |
| 4 | Moderate breeze | 6.7 | 5.5- 7.9 | Raises dust and loose paper; small branches are moved. |
| 5 | Fresh breeze | 9.3 | 8.0-10.7 | Small trees in leaf begin to sway; crested wavelets form on inland waters. |
| 6 | Strong breeze | 12.3 | 10.8-13.8 | Large branches in motion, whistling heard in telegraph wires; umbrellas used with difficulty. |
| 7 | Near gale | 15.5 | 13.9-17.1 | Whole trees in motion, inconvenience felt when walking against wind. |
| 8 | Gale | 18.9 | 17.2-20.7 | Breaks twigs off trees; generally impedes progress. |

Source: Meteorological Office - Observer's Handbook (1969) H.M.S.O.

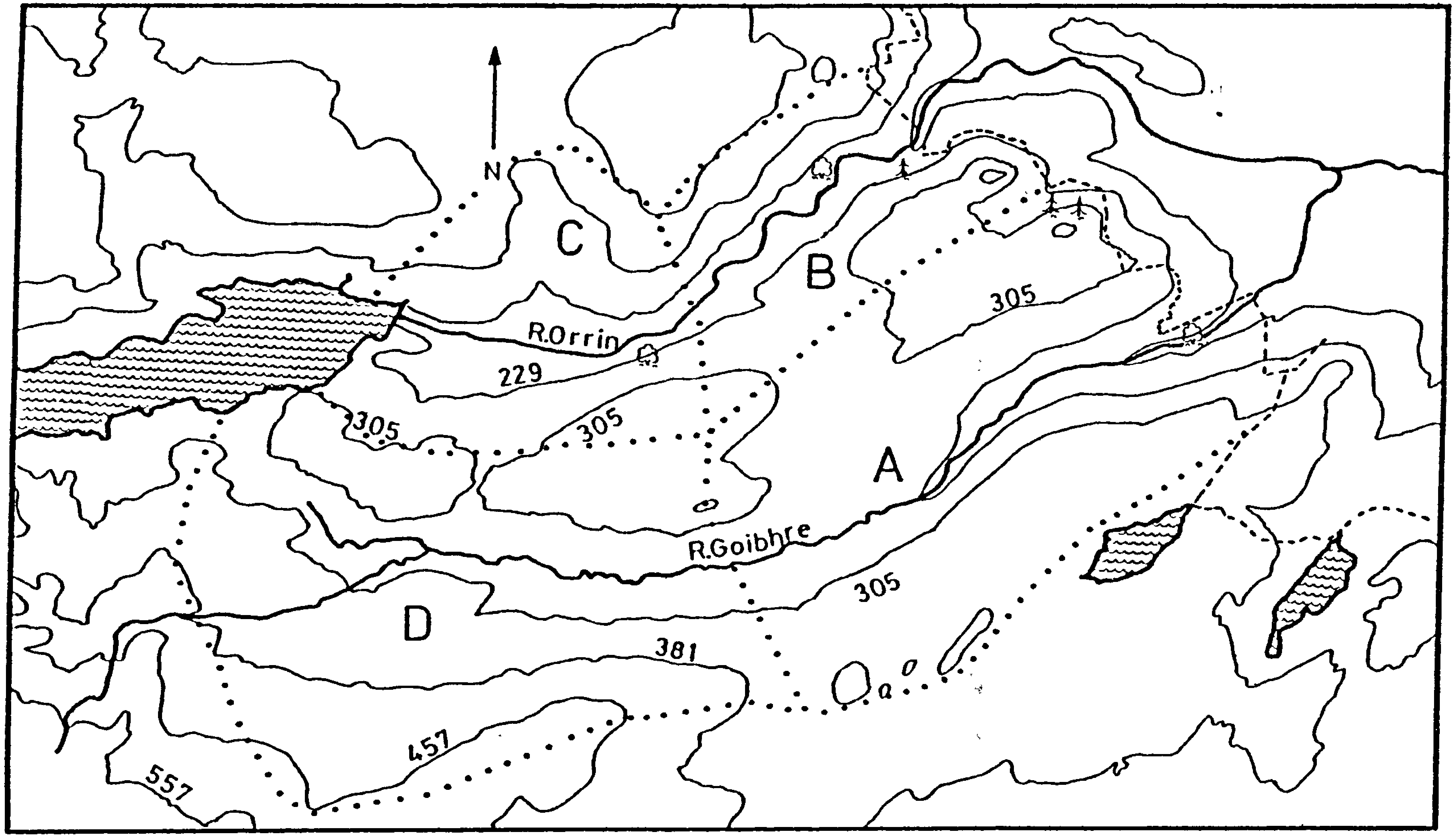


Figure 2·1 The proportion of observation time spent in different sectors of the study area
A=35·7%, B=27·3%, C=19·5%, D=17·5%

Table 2.2 The Number of Hours Devoted to Observing Deer During Fieldwork

| October | November | December | January | February | March |
|---|---|---|---|---|---|
| 30 | 43 | 74 | 60 | 51 | 61 |

If individual group members are used in the analysis, the assumption of statistical independence of the observations is violated. The activity class of a group of animals is assigned in accordance with what the majority are doing; similarly the plant community recorded for a particular activity reflects the choice of the majority of animals in a group. An examination of the animals constituting groups revealed that on average over 90% of the deer were engaged in the same activity.

Where appropriate, the procedure of Crosstabulation (Contingency Table Analysis) has been used in the analysis of the data. The sub-program 'CROSSTABS' of the computer package Statistical Package for the Social Sciences (S.P.S.S.) was utilised for this purpose. Chi-square is a commonly used statistic which can be used to test for association between two discrete-valued variables in these circumstances. As a consequence of the arrangement of the dependent and independent variables in the tables, an examination of the column percentages (figures in parenthesis) in the tables reveals the form of the association indicated by the value of Chi-square. Column percentages of adjacent cells will approach equality with increasing statistical independence (lack of association) of the variables.

## 2.4 Results

To produce figures illustrating the distribution of groups of deer during the study period, a base map was produced using a Ferranti Freescan Digitiser. Basic physiographic information was recorded from the large-scale map drawn for this study and onto which deer locations from field observations had been recorded by means of X and Y co-ordinates.

The groups of animals that had been recorded in the field were assigned to classes according to the sex of the majority of the adult animals present. Hind groups consisted of adult females, yearlings and calves; immature stags also associated with these groups. Stag groups consisted of mature male animals; immature stags and yearling males also associated with these groups. Hinds were rarely observed to associate with mature males outside of the rut. A high degree of segregation of the sexes was observed in this area and 95% of groups containing mature stags were all-male in composition (see also: Jackes 1974).

The lack of sharp discontinuities between vegetation types on the study area has been mentioned in Chapter 1. To facilitate the interpretation of the results, particularly with respect to the intergradation of certain types of vegetation, a simplified classification has been produced. Five categories based on the types recorded in Chapter 1, are recognised. The groupings are as follows:

(i) Dry Heath - *Callunetum vulgaris*; approximate area 15-20%.

(ii) Damp Heath - *Trichophoreto-Callunetum*, *Molinieto-Callunetum* and *Molinia-Myrica*, *Calluna-Eriophorum vaginatum*; approximate area 50-60%.

(iii) Grass/Heath - *Callunetum* interspersed with areas of grass as in (iv), but excluding *Juncus* grassland; approximate area < 5%.

(iv) Species Poor Grassland - Species poor *Agrosto-Festucetum*, *Nardetum sub-Alpinum* and *Juncus* grassland; approximate area 10%.

(v) Molinia - *Molinia* grassland; approximate area < 5%.

(vi) Bog - *Trichophoreto-Eriophoretum*; approximate area 5%.

Category (vi) was not considered further in this section due to its almost complete avoidance by deer during winter.

### 2.4.1 The Distribution of Deer During Winter

The overall distribution of hind and stag groups throughout the winter is presented in Fig. 2.2. Although there are areas where the range occupied by both sexes overlap, much of the ground between the two glens is mainly used by hinds, with stags tending to be distributed around the periphery.

As this aggregated picture of the distribution of the sexes may mask any temporal changes in the pattern of range use, the data has been sub-divided into discrete periods. Data are considered in monthly increments, apart from those of October and November, which were amalgamated, since few deer

## Key to Figures 2.2 - 2.7

Water bodies and rivers - blue

Deer fence - black

Stag groups - blue triangles

Hind groups - red circles

Figure 2·2
The Distribution
of Hinds & Stags
During Winter

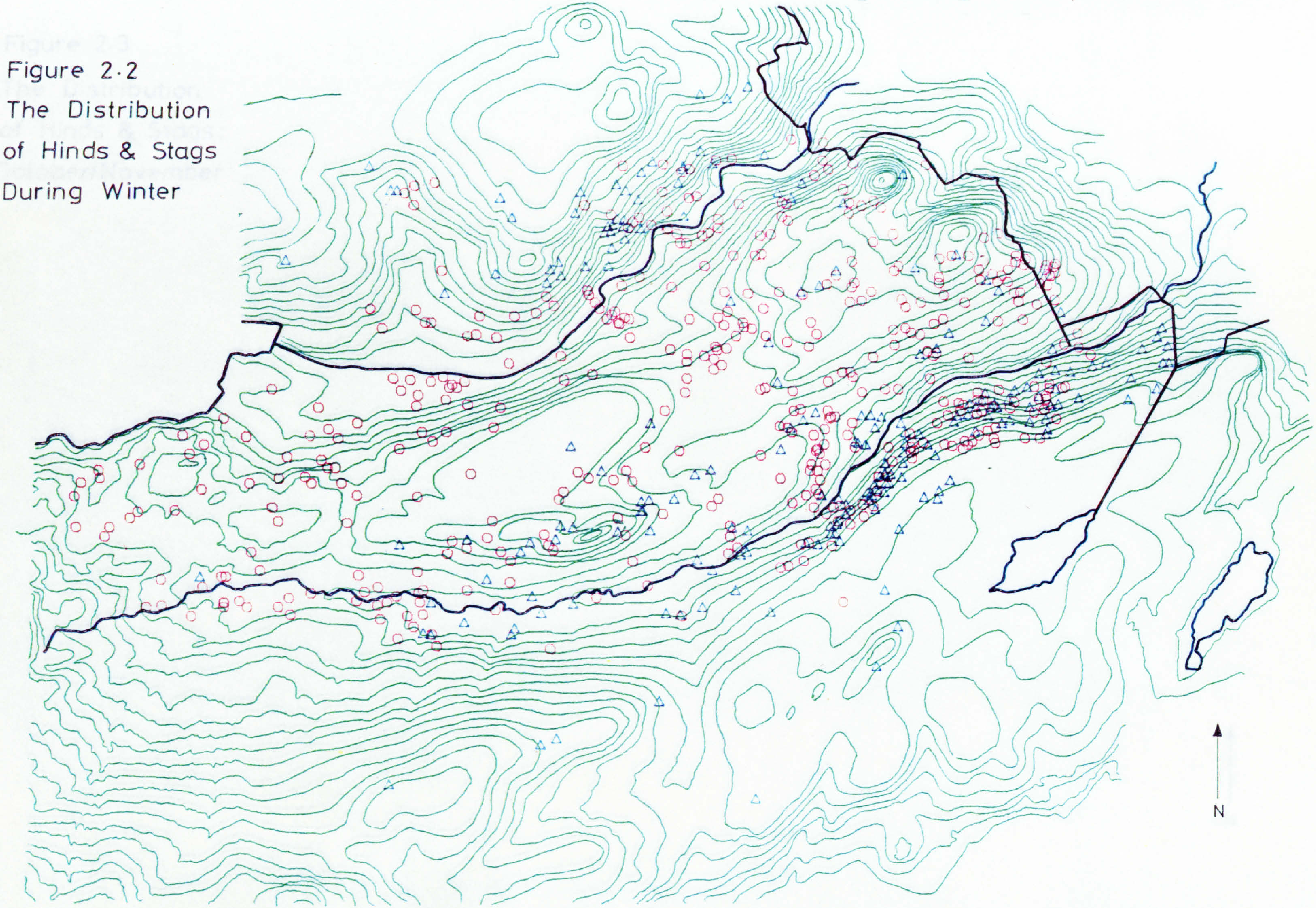


Figure 2.3
The Distribution
of Hinds & Stags:
October/November

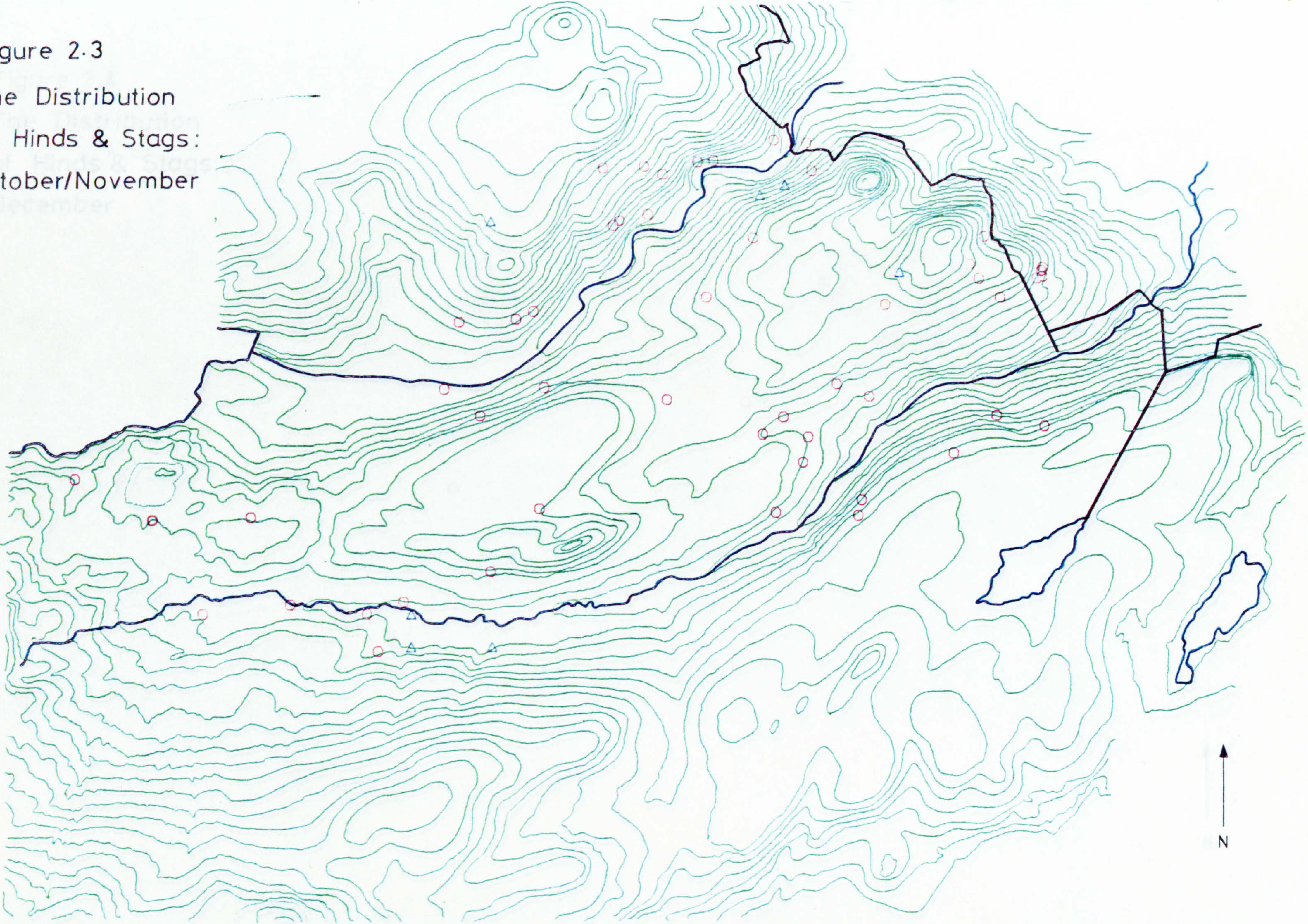


Figure 2.4
The Distribution
of Hinds & Stags:
December

Figure 2.5
The Distribution
of Hinds & Stags:
January

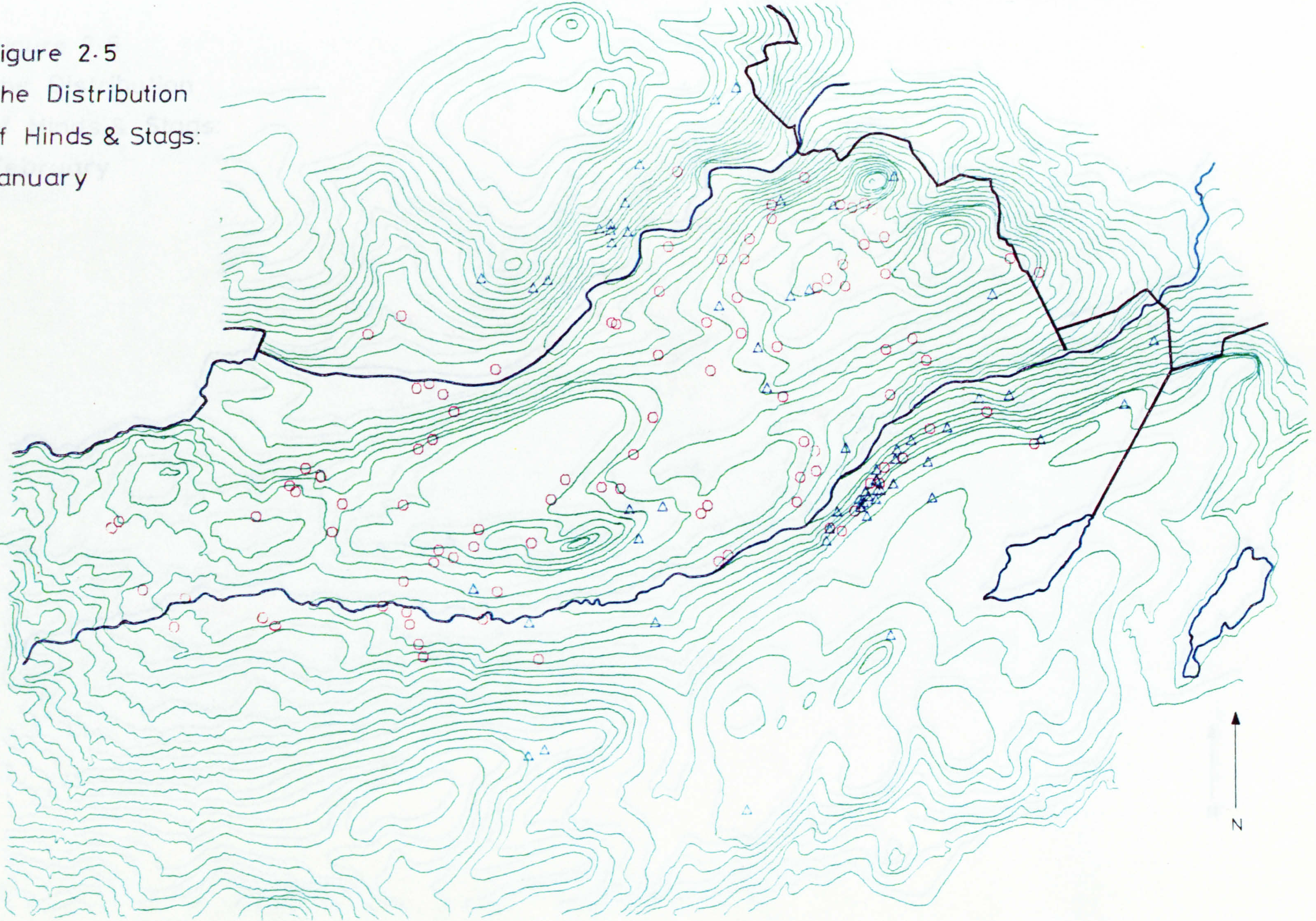


Figure 2.6
The Distribution
of Hinds & Stags:
February

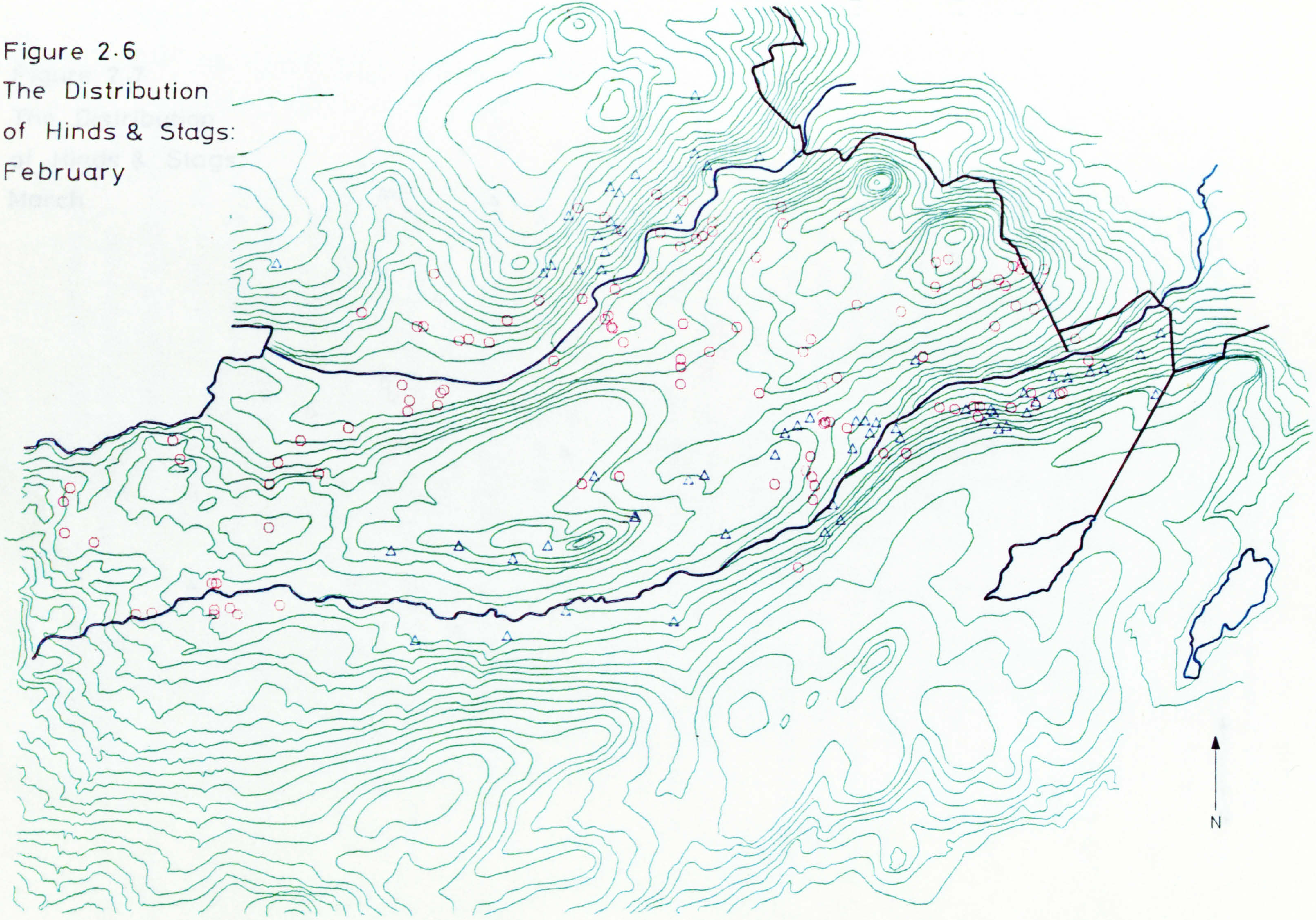
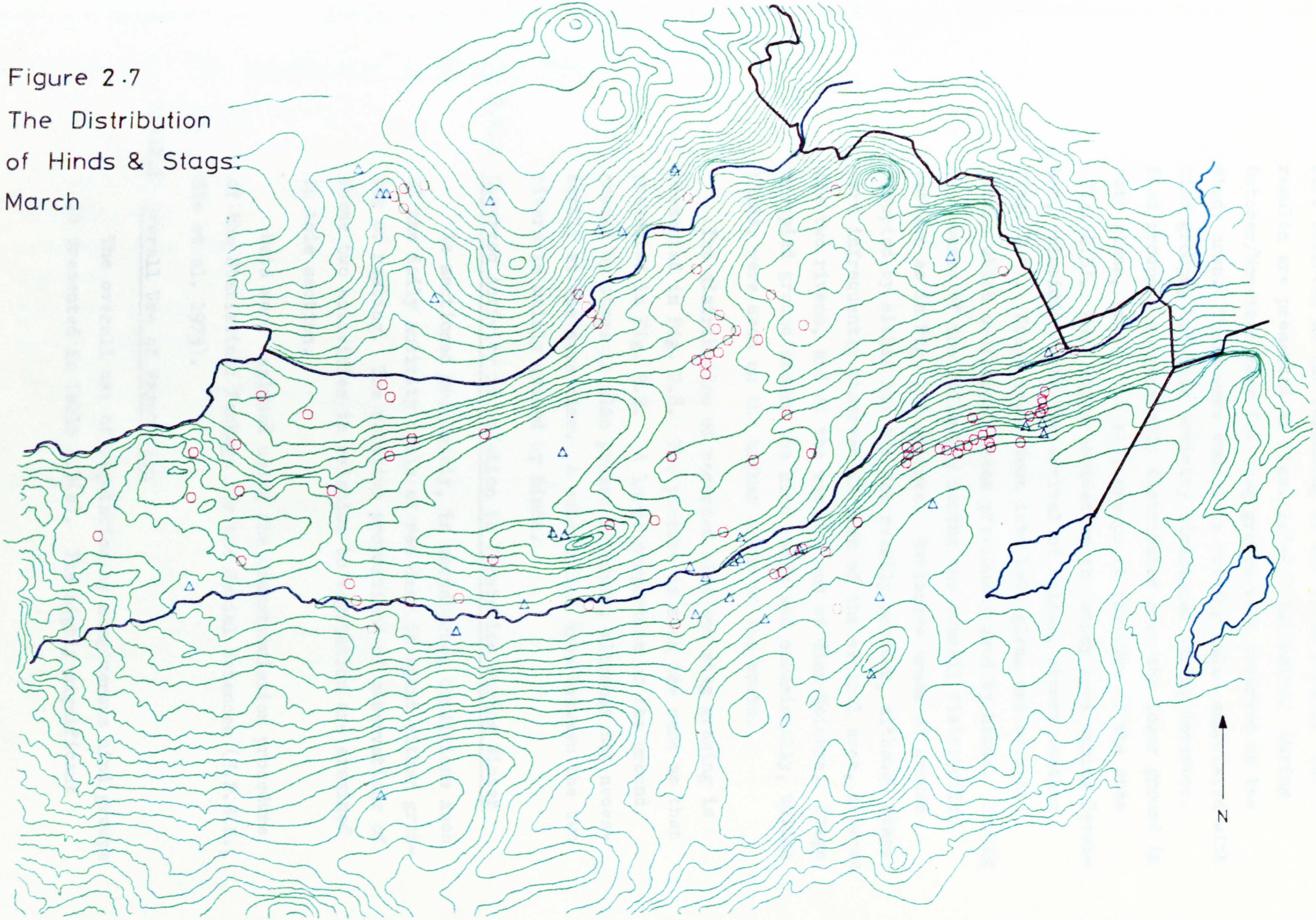


Figure 2.7
The Distribution
of Hinds & Stags:
March



were observed at the beginning of the field season. The results are presented as Figs. 2.3-2.7 inclusive. During October/November very few stag groups were observed on the study area. There were some late rutting males associated with hind groups, but this activity diminished during November. Hind groups were generally distributed over the lower ground in both glens, with a few stag groups at the edge of the area (Fig. 2.3). More stags arrived on the study area during December, coinciding with the arrival of colder, stormy weather (Fig. 2.4). Stags moved down into both glens and occupied ground which overlapped areas previously used by hinds. During the course of the following months the overall distribution pattern as in Fig. 2.2 emerges. Exclusive areas of ground occupied by either sex are not readily obvious, although stags were infrequently observed in much of the central area, between the two rivers, and at the western end of Glen Goibhre. Stags occupied ground around the hind range and occasionally, unlike hinds, were seen on the higher areas to the south.

The distribution of recorded hind and stag grazing is presented in Fig. 2.8. The picture is much the same as that presented in Fig. 2.2. A large proportion of the ground grazed by stags is also grazed by hinds, although not necessarily at the same time. A substantial area between the two rivers is mainly grazed by hinds.

### 2.4.2 Observed Activity in Relation to Vegetation During Winter

As mentioned previously, in undisturbed conditions much of the daily activity cycle of red deer is spent either grazing or resting. The relative proportions of observations of these two activities in relation to vegetation are examined in this section.

Data were analysed using the Crosstabulation procedure of the Statistical Package for the Social Sciences (S.P.S.S., Nie et al. 1975).

#### 2.4.2.1 Overall Use of Vegetation

The overall use of vegetation by stag versus hind groups is presented in Table 2.3(a). The highly significant

Figure 2·8 The distribution of grazing deer during winter

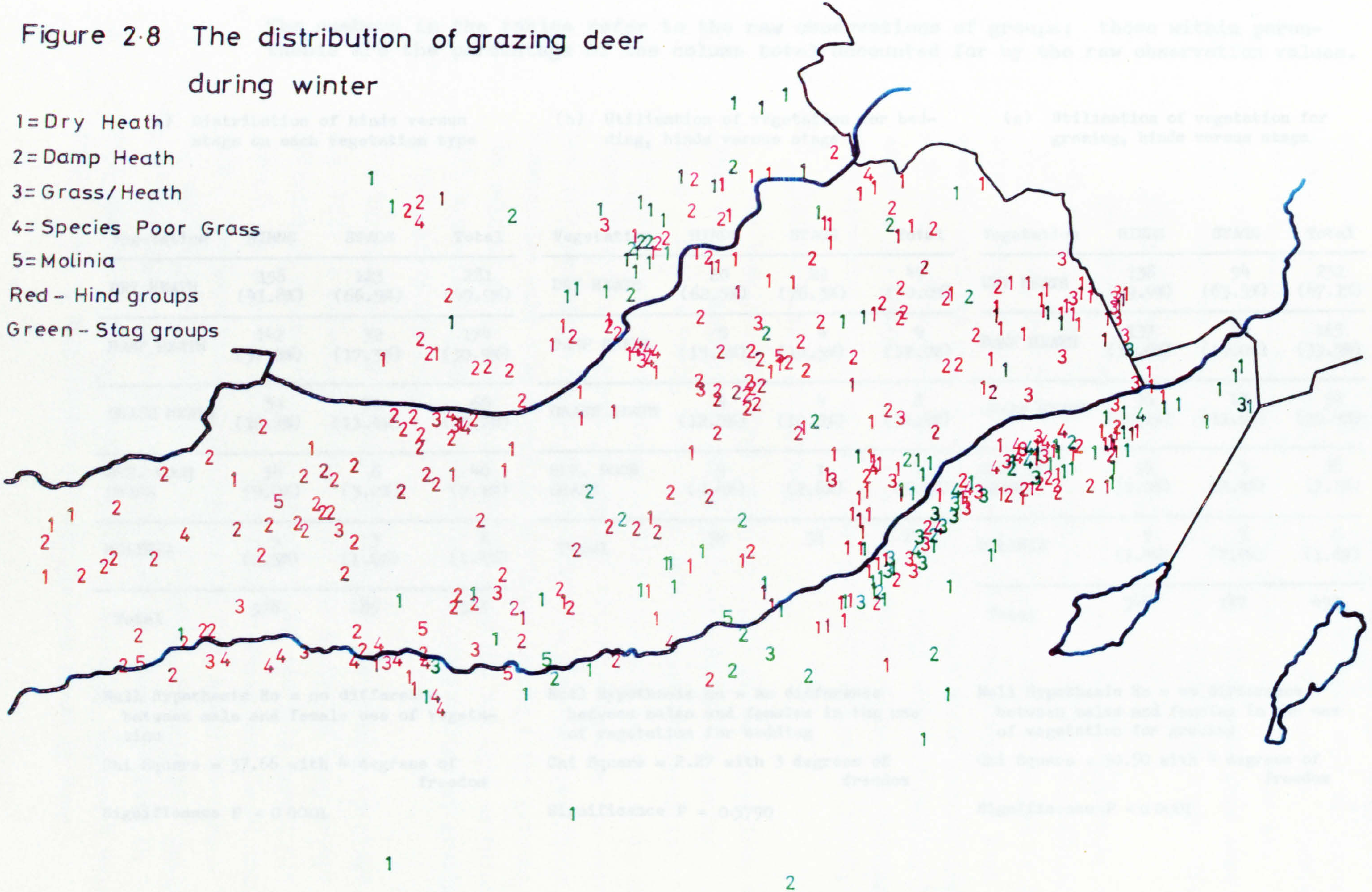


Table 2.3 The utilisation of vegetation by hinds and stags during winter.

The numbers in the tables refer to the raw observations of groups; those within parenthesis are the percentage of the column total accounted for by the raw observation values.

(a) Distribution of hinds versus stags on each vegetation type

| Vegetation | HINDS | STAGS | Total |
|---|---|---|---|
| DRY HEATH | 158<br>(41.8%) | 123<br>(66.5%) | 281<br>(49.9%) |
| DAMP HEATH | 142<br>(37.6%) | 32<br>(17.3%) | 174<br>(30.9%) |
| GRASS HEATH | 39<br>(10.3%) | 21<br>(11.4%) | 60<br>(10.7%) |
| SPP. POOR GRASS | 34<br>(9.0%) | 6<br>(3.2%) | 40<br>(7.1%) |
| MOLINIA | 5<br>(1.3%) | 3<br>(1.6%) | 8<br>(1.4%) |
| Total | 378 | 185 | 563 |

Null Hypothesis Ho = no difference between male and female use of vegetation

Chi Square = 37.66 with 4 degrees of freedom

Significance $P < 0{\cdot}0001$

(b) Utilisation of vegetation for bedding, hinds versus stags

| Vegetation | HINDS | STAGS | Total |
|---|---|---|---|
| DRY HEATH | 20<br>(62.5%) | 29<br>(76.3%) | 49<br>(70.0%) |
| DAMP HEATH | 5<br>(15.6%) | 4<br>(10.5%) | 9<br>(12.9%) |
| GRASS HEATH | 4<br>(12.5%) | 4<br>(10.5%) | 8<br>(11.4%) |
| SPP. POOR GRASS | 3<br>(9.4%) | 1<br>(2.6%) | 4<br>(5.7%) |
| Total | 32 | 38 | 70 |

Null Hypothesis Ho = no difference between males and females in the use of vegetation for bedding

Chi Square = 2.27 with 3 degrees of freedom

Significance $P = 0{\cdot}5790$

(c) Utilisation of vegetation for grazing, hinds versus stags

| Vegetation | HINDS | STAGS | Total |
|---|---|---|---|
| DRY HEATH | 138<br>(39.9%) | 94<br>(63.9%) | 232<br>(47.1%) |
| DAMP HEATH | 137<br>(39.6%) | 28<br>(19.0%) | 165<br>(33.5%) |
| GRASS HEATH | 35<br>(10.1%) | 17<br>(11.6%) | 52<br>(10.5%) |
| SPP. POOR GRASS | 31<br>(9.0%) | 5<br>(3.4%) | 36<br>(7.3%) |
| MOLINIA | 5<br>(1.4%) | 3<br>(2.0%) | 8<br>(1.6%) |
| Total | 346 | 147 | 493 |

Null Hypothesis Ho = no difference between males and females in the use of vegetation for grazing

Chi Square = 30.50 with 4 degrees of freedom

Significance $P < 0{\cdot}0001$

result ($\chi^2_{[4]}$ = 37.66, $P < 0.0001$) reveals that differential vegetation use occurs between the sexes during winter. Inspection of the column percentages in the table indicates that the major source of variation between the sexes is in the greater observed use being made of Dry Heath by stag groups and a greater use being made of Damp Heath by hind groups. Hinds also made somewhat greater use of areas of Species Poor Grass than stags did.

### 2.4.2.2 Vegetation used for bedding

The lack of significance in the result of the comparison of hinds versus stags in the utilisation of vegetation for bedding ($\chi^2_{[3]}$ = 2.27, $P = 0.52$), reveals the similarity of choice by the sexes (Table 2.3(b)). For both hind and stag groups, the most heavily utilised type of vegetation was dwarf shrub communities, with over 60% of hinds and over 75% of stags observed bedding in areas of Dry Heath. Both sexes avoid wetter areas when bedding, an observation which has also been recorded by Staines (1970).

### 2.4.2.3 Vegetation used for grazing

The highly significant result obtained in the comparison of hinds versus stags in the range of vegetation grazed during winter ($\chi^2_{[4]}$ = 30.50, $P < 0.0001$), reveals that differential utilisation occurs between male and female deer on the study area (Table 2.3(c)). The main sources of variation between the sexes are as reported for Table 2.3(a). Overall, Dry and Damp Heath communities were quantitatively the most important for grazing (as well as being the most extensive in area) and were associated with approximately 80 percent of all the observations of grazing by both hinds and stags.

The seasonal use of vegetation types for grazing by stags and hinds is presented in Fig. 2.9. The number of stag groups recorded in October/November was very low, and this result may present an atypical picture of grazing by these animals at this time. The importance of Calluna to the deer stock throughout the winter on the study area can be readily appreciated. Calluna has been shown to be important to deer in other locations in Scotland also. (See: Staines 1977 and Mitchell, Staines & Welch 1977). Use of Grass/Heath and Species Poor Grass by deer

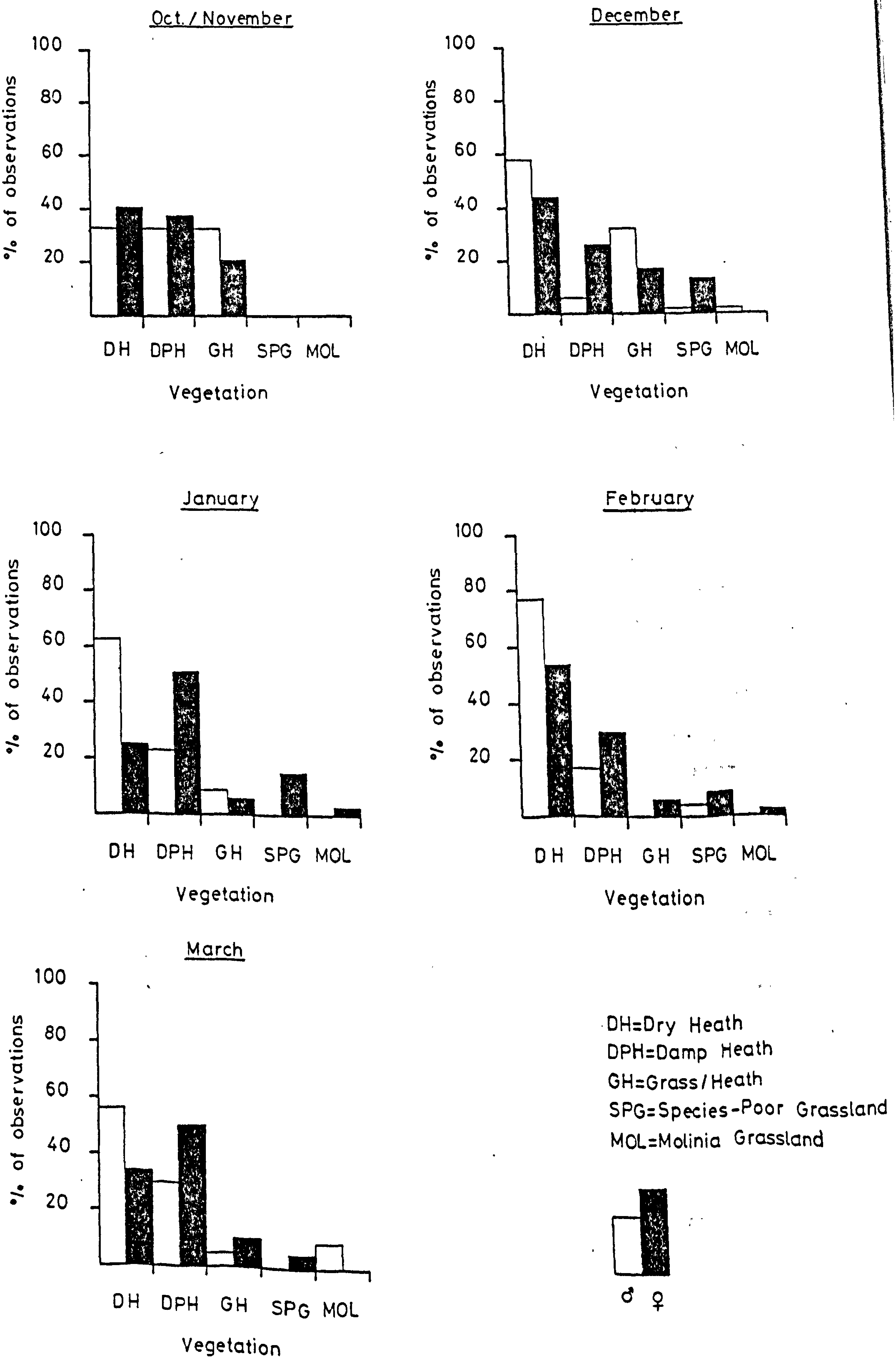


Figure 2·9 Seasonal use of vegetation for grazing by stags and hinds declined over the winter. This pattern of utilisation probably reflects the decline in availability of grass species from repeated grazing, particularly of the *Agrosto-Festucetum* communities, and the presence of snow during much of January and February. The proportion of hinds grazing on areas of Species Poor Grass was greater than that of stags; hinds also were observed to make greater use of Grass/Heath than stags in late winter. *Molinia* grassland received very low use throughout winter by both hinds and stags, which reflects the poor nutritional quality of this deciduous dominant species during winter.

### 2.4.3 Observed Activity During Winter

A highly significant result ($\chi^2_{[1]} = 15.54$, $P = 0.0001$) is obtained from the comparison of hinds versus stags in observed activity during winter (Table 2.4(a)). The column percentages in the Table reveal that hinds were observed to spend more time grazing than stags, which, conversely, were observed to spend more time bedded over the winter as a whole. The activity data have also been sub-divided into discrete periods as in section 2.4.1, and are presented in Tables 2.4-2.5 inclusive. In October/November, Table 2.4(b), the results indicate that there was no significant difference between the proportions of hind and stag groups bedded or grazing ($\chi^2_{[1]} = 1.09$, $P = 0.30$). However with such a small sample of stag groups this result must be treated with caution. For the period December to March the results are not statistically conclusive (Tables 2.4(c) - 2.5(c)). However the levels of significance for the December, January and March $\chi^2$ tests approach $P = 0.05$ (February, $P = 0.028$), and these results support the interpretation of Table 2.4(a) that overall, hind groups spent more time grazing than stag groups, which spent more time bedded during daylight hours.

Since red deer exhibit cycles of grazing and resting in undisturbed conditions, the timing of observations alone may have contributed to results obtained above, since it is possible that stags were observed predominantly at a particular time of day, when more groups were liable to be bedded rather than grazing. This situation is unlikely to have occurred, since

Table 2.4 The activity of hinds and stags during winter (i)

(a) Overall activity during winter, hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 32<br>(8.5%) | 38<br>(20.5%) | 70<br>(12.4%) |
| GRAZING | 346<br>(91.5%) | 147<br>(79.5%) | 493<br>(87.6%) |
| Total | 378 | 185 | 563 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 15.54, 1 degree of freedom

Significance P = 0.0001

(b) Activity during October/November, hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 9<br>(20.9%) | 3<br>(50.0%) | 12<br>(24.5%) |
| GRAZING | 34<br>(79.1%) | 3<br>(50.0%) | 37<br>(75.5%) |
| Total | 43 | 6 | 49 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 1.09, 1 degree of freedom

Significance P = 0.2963

(c) Activity during December, hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 2<br>(3.6%) | 6<br>(16.2%) | 8<br>(8.6%) |
| GRAZING | 54<br>(96.4%) | 31<br>(83.8%) | 85<br>(91.4%) |
| Total | 56 | 37 | 93 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 3.07, 1 degree of freedom

Significance P = 0.0800

Table 2.5 The activity of hinds and stags during winter (ii)

(a) Activity during January, hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 7<br>(8.3%) | 11<br>(20.4%) | 18<br>(13.0%) |
| GRAZING | 77<br>(91.7%) | 43<br>(79.6%) | 120<br>(87.0%) |
| Total | 84 | 54 | 138 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 3.21, 1 degree of freedom

Significance P = 0.0734

(b) Activity during February, hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 7<br>(6.5%) | 11<br>(19.0%) | 18<br>(10.8%) |
| GRAZING | 101<br>(93.5%) | 47<br>(81.0%) | 148<br>(89.2%) |
| Total | 108 | 58 | 166 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 4.86, 1 degree of freedom

Significance P = 0.0275

(c) Activity during March hinds versus stags

| Activity | HINDS | STAGS | Total |
|---|---|---|---|
| BEDDED | 7<br>(8.0%) | 7<br>(23.3%) | 14<br>(12.0%) |
| GRAZING | 80<br>(92.0%) | 23<br>(76.7%) | 103<br>(88.0%) |
| Total | 87 | 30 | 117 |

Null Hypothesis Ho = no difference between male and female activity

Chi Square = 3.60, 1 degree of freedom

Significance P = 0.0576

areas frequented by stags were not observed at the same time each day during fieldwork. In Fig. 2.10 histograms are presented which show the proportions of observations recorded during fieldwork, for hind and stag groups. Observations were distributed throughout the day, although the proportions of both male and female groups recorded during any single two hour time period do not approach parity in many cases. This is not unexpected, since the probability of observing both hind and stag groups in equal proportions, even in areas of overlapping range is highly unlikely. The results obtained above may therefore be a genuine phenomenon, and are not the result of a bias in sampling.

### 2.4.4 Observed Deer Distribution in Relation to Altitude and Aspect

It has been shown in section 2.4.1 that on the study area there is at least a partial segregation of hinds and stags. Other workers have reported hinds range to higher maximum altitudes than stags during winter (see: Lowe 1966 and Watson & Staines 1978). Furthermore the aspect of sites selected for grazing may be of considerable importance in relation to the need for shelter during winter, and the difference in sheltering requirements of stags and hinds, as suggested by Jackes (1974). In this section the distribution of hinds and stags is examined in relation to these factors.

#### 2.4.4.1 Distribution in Relation to Altitude

The study area is not characterised by an extensive range of altitude (168 - 396m). Areas occupied mainly by stags did however rise to higher altitudes than those occupied by hinds (Fig. 2.2).

The data relating to the altitude of observations was examined for normality using probability paper, and was found, in a number of cases, to be highly skewed in one tail of the distribution. In this case, with an assymetric distribution, the median* is probably a better statistic to describe the central tendency of the data, than the mean (see: Sokal & Rohlf 1969). Figure 2.11 shows median values and 95% confidence limits (Snedecor & Cochran 1967) for deer distribution with

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*Calculation of the median and approx. 95% confidence limits is described in section 3.3.2.

Figure 2.10 Daily distribution of stag and hind observations during winter

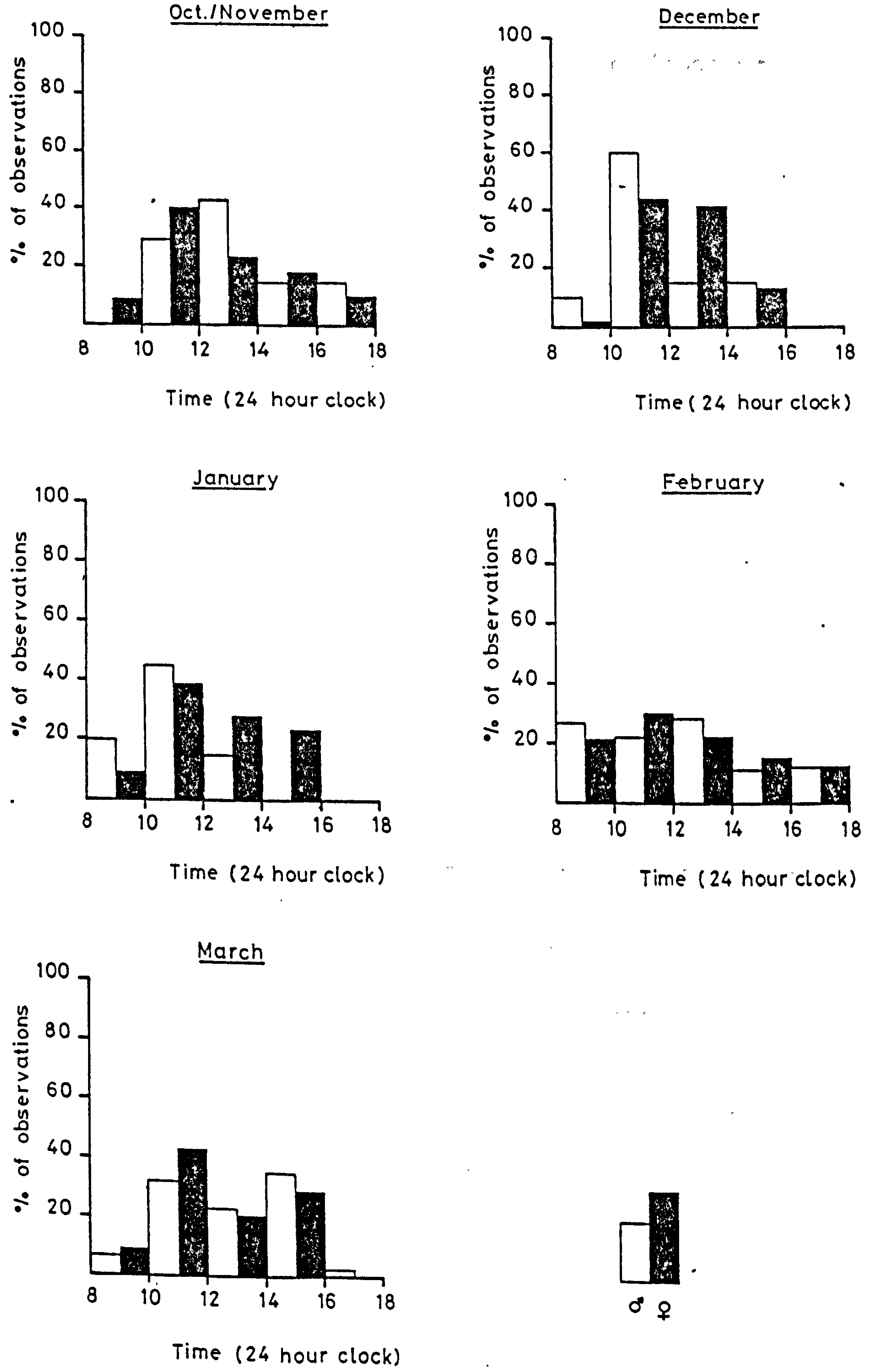
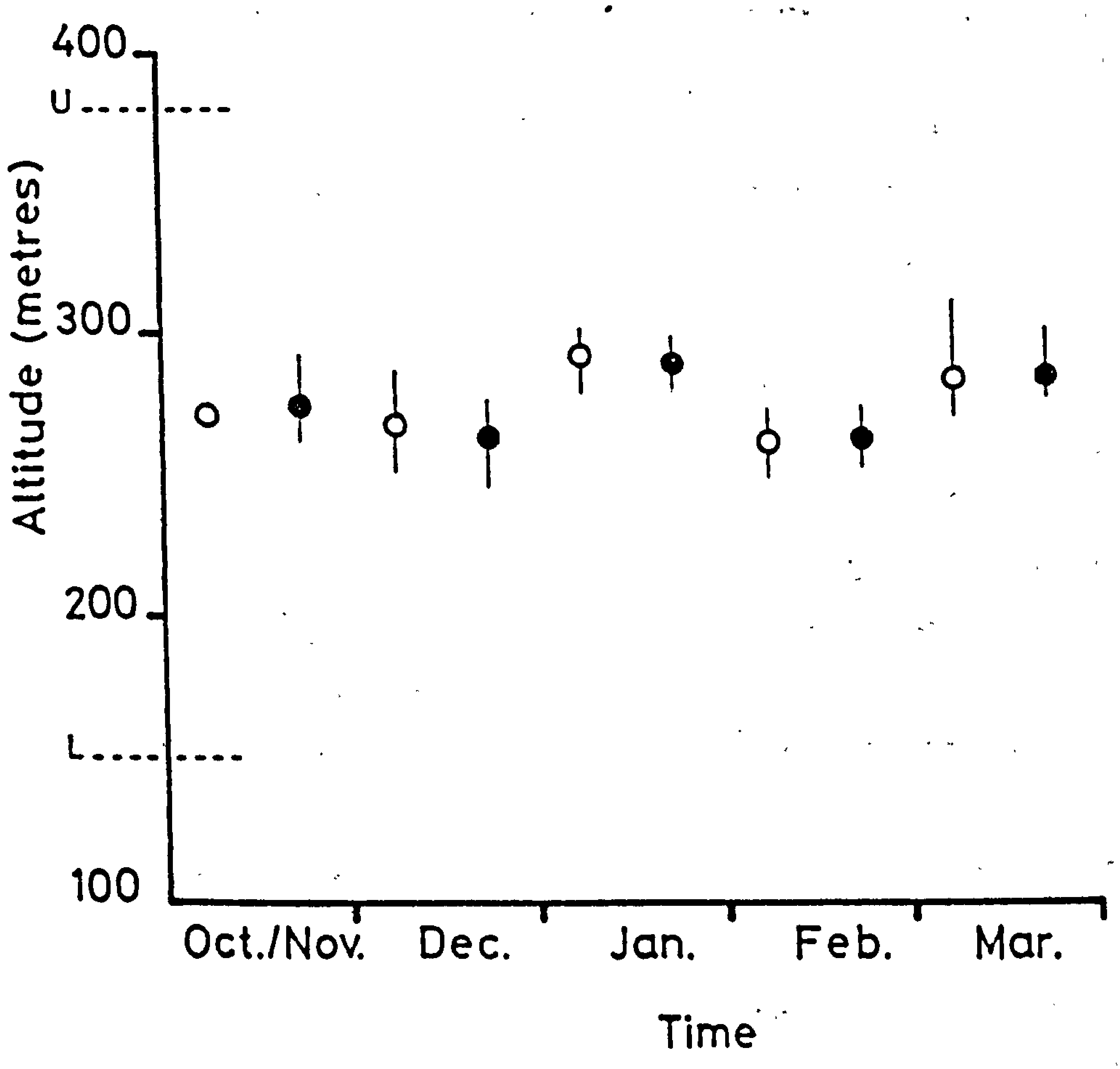


Figure 2.11 Altitudinal distribution of deer during winter

Median values & 95% confidence limits



U..... Upper altitudinal range of study area

L..... Lower altitudinal range of study area

○ Stag groups

● Hind groups

respect to altitude. Confidence limits have not been attached to the median of the first of the set of values of stag observations, because of the small sample size involved. There are no significant differences in the altitudinal use of the area for the months December to March, and little overall difference over the winter as a whole. This result reflects the limited altitudinal range of available ground in the study area, and indicates that hinds and stags utilise ground of similar altitude.

### 2.4.4.2 Distribution in relation to aspect

The distribution of deer throughout winter in relation to aspect is presented in the form of histograms in Fig. 2.12. The same constraints as mentioned above apply to the data for stag distribution during October/November. During January, February and March there is a fairly high degree of similarity in the proportion of sites of similar aspects utilised by both hinds and stags.

The proportions of available aspect on the study area were assessed by the random placement of a grid over a 1 : 63360 map, and the recording of the aspect of points which fell within 218 grid squares. This information is also expressed in the form of a histogram in Fig. 2.13. The overall use of aspect by deer (hinds and stags) has been superimposed on the proportions of available aspect in Fig. 2.13, and, when considered together with Fig. 2.12, reveals that deer are not occupying sites at random; greater use is made of certain aspects in relation to their availability.

Aspect can be of considerable importance in relation to shelter, and the selection of particular sites by hinds and stags may reflect the prevailing weather conditions and the available land forms on the respective areas of range. Use of open areas, without any readily assignable aspect, and therefore little shelter, was low throughout the winter as a whole. Seventeen per cent of hind observations were on open ground during October/November, but this declined considerably in December (4%), and remained low during the rest of the winter. Stags also avoided open areas from December to March.

Figure 2.12 Distribution of deer in relation to aspect

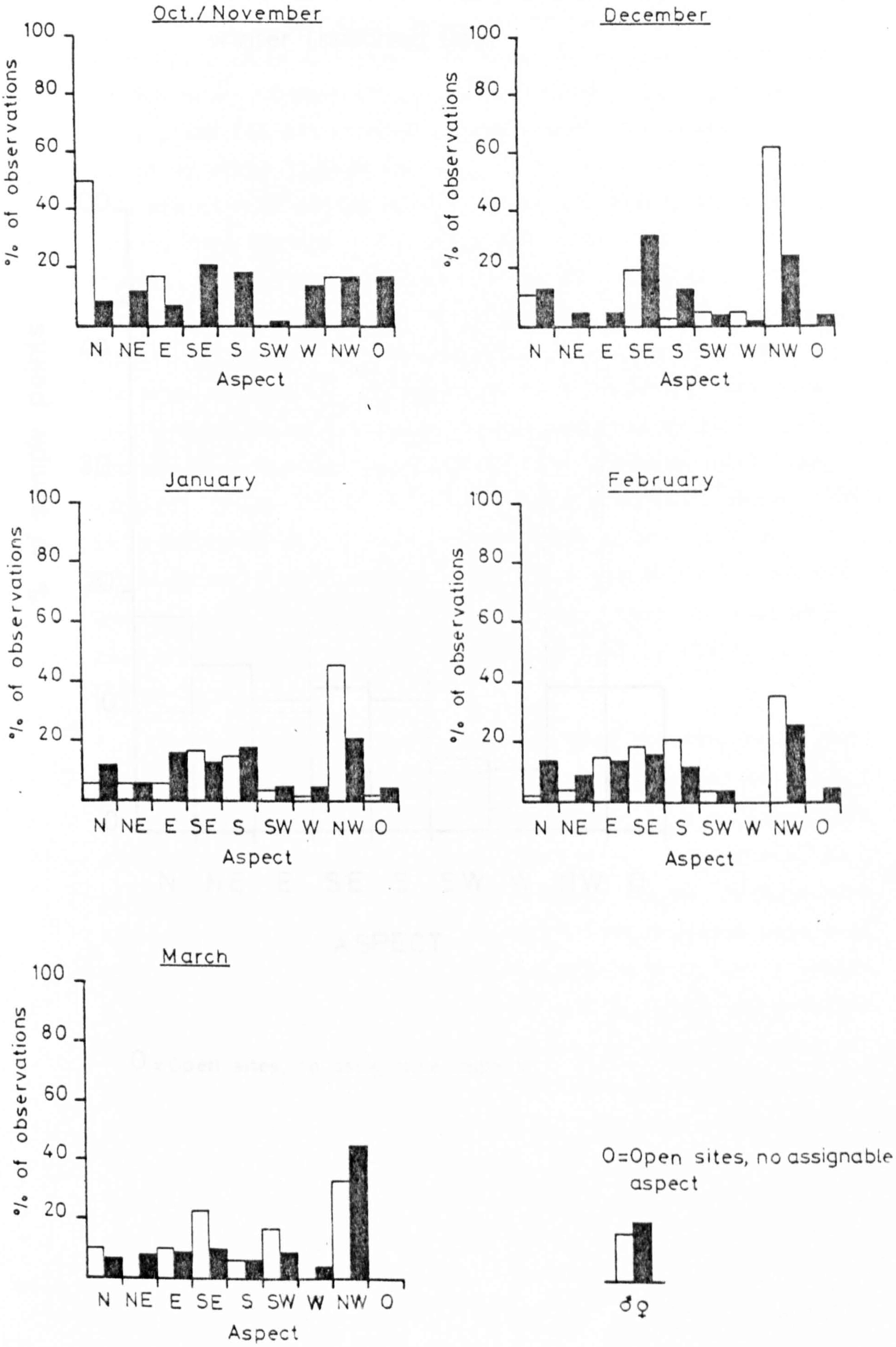
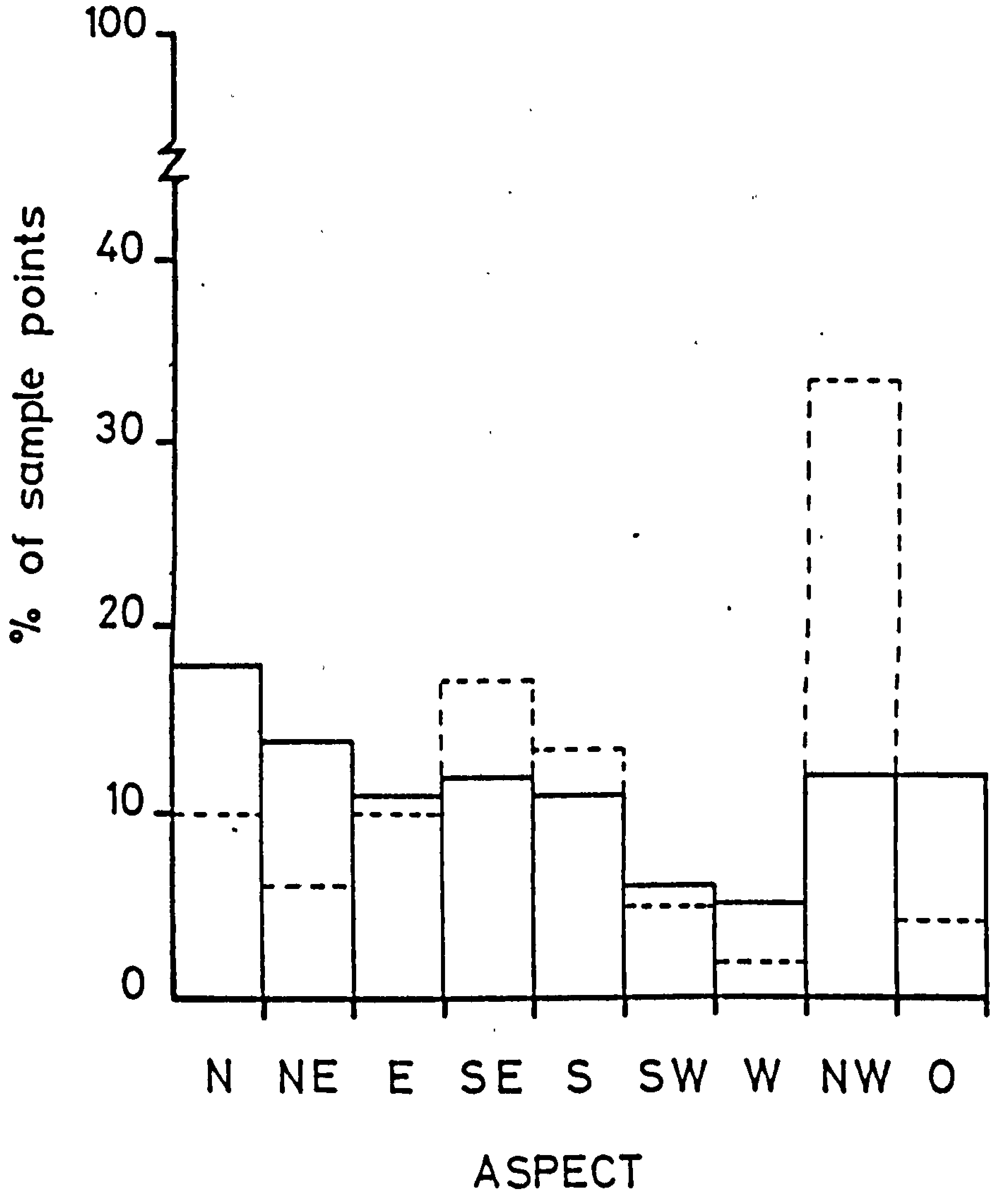


Figure 2.13 The distribution of aspect on the study area (solid line) and observed use by deer during winter (hatched line)



O = Open sites, no assignable aspect

## 2.5 Discussion

### 2.5.1 General Distribution

There are reports of the geographical separation of the sexes for much of the year from even the earlier accounts of the red deer: Evans (1890), Millais (1904) and Thorburn (1921), and the traditional occupation of such areas is mentioned by Wynne-Edwards (1962). On the study area red deer made use of much of the ground within the glens, although the higher, more exposed areas above the glens were frequently avoided. The geographical separation of the sexes in this area is not as marked as earlier reports, from elsewhere, suggest is typical of this species. When stags arrived in the area, in numbers, during November - December, they occupied ground around the areas already utilised by hinds. This pattern of occupation has been observed elsewhere with this species: Delap (1957) in Ireland and N W England, Ahlen (1965b) in Scandinavia and by Lowe (1966) on the island of Rhum. Although there were certain areas where predominantly one sex was observed, there were also areas where hind and stag home ranges overlapped, as also recorded by Darling (1937) in Wester Ross.

There have been suggestions that hind and stag range may differ in environmental quality, Jackes (1974) and Watson & Staines (1978). Watson & Staines reported, from an inspection of geological maps, that ground occupied by hinds generally overlay more base-rich rocks than that of stags. This in turn might be expected to manifest itself in the superior nature of the grazings on hind ground, which has been reported by Watson & Staines (1978) and Jackes (1974). While it was not possible to delineate home ranges on the study area with any degree of precision, through a shortage of individually recognisable animals, it is possible to generalise about the areas mainly occupied by either hinds or stags. An examination of geological maps, both solid and drift (Chap. 1), revealed that there was no evidence to suggest that either sex occupied ground overlying superior substrates. However in this area, where rocks are much more uniform, in contrast to the area investigated by Watson & Staines, an approach of this nature is liable to prove to be too superficial, and is unlikely to yield meaningful results. In such a case a detailed soil survey would probably be necessary to determine the existence of any differences in ground occupied by stags and hinds.

## 2.5.2 Distribution and Activity

### 2.5.2.1 The role of vegetation

(a) Grazing

The observations revealed that quantitatively, areas supporting Calluna were most important to deer during winter, and were associated with the majority of the observations of grazing and bedding. Although a similar range of vegetation was grazed overall by both stags and hinds, there were differences in the proportional use of particular communities, and there is evidence that hind diets may be of a higher qualtiy than those of stags during winter (see: Staines & Crisp 1978). The greater use made of Damp Heath areas by grazing hinds does not however appear to readily confer any nutritional advantage over stags, which were observed to make more use of Dry Heath areas. The range of digestibility of bog species, such as are found in Damp Heath communities, when sampled in September, has been reported to be, only at best, comparable to that of Calluna (Grant & Campbell 1979). Hinds may be grazing Damp Heath areas therefore, because of the Calluna content, rather than as a consequence of the presence of other species; a suggestion which is supported by the results of the analysis of the diet in Chap. 3. The differential use of Dry and Damp Heath areas by hinds and stags may result from the occupation of particular areas of range in the first place, rather than specific selectivity (see also: Harper et al. 1967).

Hinds were observed to make more use of, and probably had access to, a larger total area of grass communities, particularly of Agrosto-Festucetum and Juncus grassland. Areas dominated by Nardus stricta and also containing Fescue species and Deschampsia flexuosa in Glen Goibhre, were grazed by both sexes. Hinds were similarly reported to have greater areas of well-drained grassland available to them than stags, in the investigation by Watson & Staines (1978). The intensive use and significance of such areas for both sheep and deer has been reported by Hunter (1962); Rawes & Welch (1969); Mutch, Lockie & Cooper (1976); Charles, McCowan & East (1977) and Colquhoun (1971), who also reported that areas dominated by _N. stricta_ were also heavily grazed by deer. The nutritional importance of better grass species (because of the digestible nitrogen content) to sheep grazing heather moorland has been stressed by Milne (1974) and Milne & Bagley (1976); _N. stricta_ has also been considered a potentially useful grazing complement to _Calluna_, despite its popular reputation of being poor quality forage (see: Trinder 1975). In view of these points, therefore, it is possible that hinds on the study area experience a superior diet to stags during winter. However since only general conclusions may be drawn as to the nature of herbivore diets as a result of observations, an investigation of hind and stag diets based on faecal analysis was carried out. The results of this work, which are reported in Chapter 3, are inconclusive, but may indicate a greater frequency of Fescue species in hind diets.

Hinds appeared to spend more time grazing than stags during daylight hours, for much of the winter, and the reason for this may be related to the points discussed above. The amount of time a herbivore spends grazing will be influenced by the vegetation selected, and the availability of particular plant items. Grazing time for a given input of herbage will be longer when areas of closely cropped grass are incorporated into grazing bouts, than if an area of _Calluna_ alone is utilised. This is not implying that deer grazing _Calluna_ are not selective (see: Chap. 4), but there is, under most circumstances a greater availability of food items in such areas. Thus the use of grass areas in winter may entail longer periods of grazing by hinds. Furthermore, low levels of nitrogen in the rumens of Scottish red deer were considered to be possibly bacterial growth-limiting by Hobson et al. (1976), and experiments carried out in N. America have demonstrated that nitrogen and available energy supplements given to deer improved the intake of winter browse species (Ullrey et al. 1975). Similarly, an increase in voluntary intake of forage has been recorded for sheep grazing heather and receiving only small amounts of supplementary nitrogen (0.5g day$^{-1}$) by Milne, Christie & Russel (1979). Higher rumen nitrogen levels in hinds, as a consequence of a better diet, could result in improved rumen function, and a greater forage intake in comparison with stags, and thus contribute towards the observed difference between the proportions of time spent grazing by male and female deer. Systematic observations were, however, only made during daylight, which amount to as little as 8 out of 24 hours in mid-winter, and deer do graze at night also, (Colquhoun (1971) and own observations). There is no apparent reason to suggest that any differences observed between hinds and stags in the proportion of time spent grazing during daylight hours would not persist during darkness. However, results of nocturnal investigations of the red deer have yet to be published

### (b) Bedding

Although differences do exist in the selection of sites for grazing by hinds and stags, both on the study area and elsewhere in Scotland (Charles, McCowan & East 1977), there is however a high degree of similarity between the sexes in the choice of bedding sites, with a strong preference being shown for Dry Heath areas in comparison with other types of vegetation. The selection of bedding sites in areas of Calluna can reduce the energy lost by conduction to cold and wet ground and also from forced convection during windy weather. It was notable that wet areas where resting deer would be subjected to greater conductive heat loss to the ground, and evaporative cooling from the wetting of the pelage, were avoided for this purpose throughout winter. The advantages, in terms of energy conservation, in the selection of Calluna for bedding sites have been considered by Grace & Easterbee (1979), see Appendix 6.1.

### 2.5.2.2 The role of topography

#### (a) Altitude

The spatial distribution of deer in relation to topography, as examined in this chapter was similar for both hinds and stags. In contrast to reports from other studies, Lowe (1966) and Watson & Staines (1978), hinds did not range to greater altitudes than stags. Throughout winter there was no significant difference between hind and stag use of sites in relation to altitude, although it was stags which were observed to make use of the higher ground to the south of Glen Goibhre, on fine days with little or no wind.

#### (b) Aspect

Staines (1970) considered that shelter was important to red deer during winter, and that a variety of aspects, sheltered from all wind directions within the overall home range was probably necessary. Support is lent to this view by the results relating to the aspects of sites utilised by deer. During the period from January onwards, in particular, observations of deer groups were related to a variety of site aspects, the proportional use of which was broadly similar for stags and hinds. This pattern of distribution may reflect site selection in relation to the prevailing weather conditions and the topographical nature of areas of stag and hind range. The selection of sites of particular aspects can avoid the increased energy expenditure caused by chilling winds, and both hinds and stags avoided open areas throughout winter, where there was little topographic shelter. The availability of shelter may be an important overall factor in determining patterns of range use during winter. The influences of aspect and shelter on site utilisation are also examined in later sections.

## 2.6 Summary

1) Deer used much of the study area during winter, but the highest ground above the glens was generally avoided. Hinds and stags occupied separate areas of range to an extent, although there were areas of overlap (Fig. 2.1).

2) A range of vegetation was utilised by deer during the winter. Communities containing Calluna were quantitatively the most important and supported the majority of the observations of grazing and bedding. Hinds made more use of areas containing better grass species, of which there were somewhat greater areas on their range.

3) Hinds appeared to spend more time grazing during daylight hours than stags, which may reflect the availability of food items grazed, and a greater intake of forage as a consequence of higher rumen nitrogen levels.

4) Hinds and stags utilised similar ranges of altitude during winter on the study area. Deer made use of sites with a variety of aspects, but open areas were avoided. This may reflect the influence of prevailing weather conditions and the availability of shelter.

## Chapter 3 An Investigation of Hind and Stag Diets

### 3.1 Introduction

The segregation of the sexes for much of the year, which is a feature of many ungulate species, has been noted for red deer in the previous chapter. Concomitant with this may be differences in diet due to grazing on separate areas of range. In the present study observations have indicated that hind groups had access to a greater area containing better grass species than stags; hinds might therefore be including a higher proportion of such species in their diets.

Investigations of male and female red deer diets, as a consequence of the segregation outlined above, may, in common with dietary studies of other free-ranging herbivores, be difficult to achieve under field conditions. Observations of the grazing animal from even relatively close proximity can give misleading results (see: Wallmo, Gill, Carpenter & Reichart 1973); and unless tame animals are available for study, which may in any case exhibit atypical behaviour patterns, behavioural observations on many species can, of necessity, only be made at distance.

Stomach content analysis can be a useful method when considering the diet of many species; however due to its destructive nature it is frequently unsuitable. Faeces analysis has been used in many dietary studies of herbivores: Baumgartner & Martin (1939); Martin (1954); Hercus (1960); Storr (1961); Stewart (1967); Dunnet, Harvie & Smit (1973); Todd & Hansen (1973); Milner & Gwynne (1974); and Anthony & Smith (1974). Problems and limitations associated with the use of faeces analysis, such as differential digestibility, are mentioned by Stewart (1967); Dunnet, Harvie & Smit (1973); Todd & Hansen (1973) and also Milner & Gwynne (1974). Differential digestibility appears to be a problem associated mainly with soft-leaved species and young material, and is of less consequence when the diet is composed mainly of perennial species, where the degree of encasement of epidermal cells in cutin is greater (see: Storr 1961). Hansen, Peden & Rice, reported in Todd &

Hansen (1973), suggest that the degree of digestion of herbage influenced the mean weight loss per plant fragment to a greater extent than it reduced the total number of fragments. Todd & Hansen could find no statistical difference between frequencies of discernible plant fragments in the rumen contents and faeces of bighorn sheep (Ovis canadensis) during winter. Furthermore they suggest that softer more fragile species, such as encountered on a summer diet, may pass from rumen to colon intact, and could be detected by improved preparation techniques.

The purpose of this part of the study was a comparison of hind and stag diets as a consequence of differential range use. I considered that faecal analysis was a suitable method in view of the nature of the winter diet, characterised by mature perennial plant species. However since culling operations were in progress during part of the study period, rumen contents and faeces were collected to permit an assessment of the value of this method to describe red deer diets during winter.

## 3.2 Method

During the annual cull of hinds carried out on the study area during November/December 1976, samples were collected from the rumens and colons of 15 deer. Approximately one litre of mixed rumen contents and 30 faecal pellets were collected from each animal. Rumen samples were preserved in 10% formalin solution and faecal pellets in formal-acetic acid (85 parts 70% alcohol, 10 parts 40% formalin and 5 parts glacial acetic acid, Anthony & Smith 1974), until they were analysed.

Stag faeces were collected when conditions were favourable, either by observation of the animal defecating on frost or snow covered ground, or tracking in snow; stag and hind tracks were distinguishable. These samples were collected during January/February 1977 and unfortunately do not coincide with the collection of hind material, but circumstances and weather conditions mitigated against collection of stag faeces during the hind cull.

To facilitate comparisons of rumen contents and faeces, samples were air dried and milled to pass a 1.00mm screen, producing similar size fragments in both samples. Analysis was conducted with the use of a technique based on that of Todd & Hansen (1973). Hertwig's solution, a combination clearing and mounting fluid, alone was used to prepare slides, as by Baumgartner & Martin (1939). With this method, no staining was found to be necessary, nor was it necessary to dehydrate the material through an alcohol series, thereby saving much time. This method is not considered to be as potentially destructive as some others, and ensures good fragment survival during preparation. As the method relies on the identification of histological characters of epidermal cells, a reference collection of slides or similar of potential food species is necessary. Illustrations and photographs of the epidermal characters of many indigenous 'hill' species were available from previous studies carried out in the Department of Forestry and Natural Resources. Further necessary reference material was prepared using a scraping technique (Metcalfe 1960) which proved satisfactory for the species concerned.

Five slides were prepared for each sample as in the study reported by Todd & Hansen (1973), with a random distribution of thoroughly mixed fragments. Traverses were made across each slide by the use of an adjustable stage on the microscope, and the frequency of occurrence of the first 60 recognisable particles per slide was recorded, totalling 300 per sample. Recognisable but unknown species, ie. those fragments recognisable as the cuticular surface but unidentifiable with the reference material were also recorded.

## 3.3 Statistical Methods

### 3.3.1 Mann-Whitney U test

The Mann-Whitney U test was used in the comparison of hind rumen and faeces contents, and also for the comparison of hind and stag faeces composition. A non-parametric test for two independent samples was used since the assumptions of a parametric test, such as the 't' test ie. that the scores are independent observations from normally distributed populations (Siegal 1956), cannot be made.

The statistic U is calculated as follows:

$$U_1 = n_1n_2 + \frac{n_1(n_1+1)}{2} - R_1$$

$$U_2 = n_1n_2 + \frac{n_2(n_2+1)}{2} - R_2$$

Where: $n_1$ = size of the smaller sample, $n_2$ = size of the larger sample, $R_1$ = sum of ranks in $n_1$, $R_2$ = sum of ranks in $n_2$. U is the smaller of $U_1$ and $U_2$.

For samples where $n_2$ (the larger) is less than 20, the critical value of U and its associated significance level can be read from tables.

### 3.3.2 The Median

The median is the order statistic whose number is (n+1)/2 when n is odd. When n is even, the median is the average of the order statistics whose numbers are n/2 and (n+2)/2. It is a good indicator of the middle of a skewed distribution, and is appropriate for use in this case due to the non-normality of the data.

Two of the order statistics serve as the upper and lower confidence limits, and are estimated as follows:

$$\frac{(n+1)}{2} \pm \frac{z\sqrt{n}}{2} \quad \text{(Snedecor \& Cochran 1967)}$$

Where: z is the normal deviate corresponding to the desired confidence probability, and n is the sample size.

## 3.4 Results

### 3.4.1 Rumen vs. faeces composition

A comparison was made between plant species which occurred with a minimum frequency of 1% in rumen and faecal samples from the same animal. With samples from only 15 culled hinds available for this comparison, no distinction has been made between yeld and non-yeld animals; all animals are considered, regardless of their breeding status.

There was no significant difference between the frequency of occurrence of the 13 species compared, see Table 3.1. The

Table 3.1 The comparison of the frequency of occurrence of grazed species in rumen contents and faeces of hinds.

The Mann-Whitney U Test

| Species | Value of 'U' | P |
|---|---|---|
| Calluna vulgaris | 83.0 | N.S. |
| Nardus stricta | 95.5 | N.S. |
| Festuca spp. | 62.0 | N.S. |
| Deschampsia caespitosa | 96.0 | N.S. |
| Deschampsia flexuosa | 90.0 | N.S. |
| Molinia caerulea | 106.0 | N.S. |
| Eriophorum angustifolium | 84.5 | N.S. |
| Eriophorum vaginatum | 101.0 | N.S. |
| Trichophorum cespitosum | 111.0 | N.S. |
| Carex spp. | 93.0 | N.S. |
| Vaccinium myrtillus | 110.5 | N.S. |
| Pteridium aquilinum | 111.5 | N.S. |
| Myrica gale | 77.0 | N.S. |

$n_1$ = number of rumen samples = 15
$n_2$ = number of faecal samples = 15

N.S. - Not Significant at 5 per cent. level.
Null Hypothesis, Ho - no significant difference between species frequency composition in rumen and faecal samples.

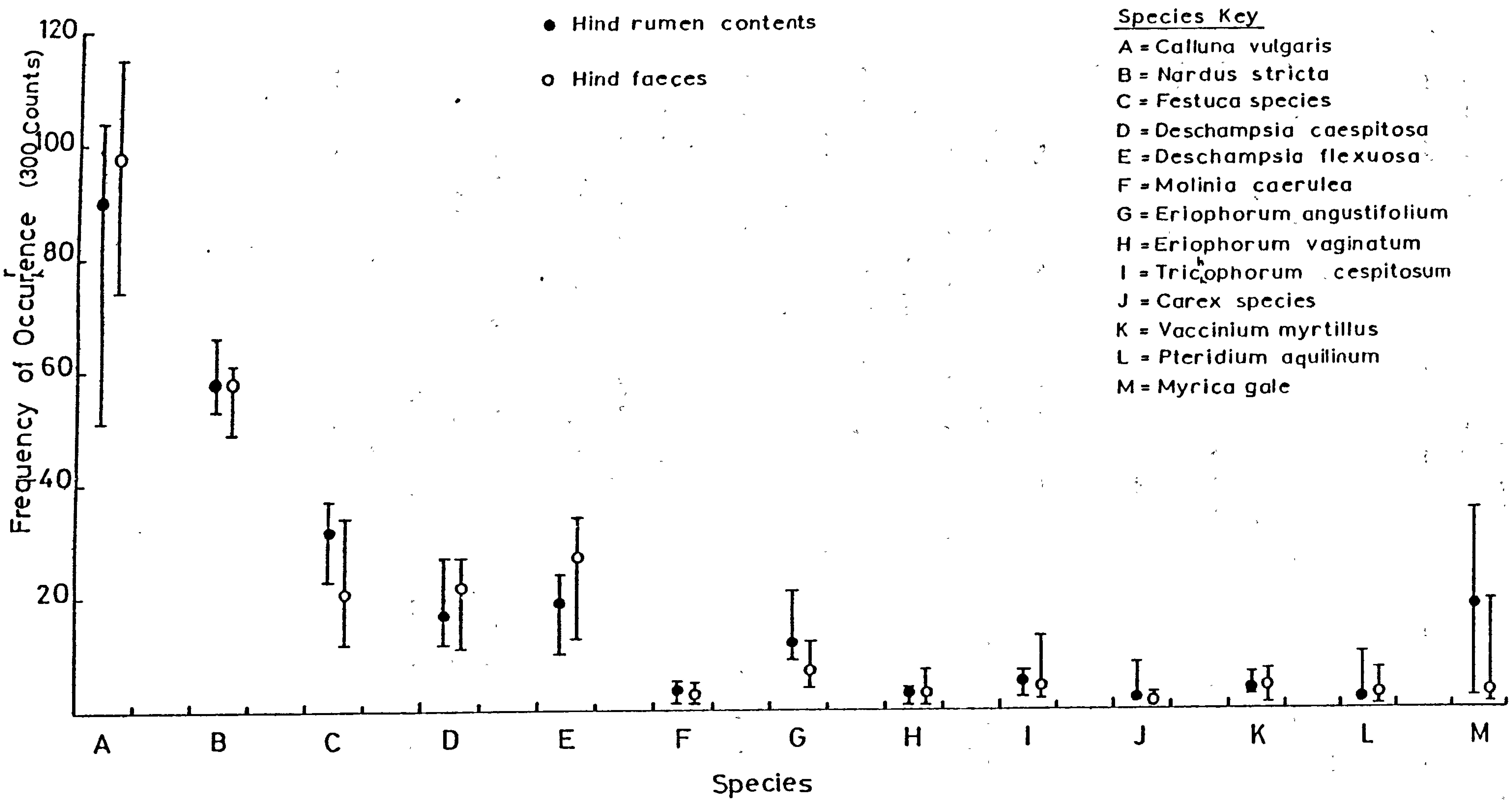


Fig. 3·1 The comparison of rumen and faeces composition, medians + 95% confidence limits graphical representation of the results is presented in Fig. 3.1, which shows the median values of the frequency of occurrence, with approximate 95% confidence intervals. The confidence interval of the medians of certain species are quite large and this may reflect the small sample size of hinds involved, and the variable occurrence of some species in the diet such as Myrica gale.

The results do suggest that the techniques of rumen and faecal analysis are reasonably comparable in their description of red deer diets on the study area during winter, except perhaps where species of a highly variable occurrence, such as Myrica gale are encountered. However the method is considered to be adequate to describe the frequencies of the major components of the diet.

### 3.4.2 Hind vs. stag faeces composition

The frequency of occurrence of the same range of plant species as previously considered, was compared in stag and hind faecal samples. There is a high degree of similarity between the diets of the sexes, with the notable exception of the two Fescue species (the frequencies of F. ovina and F. rubra are combined throughout the analysis). Hinds had significantly greater frequencies of Fescue species in their faeces than stags ($U = 11$, $P < 0.002$), see Table 3.2. The graphical representation of the results is presented in Fig. 3.2, in the same manner as above. The criticism of small sample size is more applicable to stag samples, since it only proved possible to make collections from 8 individuals. However the confidence intervals for the stag results are similar to those of the hinds, which may suggest that winter diets are not too dissimilar. A greater number of samples from both hinds and stags would obviously have been more desirable for this comparison had collection proved possible.

Table 3.2 The comparison of frequency of occurrence of grazed species in hind and stag faeces.

| Species | Value of 'U' | P |
|---|---|---|
| Calluna vulgaris | 41.0 | N.S. |
| Nardus stricta | 43.5 | N.S. |
| Festuca spp. | 11.0 | *** |
| Deschampsia caespitosa | 42.0 | N.S. |
| Deschampsia flexuosa | 31.0 | N.S. |
| Molinia caerulea | 48.5 | N.S. |
| Eriophorum angustifolium | 40.0 | N.S. |
| Eriophorum vaginatum | 35.5 | N.S. |
| Trichophorum cespitosum | 51.5 | N.S. |
| Carex spp. | 47.5 | N.S. |
| Vaccinium myrtillus | 49.5 | N.S. |
| Pteridium aquilinum | 49.0 | N.S. |
| Myrica gale | 40.0 | N.S. |

$n_1$ = stag samples = 8
$n_2$ = hind samples = 15

N.S. - Not Significant at 5 per cent. level, ***significant at 0.2 per cent. level.

Null Hypothesis, Ho - no significant difference between species frequency composition of stag and hind faeces.

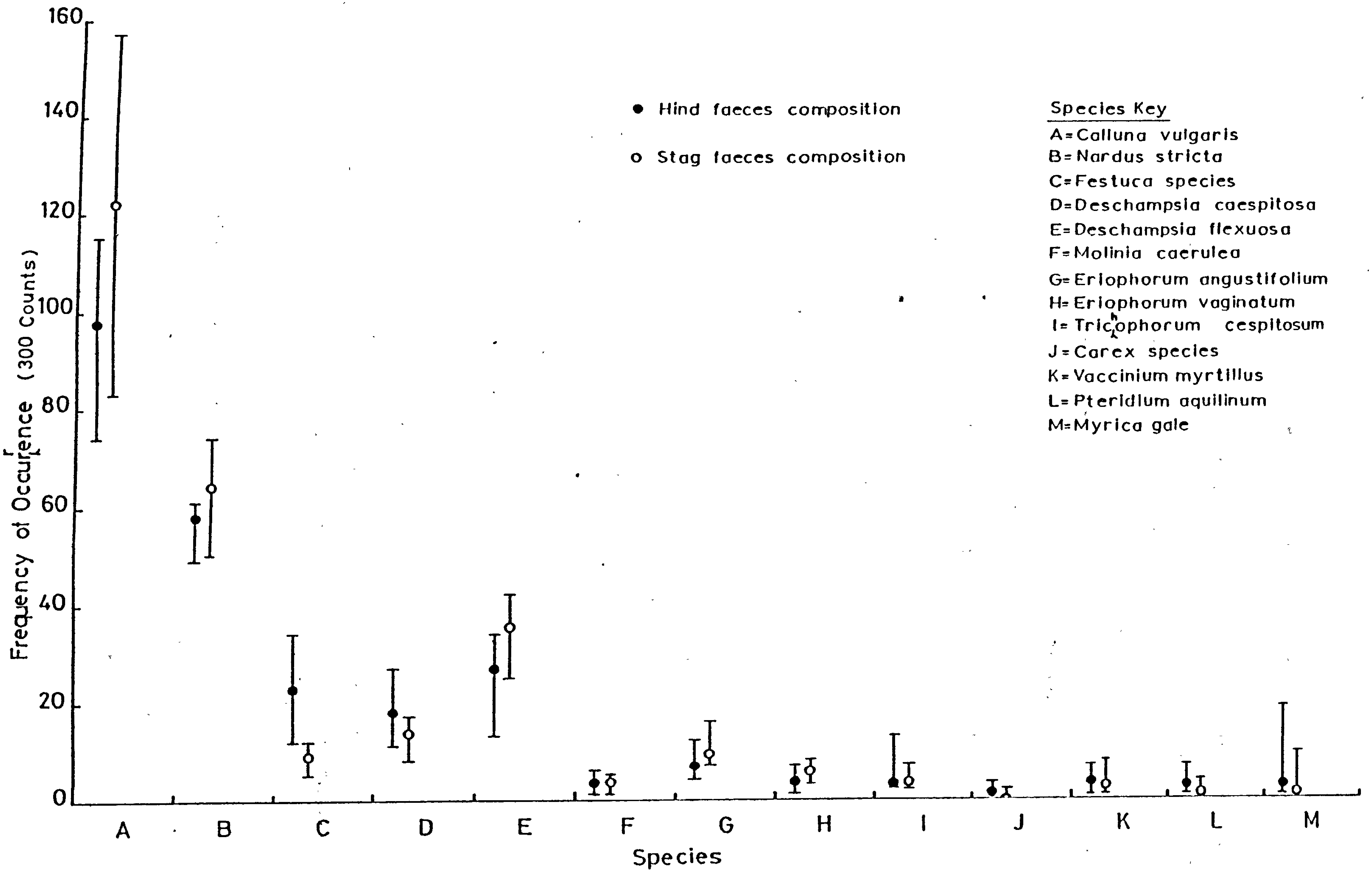


Fig. 3·2 The comparison of hind and stag faeces composition, medians+95% confidence limits

## 3.5 Discussion

### 3.5.1 The use of rumen and faecal analysis

The preliminary investigation indicates good agreement between species frequency in the rumen and faecal samples. Individual animal variation in the frequency of occurrence of particular species, which could be expected as a consequence of the time lag between ingestion and defecation, is largely overcome when all the hind samples are considered in the analysis. The time lag between ingestion and defecation in Cervids can range from less than 24 hours to approximately seven days (see: Gaare, Sorensen & White 1977 and Staines 1976a), depending on the nature of the diet.

As was noted, there is a high degree of variability associated with the frequency of occurrence of Myrica gale in rumens and faeces of individual animals. However this species had a highly dispersed distribution on the study area, and was only locally common. As a consequence, Myrica gale could be browsed one day and possibly not encountered for a number of days subsequently, depending on the distribution of the home range vegetation, and the ranging behaviour of the deer concerned. Together with digestive throughput time, this may account for the variability in the frequency of occurrence of this species in particular, in rumens and faeces of individual animals. Thus the relatively small sample of 15 animals may well be insufficient in the comparison of rumen and faecal samples, when dealing with species of a highly dispersed nature. However, overall frequencies of occurrence of the main dietary constituents found in the analysis were similar in rumen and faecal samples.

Many workers have accepted that rumen analysis can adequately represent the diet. However Gaare, Sorensen & White (1977) working with reindeer (Rangifer tarandus) point out that rumen contents may not be fully representative of the diet, if the rate of disappearance of food particles to the omasum is not taken into account. In their study it was found that lichens broke up into smaller particles than more fibrous constituents. They suggest that rumen turnover time is probably a function of the sum of the dietary components in proportion to their ruminal composition. Minor constituents of the diet are thought to be most highly affected because of the small contribution they make to turnover time. Staines (1976a) working with rumen-cannulated red deer concluded that rumen analysis could reasonably estimate the previous day's intake of heather, even when relatively little heather (10%) was included in the diet. Lichens are not likely to be of much significance in the diet of red deer in Scotland in most cases, unlike the situation with reindeer in Scandinavia; but the occurrence of more digestible species in small quantities could lead to underestimation in rumen samples. This did not appear to be the case with the better grass species such as Deschampsia flexuosa and the Festuceae, which were detected in similar frequencies in faeces and rumen contents, but may occur with delicate dicotyledonous species selected in small quantities. Nonetheless it is considered that rumen analysis is adequate to describe red deer diets in this case, and that faecal analysis because of its close agreement may also be used to describe the diet in a qualitative manner during winter, when intake is largely composed of mature perennial species.

### 3.5.2 Deer diets on the study area

Species comprising the diet reflect animal preference and the availability and distribution of vegetation on the individual's home range. Swift (1948) reported the ability of deer to select the most nutritious herbage available, and Lockie (1967) refers to the nutritional wisdom of herbivores in being able to select what they need from an environment with a variety of species of varying quality. The most important nutrient likely to be limiting ruminant performance is metabolisable energy. However low levels of available protein may inhibit digestion in the rumen (see: Hobson, Mann, Summers & Staines 1976), contributing to the inadequate supplies of metabolisable energy, and in such circumstances may also be considered to be significantly limiting performance. Anderson (1978) reports an over-winter loss of body fat in pregnant hinds of 82 per cent, and despite the lack of comparable data for stags, it is probable that metabolisable energy is again a major nutritionally limiting factor. The mature male animal is likely to have exhausted much of its fat reserves during the rut (see: Mitchell, McCowan & Nicholson 1976), and thus enters the winter in "low" condition. Any differences in hind and stag diets during winter therefore, probably reflect differences in available vegetation on the respective home ranges, rather than nutritional requirements, since it is likely that variation between the sexes is in terms of the quantitative demand for metabolisable energy, except for pregnant hinds in the latter stages of pregnancy.

It has been suggested in Chap. 2, and reported by Jackes (1974) and Watson & Staines (1978), that hinds utilised areas with greater amounts of better quality grassland than stags did; a factor which could lead to a nutritional advantage. It might be expected that hind diets would reflect the occupation and utilisation of such areas.

A confounding factor in the comparison of the species composition of hind and stag diets is that samples from both sexes were not collected coincidentally; hind samples being collected during November/December 1976, and stag samples during January/ February 1977. This temporal difference can have two consequences: i) there may be less available herbage on grass swards in the latter sampling period, due to previous grazing of these areas; ii) the greater frequency of snow-lie and freezing conditions, characterising the latter sampling period, contributes to the unavailability of material on short grass swards. This may lead to the selection of other vegetation, which through its growth habit or lack of previous grazing is physically more available under such conditions. In view of the increased frequency of snow-lie and freezing conditions as winter progressed, it is possible that deer diets, as assessed from samples collected in early winter would differ during January/February when stag samples were collected.

Despite the reservations previously voiced about sampling, it appears that hind and stag diets are not too dissimilar. Calluna was the most frequent single species in red deer diets on the study area during winter; this species has also been reported to comprise a major proportion of deer diets in other parts of Scotland and in Europe (see: Mitchell, Staines & Welch 1977). Although Calluna alone as a source of forage has been shown to be unable to maintain grazing sheep, it is of considerable value in the uplands in winter, and is capable of yielding forage equivalent to moderate-poor quality hay (see: Armstrong & Thomas 1952 and Trinder 1975). Four graminids apparently comprise a major proportion of the diets of hinds and stags (40%), and together exceed the frequency of Calluna in the diet.

D. flexuosa and the Fescues have been shown to be of considerable value to stock grazing upland areas, particularly in view of the relatively high digestible protein levels of these species in comparison with Calluna during winter (see also: Chap. 2 and Chap. 4).

The greater use of better quality grassland by hinds is not obviously reflected in these results, although significantly higher frequencies of Fescues were recorded from hind faecal samples. Reports from other studies also indicate the apparent similarity between hind and stag diets on the basis of species composition (see: Staines & Crisp 1978). Staines & Crisp (1978) have reported the results of the chemical analysis of rumen contents, which on the basis of species composition were similar. They found that hinds had higher rumen nitrogen concentrations than stags during autumn, winter and spring. It appears, therefore, that although minor differences between the sexes may exist in the species composition of the diets, it is not possible to state whether hinds experience a higher plane of nutrition, without recourse to the chemical analysis of rumen contents.

The utilisation of separate areas of range by hinds and stags does not preclude the use of the same plant species, but it is the quality and quantity of forage which is of fundamental importance to the nutritional status of the individual animal. It appears, therefore, that quite subtle variations in selection which may be undetectable by species analysis techniques, must account for the superiority of hind diets that has recently been reported.

## 3.6 Summary

1) A comparison was made between faecal and rumen analysis, on samples obtained from culled hinds.

2) Reasonable agreement was obtained between the two methods, suggesting that faecal analysis could be used to describe deer diets in winter.

3) Although samples from both sexes were not collected at the same time, stag diets, as assessed by faeces analysis, were similar to those of hinds . Hind diets, however, contained a greater proportion of Fescue species than those of stags.

4) It is suggested, in the light of recent reports, that species analysis techniques may not be able to distinguish differences in the quality of hind and stag diets.

## Chapter 4 The Value of Muirburn to Grazing Deer in Winter

### 4.1 Introduction

The proportion of Calluna vulgaris in the diet of the red deer will vary in different areas of its range in this country. depending on its palatability, abundance, distribution and the presence of other species. However it is a major constituent of the winter diet of red deer on the study area (see: Chap. 3, Fig. 3.3), and throughout much of the deer range in upland Scotland (see: Mitchell, Staines & Welch 1977).

A widely held belief throughout upland Scotland is that red deer make greater use of Callunetum after recent muirburn. There have, however, been no attempts to substantiate these claims (Mitchell, Staines & Welch 1977). Miller & Watson (1974) draw parallels between sheep, which have been shown to favour young vegetation regenerating after a fire, and red deer in their grazing preferences. However, Hewson (1976) found that the greatest use made by red deer of different aged stands of Calluna occurred on mature stands for much of the year. He considered that short pioneer stands could only be grazed with some difficulty by deer. Miles (1971) recorded considerably higher use of areas dominated by Molinia caerulea on Rhum, following burning. However Molinia is a deciduous perennial grass, and it is thus unwise to make comparisons with a dwarf shrub.

Chemical analyses of Calluna have demonstrated the higher nutritive value of young material, such as regenerated from a fire (see: Grant & Hunter 1968; Gimingham 1972 and Miller & Watson 1974). Gimingham states that the higher nutritive value of regenerating Calluna includes greater amounts of N, P, Ca, Mg, Na and K, and particularly N and P, which, as he mentions, are important nutrients to herbivores, likely to be in short supply in the upland environment. Miller & Watson (1974) have shown the rapid decline in N and P levels following the first year after burning; four year old Calluna was frequently found to be no better in this respect than plants aged 25 years and more.

There is no direct information available to demonstrate if the burning of Calluna has an effect on red deer performance.

However Evans (1890) considered that a programme of muirburn on Jura both increased birth rates and lowered mortality in the deer stock. On Rhum the lowered breeding performance of the red deer hinds and the lower average mature body weights of both sexes was attributed by Lowe (1971) to the cessation of muirburn. Despite the descriptive nature of these accounts and the lack of a control area for comparison, the suggestions of both Evans and Lowe are not unreasonable, in view of the improved quality of regrowth of plant material following fire and the greater accessibility of food items.

During winter when there is a marked decline in herbage quality in the uplands, areas of better quality herbage are attractive to grazing deer, thereby influencing ranging behaviour. It is reasonable to suppose that Calluna and the effects of muirburn are important to grazing deer, since this has been shown to be the case with sheep (see: Hunter 1954 and Grant & Hunter 1968). In this section I have presented the results of investigations into the nutrient value of different aged stands of Calluna resulting from muirburn; sampling was carried out concurrently with the observational work. The relative importance of these areas for grazing and consequently the degree of influence they are likely to have on deer distribution during winter may therefore be postulated, complementing work presented in Chapters 2 and 5.

## 4.2 Methods

### 4.2.1 The Collection of Calluna Samples

Within the study area three replicates of four age-classes were selected, representing the main growth phases of Calluna: pioneer, building, mature and degenerate, as described by Watt (1955) and Gimingham (1972). The four plots constituting each replicate were selected to be as geographically close to each other as possible, although this was not achieved in all cases to the desired extent, as the distribution of burnt sites depends on the pattern of muirburn carried out in the years preceding this study. The individual sites for replicate two were dispersed more than would have been wished under ideal conditions. Figure 4.1 shows the locations of the sampling plots on the study area.

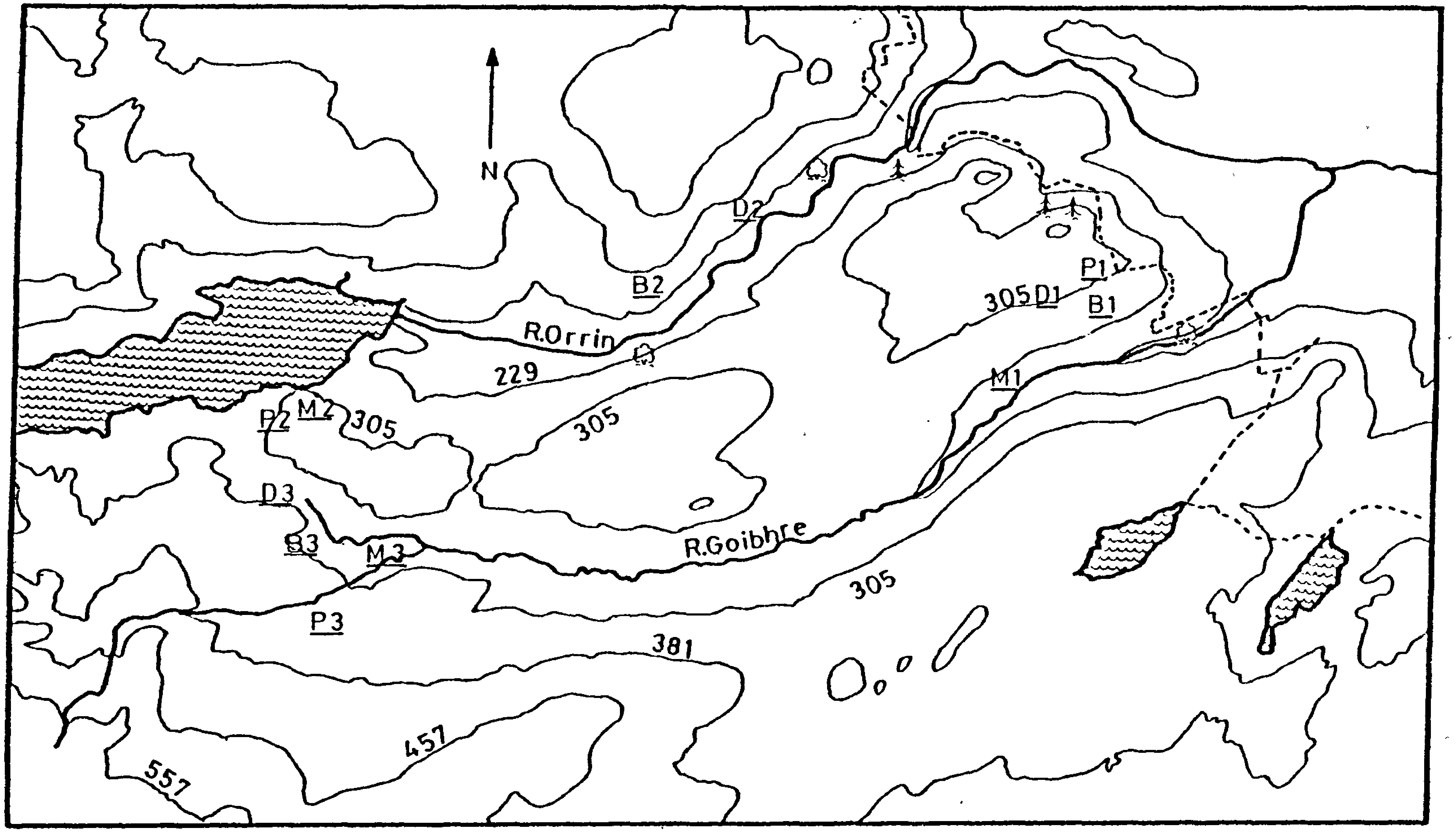


Figure 4.1 The *Calluna* sampling sites

P= Pioneer B=Building
M= Mature D=Degenerate

*Calluna* samples were collected from each plot on three occasions, in Oct./November, January and March. Samples were taken from two grazed and two ungrazed plants within each site at each visit. The proportion of the plant removed for a sample was aimed to represent the amount taken by deer. Recent grazing was inspected and the samples were cut from plants with a sharp knife in accordance with the degree of removal of herbage by deer. Other herbivorous animals were present on the study area, but I do not consider it likely that grazing by other species was mistakenly attributed to red deer in this investigation. There are obvious differences in selection by red deer and red grouse. Rabbits (*Oryctolagus cuniculus*), although present, were not found on or near the sample sites. Mountain hares (*Lepus timidus*) were extremely rare in this area. Generally, current year's growth was selected by deer, see Figure 4.2. On removal from the plant, samples were immediately immersed and maintained in 90% commercial alcohol. This action stops respiration within the plant, which could lower carbohydrate levels prior to analysis, and also preserves the plant tissue.

### 4.2.2 Analysis

Preliminary work suggests that selection of *Calluna* by grazing red deer is related to carbohydrate levels (see: Mathews 1972). Analyses were carried out therefore, for ethanol soluble carbohydrate (the main energy reserve in *Calluna*) and also nitrogen and phosphorus, since shortages may limit performance. Neutral detergent fibre was determined to provide an index of digestibility of herbage samples.

The schematic representation of the sequence of analysis is presented in Fig. 4.3.

#### (a) Ethanol Soluble Carbohydrates (E.S.C.)

The herbage samples, as described in the collection procedure above, were removed from the storage alcohol, which was retained, and placed in small containers. Each container was covered with aluminium foil, to allow the evaporation of any residual ethanol, and to minimise possible contamination with cellulose particles. (Cellulose is a common laboratory contaminant, which will interfere with the

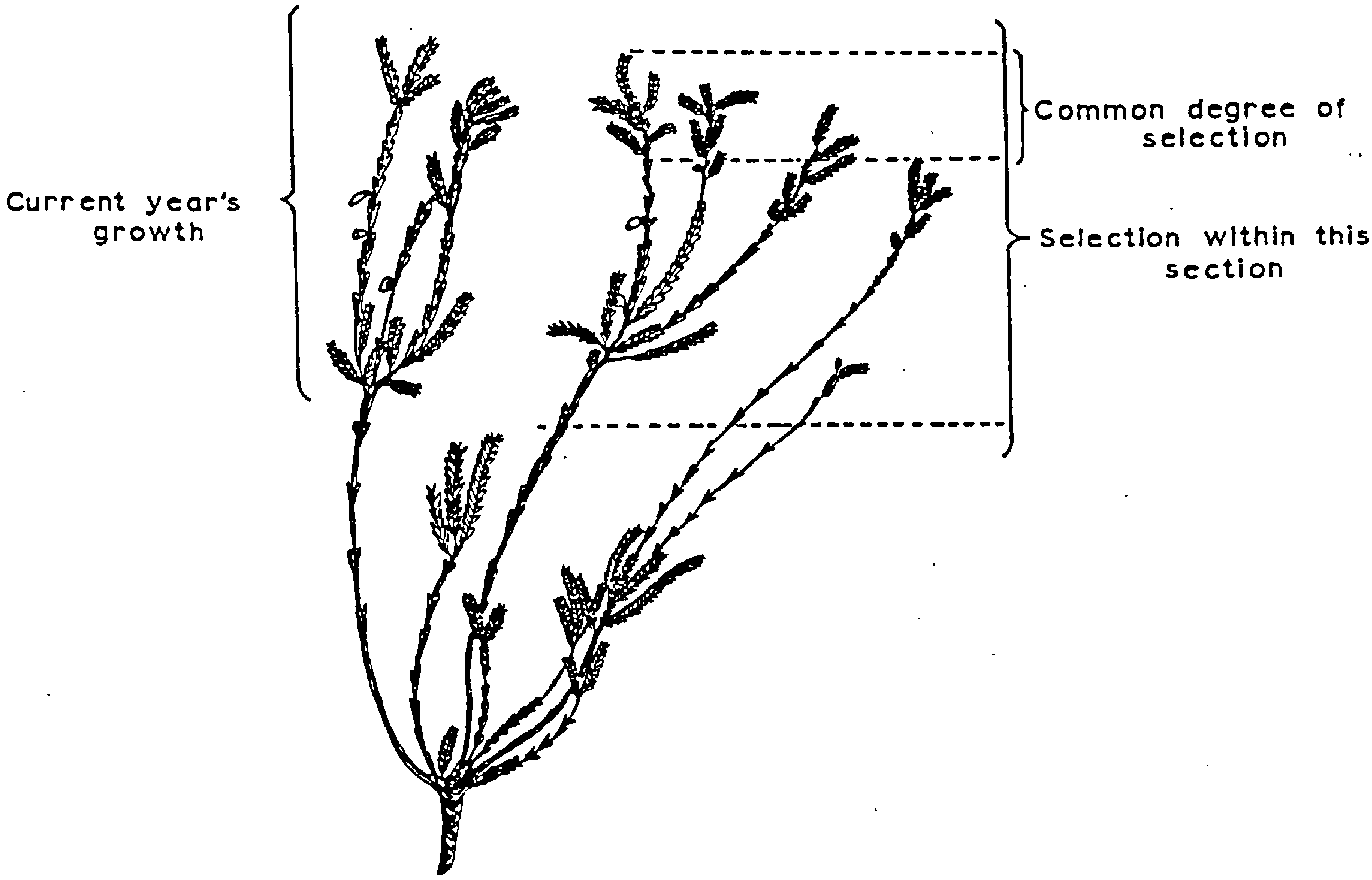
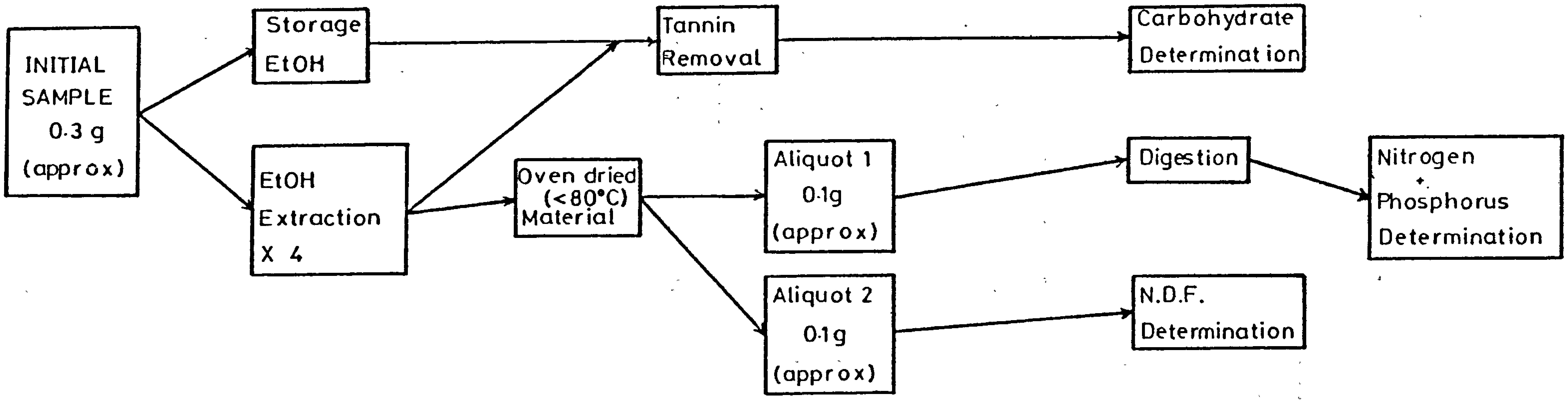


Figure 4.2 Amount of Calluna removed during sampling

anthrone reaction). When dry, the samples were macerated in their containers, to produce a much larger surface area for subsequent extractions of carbohydrates with ethanol.

Each extraction of the samples with further 90% ethanol lasted a minimum of 18 hours. The fourth extraction yielded a negative anthrone test (see Appendix 4, for details of laboratory procedures), indicating that all detectable ethanol soluble carbohydrate had already been removed. The extractions were pooled with the storage ethanol before further procedures were carried out.

Fig. 4·3 Sequence of the analysis of *Calluna* samples



### Tannin Removal

The interference with the colorimetric determination of sugars by phenolic compounds present in test material is discussed by Ebell (1969). Interference is reported to result from the colour and turbidity of condensation products, and also from the direct chemical reaction with the reagents.

Tannins were removed from the ethanol extractions with lead acetate, using a method based on that of Smith (1969). The pooled extracts for each sample were evaporated-down to less than 9 ml over a steam bath, and 1 m of neutral 10% lead acetate was added. The samples were then made-up to 10 ml with 90% ethanol, before being transferred to centrifuge tubes. Extracts were centrifuged for five minutes and the supernatant decanted into 25 ml conical flasks, containing about 100 mg of potassium oxalate, to remove any excess lead. The flasks were covered and refrigerated for four to five hours or overnight. Insufficient de-leading leads to turbidity with the anthrone reagent and erratic results, Ebell (1969). The contents of the flasks were subsequently filtered through glassfibre filter paper, before the determination of the E.S.C.

E.S.C. levels were estimated using a method based on that of Allen (1974), see Appendix 4 for details. E.S.C. values are reported in Table 4.1. Empty cells in the table are the consequence of accidental loss.

### (b) Determination of Nitrogen and Phosphorus

Following ethanolic extraction for the determination of carbohydrates, the plant material was oven dried at less than 80°C, to prevent loss of nitrogen (Schuffelen, Muller & Van Schouwenberg 1961). A micro acid digestion was carried out on this material, details of which can be found in Appendix 4.

#### i) Determination of Nitrogen

Nitrogen was determined using the automated procedure of Crooke & Simpson (1971), see Appendix 4 for details.

Table 4.1.1 The Analysis of the <u>Calluna</u> Samples - First Sampling: October/November

| Sample | % E.S.C. | | | % Nitrogen | | | % Phosphorus | | |
|---|---|---|---|---|---|---|---|---|---|
| | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 |
| Pioneer G | 8.97 | 9.25 | 11.25 | 1.46 | 1.88 | 2.02 | 0.030 | 0.058 | 0.080 |
| Pioneer NG | **** | 9.86 | 12.37 | 1.69 | 1.46 | 1.84 | 0.037 | 0.069 | 0.073 |
| Building G | 5.73 | 11.67 | 12.43 | 1.37 | 1.42 | 1.60 | 0.037 | 0.059 | 0.057 |
| Building NG | 5.17 | 9.95 | 12.12 | 1.12 | 1.36 | 1.56 | 0.039 | 0.075 | 0.045 |
| Mature G | 5.86 | 8.97 | 9.90 | 1.31 | 1.76 | 1.42 | 0.059 | 0.035 | 0.044 |
| Mature NG | 8.53 | 9.60 | 11.08 | 1.18 | 1.69 | 1.44 | ***** | 0.051 | 0.045 |
| Degenerate G | 6.02 | 10.12 | **** | 1.06 | 1.76 | 1.35 | ***** | 0.043 | 0.065 |
| Degenerate NG | 10.92 | 11.42 | 7.62 | 1.30 | 1.25 | 1.44 | 0.055 | 0.070 | 0.038 |

G = Grazed sample, NG = Ungrazed sample

S1, S2 and S3 are the three sampling areas as in Figure 4.1

*** Missing samples (accidental loss)

Table 4.1.2 The Analysis of the *Calluna* Samples - Second Sampling: January

| Sample | % E.S.C. | | | % Nitrogen | | | % Phosphorus | | | % Cell wall constituents | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 |
| Pioneer G | 16.02 | 18.69 | 12.67 | 1.12 | 1.32 | 1.55 | 0.083 | 0.075 | 0.069 | 45.9 | 41.5 | **** |
| Pioneer NG | 16.49 | 15.48 | 16.80 | 1.50 | 1.54 | 1.83 | 0.090 | 0.089 | 0.081 | 50.0 | 40.5 | 38.0 |
| Building G | ***** | 12.47 | ***** | 1.66 | 1.45 | 1.35 | 0.073 | 0.085 | 0.060 | **** | 45.8 | 47.4 |
| Building NG | 10.92 | 15.12 | 11.58 | 1.15 | 1.16 | 1.36 | 0.064 | 0.067 | 0.063 | 43.8 | 45.3 | 42.0 |
| Mature G | ***** | 13.43 | (23.80) | 1.45 | 1.23 | 1.45 | ***** | 0.080 | 0.076 | 49.8 | 34.2 | 38.3 |
| Mature NG | 11.85 | 13.95 | (23.36) | 1.40 | 1.21 | 1.58 | 0.094 | 0.065 | 0.091 | 54.9 | 40.0 | 40.8 |
| Degenerate G | ***** | 19.83 | 15.84 | 1.03 | 1.43 | 1.13 | 0.064 | 0.083 | 0.059 | 40.2 | **** | 43.0 |
| Degenerate NG | 11.50 | 15.06 | 14.23 | 1.32 | 1.08 | 1.05 | 0.058 | 0.058 | 0.047 | 44.6 | 40.5 | 37.2 |

Cell wall constituents = Neutral Detergent Fibre (N.D.F.)

Bracketed values are suspected to have been contaminated.

Table 4.1.3 The Analysis of the Calluna Samples - Third Sampling: March

| Sample | % E.S.C. | | | % Nitrogen | | | % Phosphorus | | | % Cell wall constituents | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 | S1 | S2 | S3 |
| Pioneer G | 9.85 | 13.35 | 13.22 | 1.52 | 1.50 | 1.29 | 0.061 | 0.057 | 0.075 | 35.9 | 34.9 | 40.4 |
| Pioneer NG | 14.29 | 10.08 | 8.59 | 1.38 | 1.11 | 1.24 | 0.076 | 0.045 | 0.035 | 37.9 | 41.3 | 40.7 |
| Building G | 10.26 | 13.30 | 7.73 | 1.23 | 1.46 | 1.26 | 0.046 | 0.056 | 0.062 | 43.4 | 32.8 | 46.7 |
| Building NG | 8.14 | 9.92 | 8.70 | 1.29 | 1.42 | 1.19 | 0.058 | 0.051 | 0.039 | 46.3 | 42.0 | 40.1 |
| Mature G | 10.79 | 8.80 | 16.22 | 1.37 | 1.30 | 1.45 | 0.044 | 0.061 | 0.063 | 42.0 | 42.6 | 37.5 |
| Mature NG | 8.44 | 8.44 | 17.11 | 1.29 | 1.16 | 1.59 | 0.079 | 0.059 | 0.039 | 40.0 | 29.7 | 41.1 |
| Degenerate G | 11.17 | 16.72 | ***** | 1.28 | 1.51 | 1.15 | 0.041 | 0.034 | 0.048 | 43.2 | 44.0 | 38.6 |
| Degenerate NG | 8.13 | 11.23 | ***** | 1.25 | 1.21 | 1.07 | 0.043 | 0.048 | 0.039 | 44.0 | 40.2 | 40.7 |

The values obtained for the nitrogen content of the samples are recorded in Table 4.1.

### ii) Determination of Phosphorus

Phosphorus was determined using an automated procedure based on the method of Murphy & Riley (1962), see Appendix 4 for details. The values are reported in Table 4.1.

### (c) Neutral Detergent Fibre

To gain an index of the digestibility of the herbage samples, assessments were made of the neutral detergent fibre content. The estimation of cell-wall constituents apparently separates the available fractions of a feeding stuff from those fractions which are only partially available after microbial fermentation (see: Van Soest & Wine 1967). This assessment can be useful in making comparisons of feed quality within a given plant species, but cannot on its own be satisfactorily used for interspecific comparisons due to varying levels of cellulose and lignin in the cell walls of different species.

Some of the disadvantages of the original technique of Van Soest & Wine (1967), such as the relatively large-scale of the procedure are mentioned by Waldern (1971). A micro-method based on that of Waldern (1971) was developed and tested, and found to give good agreement with Van Soest's method. The samples were subsequently analysed using this micro-method. See Appendix 4 for full details.

The average sample size for the Oct./November 1976 collection period was, unfortunately inadequate for a neutral detergent fibre determination, and thus no data are available. The results for the January and March 1977 collection periods are presented in Table 4.1.

## 4.3 Statistical Methods

When using the analysis of variance on the data in this section, the testing of the differences between individual means was not undertaken unless the result of the F-test indicated significance (see: Snedecor & Cochran 1967).

If it is desirable to make multiple comparisons between means, then precautions must be taken to reduce the risk of making Type I errors (rejection of a true null hypothesis), without unduly increasing the risk of making Type II errors (acceptance of a false null hypothesis). The multiple-range test, using the shortest significance ranges or S.S.R. can be utilised in such circumstances (Parker 1973). The shortest significant range between means can be calculated as follows:

Standard Error of treatment mean $= \surd(S^2/n)$ (S is the Standard Deviation of the Mean)

Values of Q (table of the 'Studentized Range'), for number of error degrees of freedom and for k, k-1, k-2, k-3, ........, 2 treatments.

S.S.R. is computed for k, k-1, k-2, k-3, ......., 2 as $Q\surd(S^2/n)$

Treatment means are ranked in order of magnitude, and the difference between the largest and smallest mean are tested by comparison with the S.S.R. for k means. If this is not significant, testing finishes at this point. If the difference is significant, then the differences between the largest and the next to smallest mean, and the next to largest and the smallest means are tested by comparison with S.S.R. for k-1 means. This is continued until differences prove non-significant (Parker 1973).

## 4.4 Results

An analysis of variance was performed upon the data resulting from the analysis of the Calluna samples, using the statistical package 'Genstat' (Lawes Agricultural Trust, Rothampsted 1977). A separate analysis of variance was performed upon each attribute for which there had been a chemical analysis. Factors considered to be possibly having an affect on the attributes analysed, and thus included in the analysis of variance were: site effects, sampling date, age of stand, presence or absence of grazing on the sampled plants, and the interaction of age of stand and grazing. The results of the analysis of variance are presented in Tables 4.2, 4.3, 4.4 and 4.5.

### 4.4.1 Ethanol Soluble Carbohydrates (E.S.C.) (Table 4.2)

There were significant differences between sites ($P < 0.001$) and between seasons ($P < 0.001$) in levels of E.S.C.

Site 1 plots were significantly lower than those of sites 2 and 3. Reasons for any differences between sites are not clear. The variation in altitude of the three sites is not great, nor was the distance between them such that the effects of weather might be significant (see Fig. 4.1). If aspect was a significant factor, then south-facing sites might have higher carbohydrate contents resulting from greater levels of solar radiation. However at site 1, where all plots had a southerly aspect, samples were lower in E.S.C. than sites 2 and 3, with aspects besides south.

Samples taken during the January collection were significantly higher in E.S.C. than samples collected during the previous or subsequent collections. E.S.C. levels although lower in March than in January were, however, significantly higher than the levels found in the October samples. E.S.C. levels were therefore lowest in October, rising to a peak in the January samples, before making a decline in the March samples. The seasonal differences in the carbohydrate content of Calluna are similar to those reported by Grace & Woolhouse (1970), and similar to levels reported in three species of Vaccinium by Stewart & Bannister (1973). Stewart & Bannister report that the rises in carbohydrate content in winter tended to occur during cold periods with low rainfall, resulting in longer daylengths and bright light above snow, which, coupled with low temperatures, would be expected to depress respiration, which may lead to a positive net photosynthesis. Warren-Wilson (1966) attributed the depression in assimilation of plants in arctic environments to an accumulation of sugars resulting from the depression of respiration and new growth by low temperatures. From November to March during the study, there were conditions conducive to the accumulation of E.S.C., with low temperatures and snow cover for much of the time (see: Chap. 6). The decrease in E.S.C. levels in samples collected in the latter half of March reflect the change in

Table 4.2 Analysis of Variance - Variate Carbohydrate

| Source of Variation | D. of F. | Sums of Squares | Mean Square | F-Ratio |
|---|---|---|---|---|
| Sites | 2 | 109.395 | 54.698 | 7.253*** |
| Seasons | 2 | 417.640 | 208.820 | 27.691*** |
| Ages | 3 | 37.618 | 12.539 | 1.663 |
| Grazing | 1 | 13.053 | 13.053 | 1.731 |
| Ages x Grazing | 3 | 14.290 | 4.763 | 0.632 |
| Error | 52 | 392.131 | 7.541 | |
| Total | 63 | 984.127 | 15.621 | |

***significant at 0.1% level.

F-ratios reveal significant differences between means of Sites and Seasons

i) Comparison of means - Sites

Standard Error of Sites mean = $\sqrt{(S^2/n)} = \sqrt{7.541/24} = 0.56$

Value of Q for 3 and 2 Sites = $Q_3 = 3.42$, $Q_2 = 2.84$

S.S.R. calculated for Sites 3 and 2 = $Q\sqrt{(S^2/n)}$

Sites means ranked in order of magnitude:

| Site 3 | Site 2 | Site 1 |
|---|---|---|
| 13.36 | 12.35 | 10.40 |

S.S.R. 3 = 1.91 Significant difference between Site 3 and Site 1 means.

S.S.R. 2 = 1.59 No significant difference Site 3 and Site 2.
Significant difference between Site 2 and Site 1.

ii) Comparison of means - Seasons

Standard Error of Seasons means = $\sqrt{(S^2/n)} = 0.56$

$Q_3 = 3.42$, $Q_2 = 2.84$

S.S.R. = $Q_3 \times 0.56$, $Q_2 \times 0.56$

Seasons means ranked in order of magnitude:

| January | March | Oct./Nov. |
|---|---|---|
| 15.30 | 11.26 | 9.55 |

S.S.R. 3 = 1.91 Significant difference between January and December means.

S.S.R. 2 = 1.59 Significant difference between January and March and Oct./November and March.

weather conditions that had occurred. Cloudy and wet conditions with higher temperatures before the March sampling would have the effect of raising respiration in the plants, with an associated lowering of accumulated E.S.C. levels.

### 4.4.2 Nitrogen (Table 4.3)

Significant differences were found between Calluna samples of different age ($P< 0.01$) and from samples collected during different seasons ($P< 0.01$).

Nitrogen levels were significantly higher in the October samples than in those taken during January and March. There was no significant difference between the January and March samples. The decline in nitrogen levels from October to the levels in January and March are similar to results reported by Gimingham (1972) and Powell & Malcolm (1974). Nitrogen shows an increase within the plant during periods of active growth, reaching a peak in summer, followed by a decrease in autumn to a low during winter. The October levels probably reflect the decline prior to the static low over winter, during dormancy, as reflected in the January and March levels.

Pioneer Calluna was significantly higher in nitrogen than degenerate and building material. There was no significant difference between building, mature and degenerate samples. Gimingham (1972) reports that analyses of Calluna of different ages have shown highest concentrations of nutrients in the youngest plants, and a decline with increasing age. Miller & Miles (1969) showed that nitrogen and phosphorus levels, highest in the youngest plants sampled, declined rapidly during the first six years, remaining, subsequently, at a fairly steady low level. The results follow a similar trend, with nitrogen levels being highest in pioneer material, and lower in the older age classes, although levels in building material were lower than in mature material.

### 4.4.3 Phosphorus (Table 4.4)

Phosphorus levels varied with site of collection ($P< 0.001$) and age of sample ($P<0.05$).

Table 4.3 Analysis of Variance - Variate Nitrogen

| Source of Variation | D. of F. | Sums of Squares | Mean Square | F-Ratio |
|---|---|---|---|---|
| Sites | 2 | 0.14174 | 0.07087 | 2.127 |
| Seasons | 2 | 0.41652 | 0.20826 | 6.251** |
| Ages | 3 | 0.60444 | 0.20148 | 6.048** |
| Grazing | 1 | 0.06661 | 0.06661 | 1.999 |
| Age x Grazing | 3 | 0.04416 | 0.01472 | 0.442 |
| Error | 60 | 1.99896 | 0.03332 | |
| Total | 71 | 3.27243 | 0.04609 | |

**significant at 1% level.

F-ratios reveal significant differences between means of Seasons and Ages.

i) Comparison of means - Seasons

Standard Error of Seasons mean = $\sqrt{(S^2/n)} = \sqrt{0.03332/24} = 0.037$

$Q_3 = 3.42$, $Q_2 = 2.84$

S.S.R. = $Q_3 \times 0.037$, $Q_2 \times 0.037$

Seasons means ranked in order of magnitude:

| Oct./November | January | March |
|---|---|---|
| 1.49 | 1.35 | 1.31 |

S.S.R. 3 = 0.13 Significant difference between Oct./November and March means.

S.S.R. 2 = 0.11 Significant difference between Oct./November and January means, no significant difference between January and March means.

ii) Comparison of means - Ages

Standard Error of Ages mean = $\sqrt{(S^2/n)} = \sqrt{0.03332/18} = 0.043$

Value of Q for 4, 3 and 2 Ages = $Q_4 = 3.74$, $Q_3 = 3.40$, $Q_2 = 2.83$

S.S.R. = $Q_4$, $Q_3$, $Q_2 \times 0.043$

Ages means ranked in order of magnitude:

| Pioneer | Mature | Building | Degenerate |
|---|---|---|---|
| 1.51 | 1.40 | 1.36 | 1.26 |

S.S.R. 4 = 0.161 Significant difference between Pioneer and Degenerate means.

S.S.R. 3 = 0.146 Significant difference between Pioneer and Building means, no significant difference between Degenerate and Mature means.

Table 4.4 Analysis of Variance - Variate Phosphorus

| Source of variation | D. of F. | Sums of Squares | Mean Square | F-Ratio |
|---|---|---|---|---|
| Sites | 2 | 0.0064726 | 0.0032363 | 18.709*** |
| Seasons | 2 | 0.0001525 | 0.0000762 | 0.441 |
| Ages | 3 | 0.0018275 | 0.0006092 | 3.522* |
| Grazing | 1 | 0.0000010 | 0.0000010 | 0.006 |
| Ages x Grazing | 3 | 0.0002266 | 0.0000755 | 0.437 |
| Error | 57 | 0.0098599 | 0.0001730 | |
| Total | 68 | 0.0185401 | 0.0002726 | |

*Significant at 5% level.
***Significant at 0.1% level.

F-ratios reveal significant differences between means of Sites and Ages.

i) Comparison of means - Sites

Standard Error of Sites mean $= \sqrt{(S^2/n)} = \sqrt{0.0001730/24} = 0.00268$
$Q_3 = 3.41$, $Q_2 = 2.83$
S.S.R. = $Q_3 \times 0.00268$, $Q_2 \times 0.00268$

Site means ranked in order of magnitude:

| Site 2 | Site 1 | Site 3 |
|---|---|---|
| 0.0728 | 0.0528 | 0.0525 |

S.S.R. 3 = 0.0091 Significant difference between Site 2 and Site 3 means.

S.S.R. 2 = 0.0076 Significant difference between Site 2 and Site 1 means. No significant difference between Site 1 and Site 3 means.

ii) Comparison of means - Ages

Standard Error of Ages means $= \sqrt{(S^2/n)} = \sqrt{0.001730/18} = 0.00310$
$Q_4 = 3.75$, $Q_3 = 3.41$, $Q_2 = 2.83$
S.S.R. = $Q_4$, $Q_3$, $Q_2 \times 0.00310$

Ages means ranked in order of magnitude:

| Pioneer | Mature | Building | Degenerate |
|---|---|---|---|
| 0.0657 | 0.0619 | 0.0576 | 0.0522 |

S.S.R. 4 = 0.0116 Significant difference between Pioneer and Degenerate means.

S.S.R. 3 = 0.0106 No significant difference between Pioneer and Building and Mature and Degenerate means.

Differences in the phosphorus levels of the Calluna samples from the three sites could be the result of geological variability within the area. The study area predominantly overlies undifferentiated schists, with some morainic deposits. All three sites were overlying geologically similar material, and thus if the apparently higher levels of phosphorus associated with Site 2 are not the result of between plant variability, then a localised area with higher phosphorus availability may be affecting certain of the plants. However the dispersed nature of the Site 2 plots makes it highly unlikely that they would all have a higher phosphorus status due to such soil factors.

There was a significant difference in phosphorus levels between pioneer and degenerate samples, although no significant differences were found between building, mature and degenerate samples. The results show a similar trend to other reports, and it is only the early stages of regrowth following fire that are likely to be significantly higher in phosphorus (see: Miller & Miles 1969 and Miller & Watson 1974).

### 4.4.4 Neutral Detergent Fibre (N.D.F.) (Table 4.5)

The results of the analysis of variance of the N.D.F. data are inconclusive. The significantly higher N.D.F. value for Site 1 may be the consequence of the previous grazing history of the plot. Sites 2 and 3 have lower N.D.F. values which could result from previous grazing of the plots, producing regrowth of a more juvenile nature, associated with the changed distribution of dry matter among fresh and woody material (see: Grant & Hunter 1965). However there was no significant difference between material of different ages which would have been expected had this been the case.

Since only two seasons are represented in the between seasons comparisons, any interpretation of these results is unwise. Although it has been suggested that deer will become less selective during periods when snow and ice reduce the availability of food, which was the case when the January samples were taken, the collection method is not considered sensitive enough to detect any real changes in the proportions of leaf/wood ingested. Besides it should be appreciated

Table 4.5 Analysis of Variance - Variate Neutral Detergent Fibre

| Source of Variation | D. of F. | Sums of Squares | Mean Square | F-Ratio |
|---|---|---|---|---|
| Sites | 2 | 196.87 | 98.44 | 5.602** |
| Seasons | 1 | 100.11 | 100.11 | 5.697** |
| Ages | 3 | 69.53 | 23.18 | 1.319 |
| Grazing | 1 | 0.77 | 0.77 | 0.044 |
| Age x Grazing | 3 | 8.81 | 2.94 | 0.167 |
| Error | 34 | 597.46 | 17.57 | |
| Total | 44 | 973.55 | 243.01 | |

**Significant at 1% level.

F-ratios reveal significant differences between means of Sites and Seasons.

i) Comparison of means - Sites

Standard Error of Sites mean = $\sqrt{(S^2/n)}$ = $\sqrt{17.57/16}$ = 1.048

$Q_3 = 3.63$, $Q_2 = 3.01$

S.S.R. = $Q_3$, $Q_2$ x 1.048

Sites means ranked in order of magnitude:

| Site 1 | Site 3 | Site 2 |
|---|---|---|
| 44.49 | 40.81 | 39.62 |

S.S.R. 3 = 3.46 Significant difference between Site 1 and Site 2.

S.S.R. 2 = 2.87 Significant difference between Site 1 and Site 3.

No significant difference between Site 3 and Site 2.

ii) Comparison of means - Seasons

Standard Error of Seasons means = $\sqrt{(S^2/n)}$ = $\sqrt{17.57/24}$ = 0.856

$Q_2 = 2.87$

S.S.R. 2 = $Q_2$ x 0.856

Seasons means ranked in order of magnitude:

| January | March |
|---|---|
| 43.05 | 40.16 |

S.S.R. 2 = 2.457 Significant difference between January and March means.

Table 4.6 Summary of results : analyses of variance of *Calluna* samples

Vertical bars indicate significant differences between means using multiple range test

| | | Ethanol soluble carbohydrate | Nitrogen | Phosphorus | Neutral-detergent fibre |
|---|---|---|---|---|---|
| Places | Site 1 | 10.40 | 1.32 | 0.0528 | 44.49 |
| | Site 2 | 12.35 | 1.40 | 0.0728 | 39.62 |
| | Site 3 | 13.36 | 1.43 | 0.0525 | 40.81 |
| Seasons | Oct./November | 9.55 | 1.49 | 0.0586 | |
| | January | 15.30 | 1.35 | 0.0728 | 43.05 |
| | March | 11.26 | 1.31 | 0.0525 | 40.16 |
| Ages | Pioneer | 12.53 | 1.51 | 0.0657 | 40.62 |
| | Building | 10.79 | 1.36 | 0.0576 | 43.66 |
| | Mature | 12.45 | 1.40 | 0.0619 | 40.91 |
| | Degenerate | 12.38 | 1.26 | 0.0522 | 41.24 |
| Grazing | Grazed (G) | 12.46 | 1.41 | 0.0595 | 41.48 |
| | Ungrazed (UG) | 11.61 | 1.35 | 0.0592 | 41.73 |
| Ages x Grazing | Pioneer G | 12.59 | 1.52 | 0.0653 | 39.85 |
| | " UG | 12.47 | 1.51 | 0.0661 | 41.40 |
| | Building G | 11.40 | 1.42 | 0.0594 | 44.06 |
| | " UG | 10.18 | 1.29 | 0.0557 | 43.25 |
| | Mature G | 12.42 | 1.42 | 0.0593 | 40.73 |
| | " UG | 12.48 | 1.39 | 0.0645 | 41.08 |
| | Degenerate G | 13.45 | 1.30 | 0.0537 | 41.27 |
| | " UG | 11.31 | 1.22 | 0.0507 | 41.20 |

that N.D.F. is very sensitive to any errors in sampling a uniform leaf/wood ratio, and thus such differences as are recorded may reflect this.

The results of the analyses of variance are summarised in Table 4.6.

## 4.5 Discussion

Since at least the beginning of the nineteenth century, Calluna has been managed by the use of fire. Burning, initially, was carried out on a ten year rotation for sheep, which reached peak numbers in Scotland after the middle of the nineteenth century. At about this time greater attention was being paid to the rearing of red grouse (Gimingham 1972), which in turn led to smaller individual areas of heather being burnt, in contrast to the large areas being burnt for sheep. Today upland areas are still regularly burnt, although in many cases the decision to do so sadly lacks sound justification. However where grouse are managed the burning of heather may be better regulated.

It is now recognised that heather managed for grouse is generally burnt on a 12 - 15 year rotation, depending on individual circumstances of growth (see: Miller & Watson 1974; Gimingham 1972). However due to the reduction in manpower on many estates, optimal burning cannot be carried out, which may result in the following: an insufficient area burnt annually for effective management; larger individual areas being burnt to compensate for the lack of labour, in an attempt to burn the appropriate area to maintain the rotation; an increased risk of run-away fires resulting in unsuitable or very large areas being burnt. The study area through labour shortages was underburnt in grouse management terms, and as a result only a very small proportion of suitable heather dominated ground was burnt each year.

### 4.5.1 The Composition of Calluna as Browse for Red Deer

The levels of nitrogen, phosphorus and carbohydrates found in the Calluna samples generally agree with published results of other studies. Variation in the composition of samples taken at different times during the winter are explicable in terms of the physiological response of the plant to seasonal and other environmental factors. The minor differences that occurred between sites, in some instances, may reflect the range of natural variability that exists in natural populations.

The results of the analyses support the views of Gimingham (1972) and Miller & Watson (1974), that any affects of muirburn are of relatively short duration, and once out of the pioneer stage, the quality of Calluna is fairly uniform. Samples in this study from pioneer stands, with a mean age of four years, were found to be higher in nitrogen and phosphorus than older material, but often only marginally so. However Miller & Watson (1974) found considerably higher levels of nitrogen, phosphorus and soluble carbohydrate in very young Calluna of one to two years of age, with a rapid decline in such levels subsequently.

Nutrient content per se is of limited value when considering the potential nutritive value of herbage for deer without some measure of digestibility of the material involved. In January and March the N.D.F. contents of the different aged samples were similar, and results presented by Milne (1974) also show a lack of significant differences in N.D.F. and also the digestibility of organic matter between pioneer, building and mature Calluna taken in summer. This suggests that the cell wall constituents are similar between the material sampled, and it is unlikely therefore that the digestibility will differ significantly also. The presence of tannins in Calluna may complicate this overall picture however. These compounds when found in similar amounts in other species have been implicated in the reduction of the in vitro and apparent digestibility of nitrogen in the diet (see: Milne 1974), probably as a result of the formation of protein-tannin complexes. A proportion of the nitrogen content of the diet may thus be unavailable to the rumen microflora. As Milne (1974) points out, more detailed work is required to determine the importance of such compounds in the digestion of nitrogen when Calluna is included within the ruminant diet.

### 4.5.2 The productivity and availability of Calluna as a grazing resource for red deer

The productivity and availability of Calluna shoots for grazing by deer varies with different stages of the growth cycle. Barclay-Estrup (1970) measured the primary productivity of different aged stands of Calluna, and found that the lowest annual production of short shoots was in pioneer stands with 148.8 g $m^{-2}$, in contrast to 442.4 g $m^{-2}$ and 363.6 g $m^{-2}$ in building and mature stands respectively. The open nature of pioneer, in contrast to older stands has been documented by Barclay-Estrup & Gimingham (1969). Thus despite the higher nutritive value of the current year's growth in the very youngest material, grazing time for a given input of forage is likely to be considerably longer than for older stands with a greater productivity. This may have important consequences, since the act of grazing in winter can be expensive in energy terms, due to the increased exposure of body surface compared with the bedded posture, under chilling conditions (see: Appendix 6.1 and Chap. 6). Thus the higher nutritive value of more dispersed food items may be offset by the increased energy cost involved in their exploitation.

Pioneer stands resulting from muirburn, unless of very small area, are less winter hardy than older material (see: Hunter 1954 and Grant & Hunter 1968). Watson, Miller & Green (1966) suggested that both pioneer and degenerate Calluna may suffer most from winter browning, due to the presence of a more open canopy, with more exposed foliage than building and mature stands. Areas suffering from winter browning are unlikely to be used by grazing deer. Furthermore during periods of snow-lie, particularly when coupled with freezing conditions, young heather will be far less available than older material, and experience low levels of utilisation. Hunter (1954) observed that although young heather was used intensively by sheep during summer, it was almost completely avoided during winter. During snowy conditions deer were observed to make much use of areas of longer heather, which has also been recorded by Darling (1937).

### 4.5.3 The selection of Calluna by red deer

Although deer have been reported to be able to select the richer areas of a sward, or even individual plants that are higher in nutrients (see: Mitchell, Staines & Welch 1977), the consistent lack of any significant difference between grazed and ungrazed plants within a given single-aged stand of Calluna for any of the attributes in the analysis, suggests that much of the available browse that can be utilised by red deer in upland Scotland during winter is of relatively uniform quality. There was also no evidence that any particular nutrients out of those evaluated were being specifically selected; deer were including the most nutritious parts of the plant by exploiting mainly the current season's growth. Such a conclusion is in contrast to reports by Mathews (1972), who considered that red deer were selecting a winter diet of Calluna on the basis of its carbohydrate content. In that study, the pooled data from Calluna samples taken from a range of altitudes during the March sampling period revealed significantly higher levels of soluble carbohydrate in previously grazed compared with ungrazed material. The analysis of what was termed 'grazed material', was in fact the shoot remainder subsequent to grazing in the randomly grabbed samples. This material analysed by Mathews may have had a higher soluble carbohydrate content as a consequence of grazing, since the removal of the terminal portion of the shoot may have the effect of causing a build-up of sugars beneath the point of removal. In this study ungrazed shoots adjacent to those which had experienced recent grazing were removed to the same estimated extent, on each sampling occasion. Thus a close approximation to what the deer actually consumed was sampled, rather than material remaining after grazing had taken place.

Selection of Calluna by deer on the study area throughout the winter was generally of the current season's growth only, which has also been noted for sheep by Armstrong & Thomas (1952); but during prolonged spells of snow, when the availability of herbage declined, more than the current season's growth was observed to have been grazed. Increased selectivity by the deer could result in a higher quality input, but at the expense of forage intake, since the most nutritious parts of Calluna plants constitute but a small fraction of the total biomass; consequently there is a limit to the amount of such material that can be obtained in a grazing day, apart from any physical constraints imposed by such a feeding strategy.

In view of the points raised in this discussion it is likely that during winter much of the available Calluna for deer browse is of a relatively uniform quality. Areas of pioneer Calluna may receive little use by grazing deer due to low productivity and lack of availability, in contrast to older stands, offering both available browse and in many cases valuable sheltered bedding sites. Newly burnt areas may be of most benefit to grazing deer in terms of availability during summer and autumn, when energy reserves are being built-up before the onset of winter. Thus well executed muirburn for grouse management, in suitable areas, as prescribed by Watson & Miller (1970) may be of value at such times. However, badly performed and inappropriate muirburn can destroy Calluna in marginal areas and encourage its replacement by other species, such as: M. caerulea, T. cespitosum, Eriophorum species and N. stricta (McVean & Lockie 1967 and Gimingham 1972); the first three named species being of negligible value to grazing deer for most of the winter. Extensive fires can destroy, at least in the short-term, substantial areas of heather, which may compel deer to seek other and possibly inferior areas of range; this may entail greater expenditure of energy. Injudicious burning may be particularly serious if heather stands in sheltered localities are decimated, since such areas may receive extensive use during winter (see: Chap. 5 and Gimingham 1972).

## 4.6 Summary

1) Deer grazed and adjacent ungrazed Calluna plants were sampled three times during winter at different sites on the study area.

2) Chemical analyses were conducted on the samples, for attributes considered to be of significance in the nutrition of deer in the uplands. Nutrient levels in the samples, as determined by the analyses, are in agreement with the published results of other studies.

3) There was no evidence to suggest that deer were selecting for any particular attribute out of those analysed. On the whole only the current year's growth was grazed, except during conditions of deep snow, when *Calluna* was grazed to a greater extent.

4) Although superior in nutritional quality, the low productivity of young pioneer *Calluna*, coupled with its susceptibility to winter browning and lack of availability during snow-lie, may result in low levels of use during winter.

5) It is suggested that it may be most advantageous, with respect to the energy budget, for deer to graze older stands of a higher productivity rather than the early regrowth after a fire.

# Chapter 5 Utilisation of the Habitat by the Red Deer during Winter

## 5.1 Introduction

The use of its habitat by an animal is the result of responses to the physical and biological environment, and to both inter and intra-specific behavioural factors, and, while it may not be possible to quantify all the factors mentioned above, specific aspects of the physical and biological environment can be assessed, which may explain, at least in part, the distribution and activity of a species within its habitat.

Wildlife managers in North America have made extensive use of methods involving habitat appraisal and pellet-group counts. The assessment of vegetational trends, animal impact on the habitat, the location and degree of utilisation of feeding areas and the determination of population size, have all been performed by the use of such methods (see: Neff 1968 and Korschgen 1969). Similar techniques have also been used in British studies, Table 5.1.

The popularity of pellet-group techniques has lead to the build-up of a considerable volume of literature on this subject, which has been reviewed by Neff (1968). Despite the popularity of use, such techniques have been criticised by some workers. Van Etten & Bennet (1965) reported that misclassification of pellet-groups by age was a serious problem in the use of pellet-group counts to census deer populations. However other authors (not all of whom were attempting to make an actual census of deer populations, thereby demanding less of such methods) have classified pellet-groups with respect to age, with apparent success (see: Riney 1957; Rogers, Julander & Robinette 1958; Charles, McCowan & East 1977). Dzieciolowski (1976) considered that pellet-group counts could provide an index of deer use in different habitats, although concluding that this technique was not adequate for censusing roe deer (Capreolus capreolus) populations.

In the part of the study reported in this section, I required an index of deer utilisation in different parts of the study area, to augment the observations reported in Chapter 2,

Table 5.1 British studies which assess animal utilisation by faecal deposition

| Author | Technique |
|---|---|
| Charles & McCowan 1967 | Numbers of faeces counted from collections made along transects five times per annum. |
| Rawes & Welch 1969 | Dung volume measurements made on permanent plots. |
| Miles 1971 | Faecal-pellets counted and removed from permanent plots. |
| Miller 1971 | Yearly faecal counts on permanent plots. |
| Welch 1971 | Dung volume measured at three week intervals on belt transects. |
| Hewson 1976 | Pellet counts and dung volume measurements on permanent plots. |
| Staines 1977 | Faecal-pellet counts made every two months along belt transect. |
| Charles, McCowan & East 1977 | Fresh faeces counted on permanent transects. |

and the use of pellet-group counts is considered justifiable. While carrying out the pellet-group counts, an attempt was also made to assess the degree of any grazing on the sampling sites. However I consider the grazing assessment results are too unreliable for inclusion in any estimate of habitat utilisation. This is due to the difficulties in making field measurements of grazing on species with different growth-forms eg. dwarf-shrubs and grasses, in such a way that valid comparisons can be made between sampling sites. Furthermore rabbits were present in the study area, and contributed to the total grazing on some of the sampling sites. However, utilisation, as assessed by pellet-group counts, can also estimate the relative amount of feeding in a specific area. The digestive physiology of the deer is such that most faeces are likely to be voided during bouts of feeding: 'ingestion stimulates egestion'. Undisturbed deer are reported by Moen (1973) to bed-down near their feeding sites, and thus faeces voided other than when grazing will tend also to be near the feeding area. Charles, McCowan & East (1977) report that feeding deer defecated frequently, and resting deer usually used the same ground as feeding deer; so faeces counts were considered to give a good indication of feeding distribution.

## 5.2 Method

Representative areas of homogenous vegetation (subsequently referred to as sites) were sampled throughout the study area, during the period mid-November 1976 to April 1977. The major vegetation associations and their variants had been identified during the preliminary reconnaissance of the study area during the summer of 1976. Data from forty three sites have been included for analysis.

### 5.2.1 Sampling

At each site selected on the study area, ten transects were sampled in a random fashion (see Appendix 5 for details). Five sample points were evaluated for each transect in most instances. The sampling unit in this scheme is the individual transect. Evaluation of sampling points along each transect involved counts of pellet-groups within a quadrat of 0.8 $m^{-2}$ at each of the five sample points. In borderline cases where a pellet-group was not entirely within the sample quadrat, it was included if more than 50 per cent of it was within the sampling area.

A value for a single transect is obtained as the average number of pellet-groups per transect, divided by the number of sampling points (usually five). This form of weighting of the values is used because the number of sampling points can be variable between transects through any errors in the estimation of the site dimension, and the inevitable irregularities of shape of areas of vegetation (see: Appendix 5).

Pellet-groups were assigned an age-class, either 'old' or 'recent'; although the ageing of pellet-groups is a continuous process without sudden transitions from one class to another. Old pellet-groups ranged from those that had commenced disintegration, to those which were intact, but with obvious signs of weathering: bleaching and surface disintegration. Recent pellet-groups consist of the freshest pellets, which are smooth, dark coloured and coated in mucous, and those pellets which have lost the mucous coating, but still show signs of recent origin viz. darkness of colour and little sign of surface weathering. For those pellets which are not clearly in one class or the other, there exists a potential source of error in the classification. In borderline cases such as this, pellets can be broken open to reveal the extent of internal weathering, which can assist in classification.

A trial was conducted during the winter of 1976-1977 to check on the rate of pellet decomposition. Freshly voided faeces from one pellet-group were placed in four different sites: dry open, dry closed, wet open and wet covered. Pellets remained in the 'recent' category longest in the wet covered site, 14 weeks. At the other sites, pellets remained as 'recent' for approximately 12 weeks. This is in contrast to reports of Dzieciolowski (1976), in which a maximum survival time of three months is given for red deer pellets under tree canopy in winter. The 'old' category generally represents faeces voided some months prior to sampling, although pellets can survive more than a year in the study area.

Discovery of all pellet-groups, while simple on short vegetation, is much more difficult in tall heather. In such cases thorough searching is necessary to ensure all pellet-groups are found. Van Etten & Bennet (1965) report that missed pellet-groups were a further source of error in using the method. However as the individual sampling point used in this study is of small area, intensive searching can be completed in a relatively short space of time.

### 5.2.2 Site Factors

An assessment was made of the following factors which were considered to be of possible significance in site utilisation for each area of vegetation that was sampled.

(i) Aspect

The aspect of each site to 8 cardinal compass points was recorded.

(ii) Slope

The slope of the sites was measured with an Abney level and a ranging pole. Sites were classified as follows:

1 Steep, angle of slope $\geq 25^\circ$
2 Moderate, angle of slope $> 10^\circ$ and $< 25^\circ$
3 Gentle, angle of slope $> 3^\circ$ and $< 10^\circ$
4 Flat, angle of slope $\leq 3^\circ$

(iii) Drainage

The drainage of sites was assigned to one of the following classes:

1 Wet (standing water or squelchy under foot)
2 Intermediate
3 Dry

This classification is applicable to winter conditions only, since site characteristics are liable to change with periods of dry weather during summer.

(iv) Shelter

The potential geomorphic shelter of sites was assessed by the use of the Topex Method of the Forestry Commission (see: Howell & Neustein 1965). In a revised form (Pyatt, Harrison & Ford 1969), measurements are taken with an Abney level of the angle subtended by the horizon at the eight cardinal compass points. The sum of the eight angles gives an estimate of the relative exposure of the site.

Any other factors which it was felt might have been of possible influence on site utilisation were recorded. These included: proximity to woodland; adjacent vegetation; any burning.

## 5.3 Results

In the computations that are presented in this section, I have used only those pellet-groups assigned to the 'recent' category. This category represents the integrated use of an area during a suitably short period of time since deposition and hence is most appropriate for considerations of site utilisation over the winter period. The first four sites sampled have been excluded from the overall data-set because of inconsistencies with sites subsequently sampled; this arose from a development in the technique during the early stages of sampling. A score for each site, based on the pellet-group values of the ten individual sampling transects has been calculated. The values of the individual transects for a particular site have been summed to give an overall score. The scores of the 43 sites included for analysis are presented graphically in Fig. 5.1. Sites have been allocated to the vegetation classes adopted in Chap. 2, with the exclusion of Molinia Grassland which was of limited distribution on the study area. The Species Poor Grass category is referred to as Grass, for convenience throughout this section.

The designation of the categories 'low', 'medium' and 'high' scores is on an arbitrary basis, and is determined by the division of the range of site scores into three categories of approximately equal size.

### 5.3.1 Shelter

To test for any relationship between the degree of utilisation of sites, as assessed by the pellet-group scores, and available geomorphic shelter (Topex Value), Spearman's rank correlation

Fig. 5·1 Site Utilisation As Determined From Pellet-Group Scores

coefficient, $r_s$, was calculated. The correlation coefficient is presented in Table 5.2; there is no significant relationship at the five per cent level between site utilisation and geomorphic shelter ($r_s = 0.158$, $t_{(38)} = 0.99$, N.S.). However the possibility that shelter from specific directions might influence site utilisation under certain weather conditions was investigated, by breaking the shelter data up into its constituent quadrants as in Fig. 5.2. The correlation coefficients are presented in Table 5.2 for each of the quadrants of the shelter values and site utilisation. A significant correlation was obtained with shelter to the west and site utilisation ($r_s = 0.433$, $t_{(38)} = 2.96$, $P < 0.01$). Correlations were subsequently calculated for shelter to the south-west and north-west and site utilisation; a further significant relationship was obtained for shelter to south-west ($r_s = 0.446$, $t_{(38)} = 3.07$, $P < 0.01$).

If deer are seeking shelter from wind then a variety of sites with a range of available shelter would be necessary to account for the range of wind directions that may be experienced over the course of the winter. However site use, as assessed by pellet-group counts, is apparently associated with shelter from the south-west to west. High pellet-group scores suggest repeated use of a site, which in this instance could come about if winds were frequently blowing from south-west to west and causing deer to seek shelter. An examination of the weather data collected on the study area during fieldwork (see: Chap. 6), reveals that the prevailing winds recorded during the period November 1976 to April 1977 originated from south-west and westerly directions. A minimum of 50% of total winds originated from these directions (see: Fig. 5.3). This supports the results presented above. During fieldwork, undisturbed deer could be found in areas where they had been observed on previous occasions when winds were blowing from a similar direction.

### 5.3.3 Aspect, Slope and Drainage

The sub-program CROSSTABS of S.P.S.S. (Nie et al. 1975) was used to test for any association between the degree of site utilisation and the variates: aspect, slope and drainage. Sites have been assigned as low use (pellet-group score $\leq 7$,

## Table 5.2 Spearman Rank Correlation Coefficients for Site Utilisation and Geomorphic Shelter

| Direction of Shelter | Correlation Coefficient | 't' value |
|---|---|---|
| Total shelter | $r_s = 0.158$ | $t_{(38)} = 0.99$ N.S. |
| North | $r_s = 0.135$ | $t_{(38)} = 0.84$ N.S. |
| East | $r_s = -0.056$ | $t_{(38)} = 0.35$ N.S. |
| South | $r_s = 0.260$ | $t_{(38)} = 1.66$ N.S. |
| West | $r_s = 0.433$ | $t_{(38)} = 2.96$ $P < 0.01$ |
| South-west | $r_s = 0.446$ | $t_{(38)} = 3.07$ $P < 0.01$ |
| South-east | $r_s = 0.163$ | $t_{(38)} = 1.02$ N.S. |
| North-west | $r_s = 0.186$ | $t_{(38)} = 1.27$ N.S. |

Fig. 5·2 The Division Of The Shelter Data

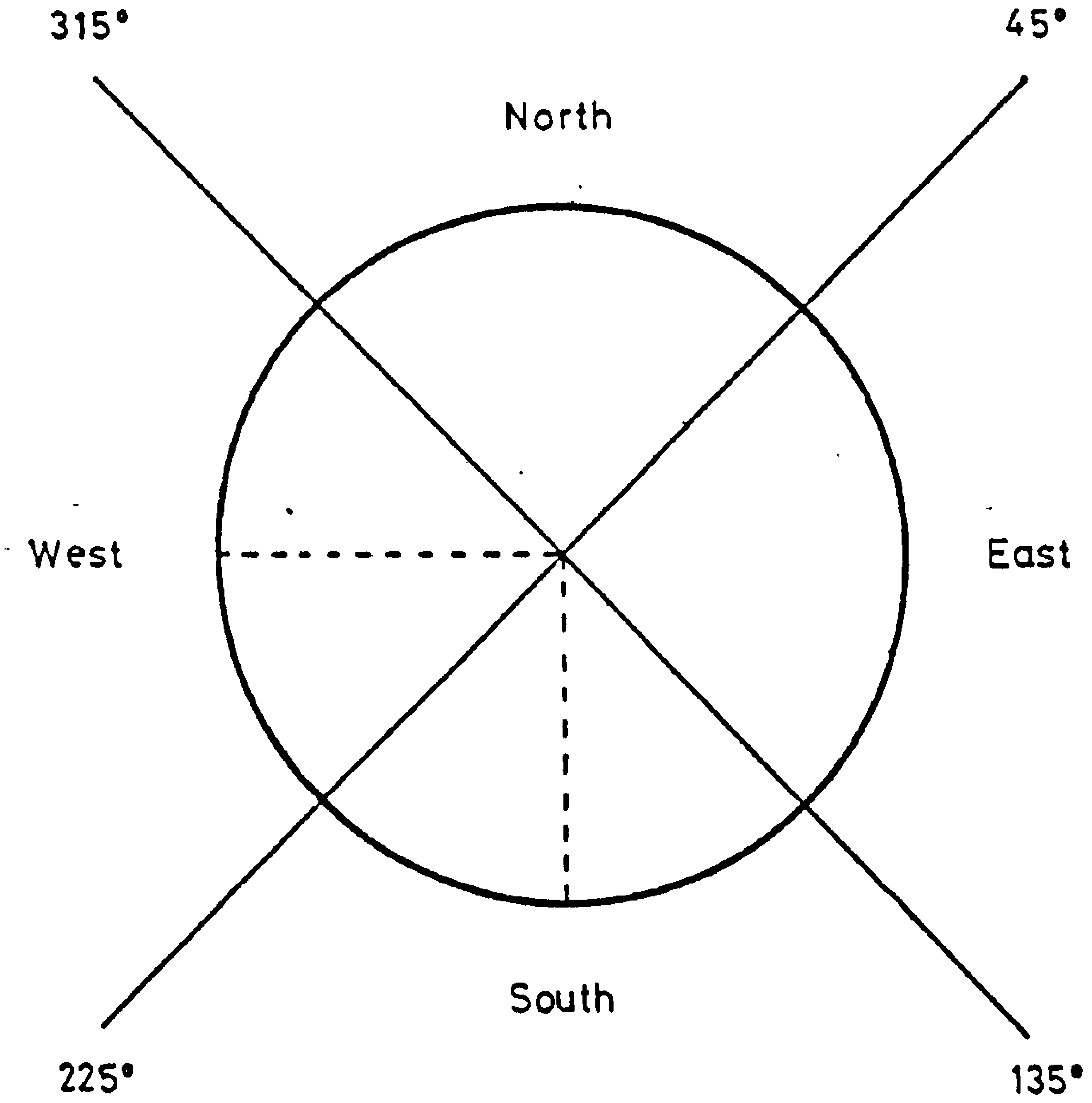
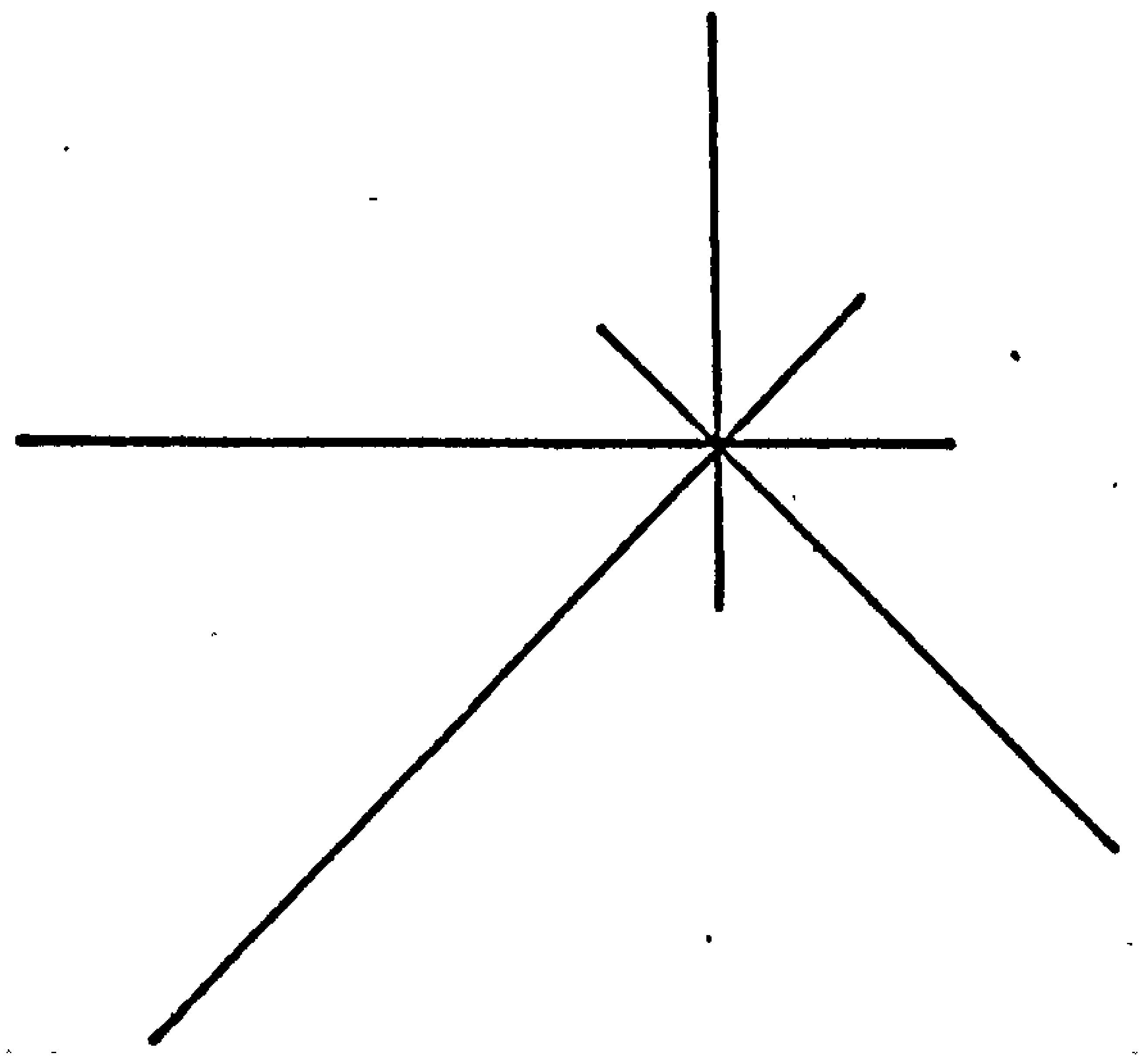


Figure 5.3 Windrose for the study area

November 1976 to April 1977



low category in Fig. 5.1) and high use (pellet-group score $> 7$, medium and high categories in Fig. 5.1).

(i) Aspect - Table 5.3(a)

Site aspect was related to utilisation ($\chi^2_{[3]} = 15.23$, $P = 0.0016$). The comparison of adjacent column percentages in the table, as mentioned previously, reveals that the greatest heterogeneity occurs with site aspects of north to east and south to west. Sites with a north to east aspect were high use (35.3% vs. 0.0%), whereas those with aspects of south to west were predominantly low use (46.2% vs. 5.9%). This result is likely to be related to shelter from the prevailing winds; south-westerly sites tending to be exposed more frequently in contrast to north easterly sites, which would offer shelter under such circumstances.

(ii) Slope - Table 5.3(b)

The slope of sites, as measured in this study, does not appear to be directly associated with the degree of utilisation by deer ($\chi^2_{[3]} = 2.60$, $P = 0.4578$). Steep areas appear to receive as much use as flat areas. Slope does of course interact with drainage and vegetation, which may influence deer utilisation. Steep slopes although tending to be well drained do not necessarily support attractive vegetation which may encourage high levels of use. Similarly, flat areas were in some instances poorly drained and supported bog-type vegetation, whilst others with better drainage supported better quality grass species. This interaction with other variables complicates the interpretation of the results.

(iii) Drainage - Table 5.3(c)

Site drainage was also associated with utilisation by deer ($\chi^2_{[3]} = 6.07$, $P = 0.0480$). As before the comparison of adjacent column percentages in Table 5.3(c), reveals that the greatest contribution to heterogeneity exists in the wet and dry categories. Most of the wet sites fall into the low use category (34.6% vs. 11.8%) and conversely the majority of dry sites are in the high use category

Table 5.3 Site utilisation as determined from pellet-group scores

The numbers in the tables refer to the frequency of sites in either low (pellet-group score $\leq 7$) or high ($> 7$) use categories; those in parenthesis are the percentage of the column total accounted for by the site frequencies.

(a) Site utilisation in relation to aspect

| | Pellet-group score | | |
|---|---|---|---|
| Aspect | Low | High | Total |
| North to East | 0<br>(0.0%) | 6<br>(35.3%) | 6<br>(14.0%) |
| East to South | 9<br>(34.6%) | 5<br>(29.4%) | 14<br>(32.6%) |
| South to West | 12<br>(46.2%) | 1<br>(5.9%) | 13<br>(30.2%) |
| West to North | 5<br>(19.2%) | 5<br>(29.4%) | 10<br>(23.3%) |
| Total | 26 | 17 | 43 |

Chi Square = 15.23, 3 degrees of freedom

Significance P = 0.0016

(b) Site utilisation in relation to slope

| | Pellet-group score | | |
|---|---|---|---|
| Slope | Low | High | Total |
| Steep | 2<br>(7.7%) | 3<br>(17.6%) | 5<br>(11.6%) |
| Moderate | 12<br>(46.2%) | 5<br>(29.4%) | 17<br>(39.5%) |
| Gentle | 9<br>(34.6%) | 5<br>(29.4%) | 14<br>(32.6%) |
| Flat | 3<br>(11.5%) | 4<br>(23.5%) | 7<br>(16.3%) |
| Total | 26 | 17 | 43 |

Chi Square = 2.60, 3 degrees of freedom

Significance P = 0.4578

(c) Site utilisation in relation to drainage

| | Pellet-group score | | |
|---|---|---|---|
| Drainage | Low | High | Total |
| Wet | 9<br>(34.6%) | 2<br>(11.8%) | 11<br>(25.6%) |
| Intermediate | 14<br>(53.8%) | 8<br>(47.1%) | 22<br>(51.2%) |
| Dry | 3<br>(11.5%) | 7<br>(41.2%) | 10<br>(23.3%) |
| Total | 26 | 17 | 43 |

Chi Square = 6.07, 3 degrees of freedom

Significance P = 0.0480

(41.2% vs. 11.5%). The sites classified as wet fell into the Bog Category with two exceptions, both of which were grass dominated. These two sites containing Deschampsia and Festuca species both received relatively high levels of use, and had become wet during the winter period.

### 5.3.4 Vegetation

A further variable which may exert a major influence on the distribution of animals is the vegetation complex. Inspection of Fig. 5.1 reveals the considerable variation between sites in any given vegetation class. Fig. 5.4 summarises the data for the degree of utilisation of sites in relation to vegetation. The low overall use made of Damp Heath and Bog sites can be seen. Dry Heath sites show the greatest variability with 58% of the sites in this category falling in the 'low category'. However 26% of the sites fell in the 'high category'. Overall, Grass sites received the highest use during winter, with 77% falling into the medium and high categories. The heaviest overall use recorded however, was amongst Dry Heath sites.

### 5.3.5 Other Factors

(a) Trees and Shrubs

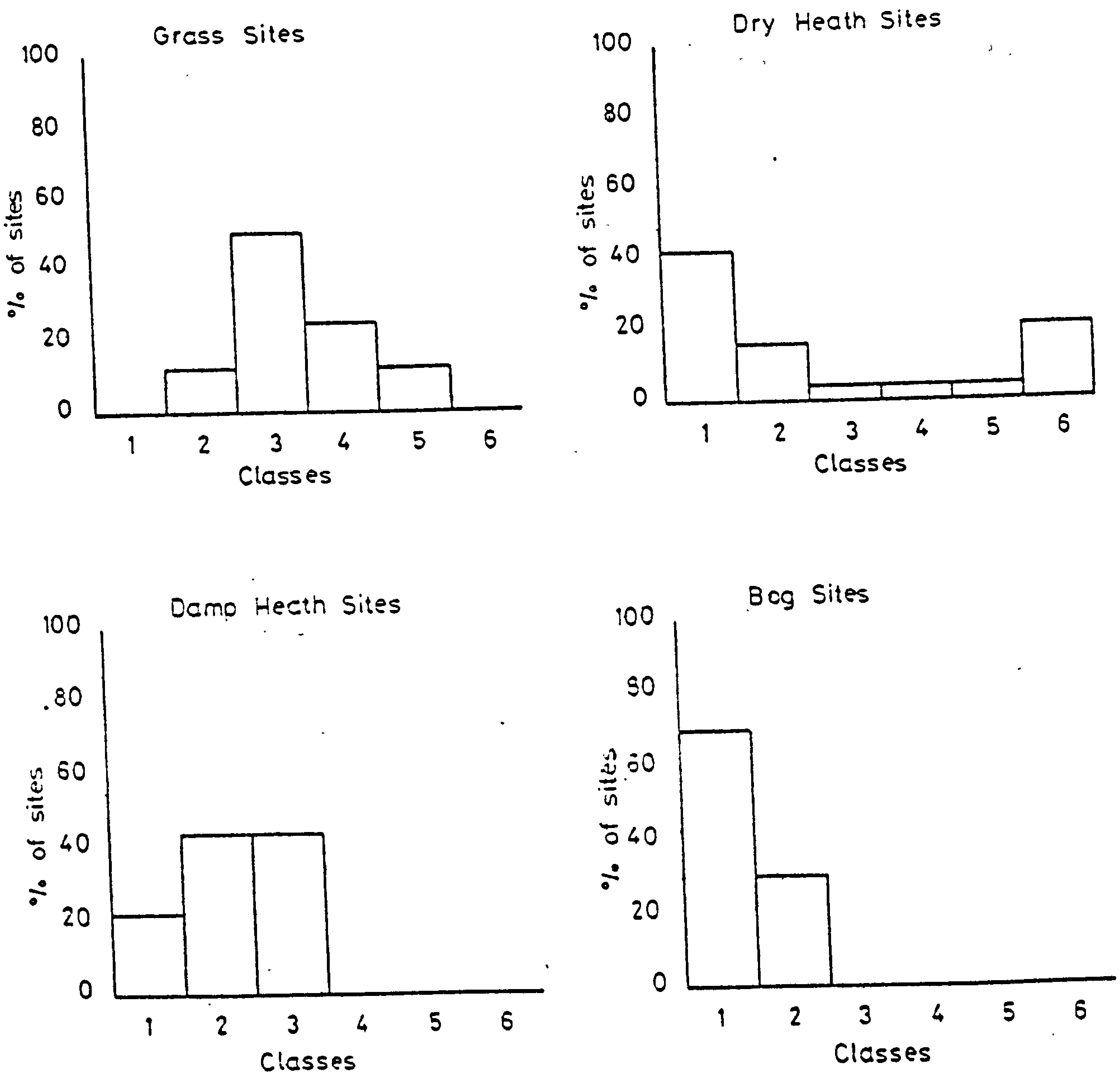
Trees and shrubs may influence the utilisation of a particular site in two ways:

(i) augmenting geomorphic shelter and thus reducing potential convective and radiative heat loss;

(ii) providing browse - an important constituent of the winter diet of red deer in more 'natural' areas of their range.

Sites associated with trees can be seen in Fig. 5.1, illustrated with the symbol ↟. Site details are summarised in Table 5.4. The small sample of sites involved precludes the drawing of any firm conclusions in this instance; however of the four sites involved, two fall in the high use category and two in the medium. Site 9, although potentially a suitable site as assessed from the tree cover and understorey vegetation, received comparatively little use.

Fig. 5·4 Site Utilisation In Relation To Vegetation



Class Intervals of Pellet-Group Scores

1=0-3·5
2=3·6-7·0
3=7·1-10·5
4=10·6-14·0
5=14·1-17·5
6=17·6-21·0

Table 5.4 Sites associated with trees and the understorey vegetation

| Site Number | Tree Species | Understorey Vegetation | Pellet-group Score |
|---|---|---|---|
| 5 | Pinus sylvestris | Calluna | 12.82 |
| 9 | Larix deciduous<br>P. sylvestris | Calluna<br>Pteridium aquilinum<br>Agrostis species | 7.23 |
| 48 | P. sylvestris | Calluna<br>Vaccinium myrtillus<br>Vaccinium vitis-idaea | 20.57 |
| 49 | P. sylvestris<br>Betula pubescens<br>Salix species | Calluna<br>Ulex europeus<br>Sarothamnus scoparius<br>Vaccinium myrtillus<br>Vaccinium vitis-idaea | 16.25 |

Categories of utilisation used with pellet-group scores: less than 7 = low, greater than 7 but less than or equal to 14 = medium, greater than 14 = high.

## Table 5.5 Kruskal-Wallis One-Way Analysis of Variance by Ranks: Utilisation of Different Aged Stands of Calluna

| Site Scores | Pioneer Stands | Building Stands | Mature Stands | Degenerate Stands |
|---|---|---|---|---|
| | 3.25 | 5.65 | 1.84 | 2.64 |
| | 1.35 | 3.48 | 4.15 | 1.75 |
| | 7.57 | 2.17 | 8.39 | 7.14 |
| | 9.20 | 21.64 | 10.45 | 2.47 |
| | 1.87 | 18.04 | | |
| | 17.82 | | | |
| **Ranks** | 8 | 11 | 3 | 7 |
| | 1 | 9 | 10 | 2 |
| | 13 | 5 | 14 | 12 |
| | 15 | 19 | 16 | 6 |
| | 4 | 18 | | |
| | 17 | | | |
| | $R_1 = 58$ | $R_2 = 62$ | $R_3 = 43$ | $R_4 = 27$ |

$$H = \frac{12}{N(N + I)} \sum_{J=1}^{k} \frac{R_J^2}{n_J} - 3(N + 1)$$

$$\frac{12}{19(19+1)} \left[ \frac{(58)^2}{6} + \frac{(62)^2}{5} + \frac{(43)^2}{4} + \frac{(27)^2}{4} \right] - 3(19+1)$$

$H = 3.24$

Degrees of Freedom = k-1 = 4-1 = 3

$H_0$ 3 df = 7.82, P = 0.05

Accept null hypothesis of no significance difference between stands in levels of utilisation.

Table 5.6 Summary of statistical analyses

| | Test | Result | Significance |
|---|---|---|---|
| Shelter | | | |
| Total | Spearman Rank Correlation | $r_s = 0.158, t_{(38)} = 0.99$ | N.S. |
| North | " | $r_s = 0.135, t_{(38)} = 0.84$ | N.S. |
| East | " | $r_s = -0.056, t_{(38)} = 0.35$ | N.S. |
| South | " | $r_s = 0.260, t_{(38)} = 1.66$ | N.S. |
| West | " | $r_s = 0.433, t_{(38)} = 2.96$ | $P < 0.01$ |
| South-west | " | $r_s = 0.446, t_{(38)} = 3.07$ | $P < 0.01$ |
| South-east | " | $r_s = 0.163, t_{(38)} = 1.02$ | N.S. |
| North-west | " | $r_s = 0.186, t_{(38)} = 1.27$ | N.S. |
| Aspect | Contingency Table Analysis | $\chi^2_{[3]} = 15.23$ | P=0.0016 |
| Slope | Contingency Table Analysis | $\chi^2_{[2]} = 2.60$ | N.S. |
| Drainage | Contingency Table Analysis | $\chi^2_{[2]} = 6.07$ | P=0.0480 |
| Calluna Stands | | | |
| Pioneer, Building<br>Mature, Degenerate | Kruskal-Wallis One-way Analysis of Variance | H = 2.34 | N.S. |

### (b) The Burning of Heather

It has been suggested in Chapter 4 that heather burning may affect the subsequent utilisation of a site. Data from nineteen sites with a variety of exposures and aspects, representing the four growth phases of Calluna, were analysed with the Kruskal-Wallis one-way analysis of variance by ranks, to assess any variation in the utilisation of different aged material. A non-parametric statistical test was performed on the data, due to reasons of non-normality, as has been noted previously. Sites 5, 48 and 49 have been excluded from this analysis because of the presence of trees, thought to represent a source of unwanted variation in this case.

The result of the Kruskal-Wallis one-way analysis of variance, Table 5.5, reveals no significant differences at the 5% level, between utilisation of the different aged stands ($H = 2.34$, $P > 0.50$). An examination of the raw data in Table 5.5 shows the tendency for the higher pellet-group scores to occur in the pioneer and building stands respectively. However the variation between sites of the same age-class is considerable, and this contributes to the lack of statistical significance in the comparison of different aged stands.

The statistical results presented in this section are summarised in Table 5.6.

## 5.4 Discussion

The winter experienced in the Scottish uplands is, as mentioned elsewhere, usually considered to be a period of great stress for the red deer. The two most important ultimate factors affecting red deer at this time are the severity of the weather and the quality and quantity of available food. The use of the winter range may be expected to reflect these factors to some considerable degree.

The results have shown that shelter, aspect and vegetation (drainage also through its influence on the vegetation) apparently influenced the usage of sites, as estimated by pellet-group counts. However there are considerable interactions between variables, which tends to complicate the interpretation of these results.

### 5.4.1 Shelter and Aspect

Staines (1970) found that although red deer tolerated worse weather conditions when feeding than resting, the gross distribution during winter was associated with the availability of good shelter from wind, and not the quality and quantity of their food. Moen (1968a) reported the independence of shelter exhibited by white-tailed deer during winter when feeding on high energy agricultural crop residues. The circumstances reported in Moen's study are, by Scottish standards, exceptional, and the benefits to deer in Scotland from the exploitation of better areas of range are unlikely to preclude the need to utilise shelter under normal conditions. Deer in such areas will be compelled to exploit shelter during poor weather, to conserve energy. Thus the situation as reported by Staines (1970) is more likely to be typical of upland Scotland.

From breakdown of the shelter data, land-forms providing shelter from the south-west to west direction were seen to be most significant in determining overall utilisation of sites during winter. In view of the prevailing wind over the winter period, this, perhaps, is not an unexpected result. The results from the examination of aspect tend to support this view, since the presence of landforms to the south-west was apparently associated with sites in the high use category, in contrast to areas open to the south-west, with a preponderance of low use sites. However this may well be an over simplification of the situation; adjacent landforms may modify windflow such that sites are not exposed to the extent that considerations of aspect alone would suggest. Aspect has, for different reasons, been considered to be important in studies of wintering deer in N. America. Mule deer (Odocoileus hemionus) have been observed to make use of south-facing slopes, and to follow the sun shadow throughout the day (see: Loveless 1964). There was no tendancy in the present study for south-facing slopes to receive higher use as a matter of course, but fundamental differences exist between the climate of the study area used by Loveless, which is continental, and N. Scotland, which is decidedly oceanic in nature. In the cool, cloudy, wet and windy conditions experienced on the study area, the use of south-facing slopes for their potential insolation is likely to be of minor importance in comparison with the avoidance of the prevailing winds. This is not to say however, that red deer will not make use of direct solar radiation when it can be exploited without exposure to chilling winds.

Reports by Lowe (1966) that 60% of observed red deer on Rhum were distributed on ground insolated from the south, despite the prevailing south-west wind, appear to conflict with results obtained in N. Scotland. An inspection of the data from Rhum revealed the following distribution of winds: NW-NE, 63%; E-SE, 24%; W, 10%; and SW, 2.5%. This coupled with the complex and broken topography of the Isle of Rhum suggests that deer were likely to have been sheltered from the wind when the particular observations were made. Furthermore the number of hours of sunshine for the periods when observations were made, are not given, and thus it is not clear how much insolation would have been received on such south-facing slopes. Consequently shelter is considered to be a major influence on site utilisation by deer, and aspect, with regard to insolation, may be of minor importance for much of the time in the oceanic conditions of N. Scotland.

Although the existence of a relationship was established between utilisation and the sheltering potential of a site, the use of the Topex Method may not be as sensitive for site appraisal for red deer as might be desired. Staines (1977) has used this method with apparent success for classifying sites used by deer. He was able to relate shelter from the wind at the time of observation to the mean sum of the three uphill bearings. Such an approach was not applicable in this part of the study. While apparently adequate for describing relative site exposure for forest trees, which at maturity may be 20-30m in height, the Topex Method probably underestimates site values for red deer, since the trunk of an adult animal is only about one metre above ground level.

Microtopographic relief, insignificant to trees, which is overlooked by this method, can, nonetheless be of considerable value to grazing or bedded deer (see: Appendix 6.1).

Tree cover will also provide shelter, reducing both convective and radiative heat loss; evergreen species naturally being of far greater value than deciduous trees in this respect during winter (see: Appendix 6.1). Sites 48, 49 and 5 have Scots Pine present or immediately adjacent to them, which as well as providing shelter may provide valuable browse, particularly from wind-blown branches. Mutch, Lockie and Cooper (1976) attribute, at least in part, the high numbers of deer found in certain glens in S. Ross-shire to the presence of woodland (mainly Scots Pine and Birch), providing valuable browse and storm shelter, and while it is not suggested that the small areas of woodland in the study area are contributing to overall deer numbers, their presence may be attractive to wintering deer. Site 9 also had tree cover of Larch and Scots Pine, and despite the already high geomorphic shelter of this site, it was not highly used. This site was however considerably wetter than many others. The low use made of this area may suggest that there are certain traditional areas adopted for use by red deer. Staines (1977) also mentions the possibility that tradition or fidelity to a home range determined to which areas deer moved to get better shelter.

### 5.4.2 Drainage

Drainage also appeared to influence site utilisation during winter; wet areas being characterised by low use sites, and dry areas by high use sites. Site drainage will influence the vegetation which in turn will influence the selection of grazing and bedding areas by deer. Continuously impeded drainage leading to the development of bog communities led to low levels of utilisation in such areas during winter in this study. However, sites which became wet during winter, but containing attractive grass species still received relatively high levels of use.

### 5.4.3 Slope

Moen (1976) reports the use of flat land by white-tailed deer during winter, and an avoidance of steeper terrain, which, he suggested, is partially explicable in terms of energy conservation: less energy being expended in locomotion on level as opposed to vertical ascents. There is no suggestion that the intensity of use of sites on slopes is any less than on sites on flatter ground in the present study. Again there are probably considerable differences between the deer range under study and that in N. America, where the scale of the topography may be much greater, and the habitat more 'natural' than in the Highlands. In the sub-optimal range occupied in much of Scotland the use of topographic shelter is more likely to be an appropriate means of conserving energy than the avoidance of steeper terrain. The most likely influence of slope on site utilisation is, indirectly, through its affect on drainage and hence vegetation.

### 5.4.4 Vegetation

It has been reported that red deer have the capability to select the most nutritious diet from the plant material available to them, although the extent to which this occurs is unknown (see: Mitchell, Staines & Welch 1977). The importance of 'better' grasses to both sheep and deer in upland areas has been discussed in Chapter 2. The results have also demonstrated the generally high use made of grass sites during winter, with the notable exception of site 36. This site had, however, been grazed very severely earlier in the season, and offered negligible, if any, herbage for subsequent grazing. Charles, McCowan & East (1977) report the reduction in the use of herb-rich grassland by hinds between summer and winter on Rhum, which they attributed to previous heavy grazing. Similar observations have been reported for feral Soay sheep (<u>Ovis aries</u>) by Grubb & Jewell (1966). The study area has a small population of red deer during summer, but many more during winter. Site 36 was in an area frequented by hinds during summer and stags during winter. Other grass sites had not been so extensively used before winter and therefore offered utilisable herbage later in the season.

It is reasonable to expect that grass sites would receive repeated use during winter as long as herbage was available. Miller (1971), working in Glen Feshie, reported that grass areas were used intensively when free of deep snow, until the supply of green herbage reached a minimum in March. Glen Feshie is also a wintering area for red deer and received low levels of grazing during summer, as did much of the study area, which left utilisable herbage for winter use. This is in contrast to the situation on Rhum, as reported by Charles, McCowan & East (1977), where seasonal movements are much less than on the mainland.

Interactions between the exposure of grass sites and their utilisation would be interesting to investigate. However all grass sites sampled showed some degree of geomorphic shelter, as evaluated by the Topex Method. If, as postulated earlier, shelter is the most important variable determining site utilisation during winter, which is in accordance with conclusions made by Staines (1970), then the selection of grass sites might have been a consequence of a sheltering effect in the first instance; selection for optimum grazing being a factor of secondary importance.

The bog areas received generally low use, which appeared to be independent of shelter. These areas, characterised by *Eriophorum vaginatum*, *Erica tetralix*, *Trichophorum cespitosum*, *Eriophorum angustifolium* and *Molinia caerulea* (not individually important dietary components during winter), contain little *Calluna*, which although not of a particularly high feeding value, is a major food item during winter (see: Chap. 3). *Calluna* in the bog associations is not vigorous, and of only sparse distribution. Grazing intensity is light, and as reported by Staines (1976) and in Chapter 2, such areas were avoided by bedding deer, being wet, and offering little of the insulation from the ground (a significant avenue of heat loss to a bedded animal, see: Gatenby 1977), or the shelter that *Calluna* stands can offer.

Damp Heath sites show somewhat higher utilisation values than the Bog type, and possibly reflect the greater abundance and vigour of the *Calluna* associated with these sites. Although not receiving high grazing overall, these sites are important quantitatively due to their extensive nature, covering an estimated 60% of the study area.

Within the Dry Heath sites there were some high use areas, and other areas receiving comparable use to the Damp Heath areas. However the dividing line between Dry and Damp Heath areas is, in some cases, rather fine; these two classes of vegetation representing different areas of a continuum rather than discrete categories.

The influence of shelter on these sites has already been discussed, but a further factor of possible influence is that of burning _Calluna_ stands.

### 5.4.5 Burning Calluna Stands

It has been suggested in Chapter 4 that pioneer _Calluna_ was unlikely to be a major attraction to grazing deer in winter, due to the low productivity of only marginally superior herbage. The results of the Kruskal-Wallis One-Way Analysis of Variance, Table 5.5, at first sight do not support such a view. Although there is considerable variation within sites, the pellet-group scores for pioneer stands are often high. However of the three higher value sites within this particular category, two contained substantial amounts of _Festuca_ species and _Deschampsia flexuosa_, which had colonised following burning. The presence of the grasses may have encouraged higher overall levels of utilisation. The other higher value site, with the highest pellet-group score per $m^2$ of sites in the pioneer stage, was a small ridge adjacent to an extensive area of _Festuca_-rich grassland, and was frequently used as a sheltered bedding area between bouts of feeding. _Calluna_ in association with grass areas has frequently been observed to be heavily grazed (see: Staines 1970), which may also contribute to the high recorded use made of this site.

Hewson (1976), working on Deeside, found that for much of the year mature stands of _Calluna_ were utilised most by red deer. However during late winter and early spring, he found that stands of building _Calluna_ received most use. It is possible that more uniform site conditions existed in Hewson's study area, which facilitated the establishment of significant differences between stands. Furthermore in the drier Eastern Highlands, more suitable for the vigorous growth of Calluna, regeneration following fire is likely to be more rapid than in the Northern Highlands; invading graminoids may be more readily supressed, making pioneer areas less attractive than on the study area.

Burning of Calluna can have an affect on the subsequent utilisation of an area, but other factors such as the shelter of the site and its proximity to areas of better quality grass, appear to exert a major influence.

## 5.5 Summary

1) The degree of utilisation by deer of a range of sites on the study area was assessed by the use of pellet-group counts.

2) Of the variables considered, shelter and vegetation had a direct influence on the use of sites by deer. Shelter has, apparently, the most significant effect, with vegetation of secondary importance.

3) Although only occupying an estimated 5% of the area, sites supporting better quality grasses were generally heavily used while herbage was available.

4) Trees and shrubs can influence site utilisation through the provision of shelter, and by supplying browse.

5) The use of Calluna stands may be influenced by muirburn; pioneer stands may receive little use, depending on the amount of grass that invades subsequent to the fire.

6) The comparatively low use occasionally made of what appeared to be favourable sites, probably indicates that an element of tradition exists in the overall use of range.

# Chapter 6 The Influence of Weather on Red Deer in Winter

## 6.1 Introduction

Thermal homeostasis involves the continuous balancing of heat exchange with the environment, and endogenous heat generated by metabolism, activity and productive processes, resulting in a relatively constant body-core temperature. During winter in the higher latitudes, homeotherms which remain active have to contend with weather conditions which promote heat loss from the body; in particular, low temperatures, high wind speeds and precipitation. Such losses will result in a drain on the animal's energy budget if thermal homeostasis is to be maintained.

There are two possible responses to this drain on the energy budget of the animal: i) it may increase food intake, although this will incur a penalty of increased energy expenditure; ii) it may adopt a strategy of conservation, restricting activity and minimising energy expenditure and loss. In upland Scotland the energy drain which winter weather may impose upon red deer cannot be counter-balanced by an increase in forage intake, as the digestibility of food species declines at this time, and the availability of the most nutritious species may be limiting. Also, deer have been observed to decrease food intake during winter (see: Ozoga & Verme 1970 and Blaxter et al. 1974). This phenomenon is believed to be a physiological adaptation to reduced food supplies in winter.

The significance of the physical environment to wintering deer in N. America has been documented in a number of studies, including: Severinghaus & Cheatum (1956), Loveless (1964), Verme (1965), Ozoga (1968) and Moen (1968 (a) & (b), 1973, 1976). In comparison, less attention has been paid to the effects of winter weather on red deer. Flerov (1952) in his general account of the species, mentions the importance of shelter, and also snow depth, which he considered limited the northerly distribution. There are reports from central Europe of the value of shelter for red deer in winter eg. Dzieciolowski (1969). Studies in Scotland on this topic are few, and it is regrettable that the pioneer work of Darling (1937) was not followed up sooner.

Darling considered that deer selected areas with the most uniform conditions of weather. He did not consider that wind was one of the more important factors influencing movement, except for strong winds, which he mentions brought deer down hill or into sheltered places. Staines (1970), however, reported a general avoidance of wind by red deer in winter, which tended to shelter more at higher wind speeds and lower temperatures. Jackes (1974) also recorded that shelter was important to red deer during winter, but she considered this to be more so for stags than hinds.

Winter weather may therefore be expected to have a considerable influence upon homeotherms during winter, and Moen (1968b) considered that the interpretation of observed behaviour patterns of deer during winter may be difficult, without a quantitative application of heat transfer parameters. Attempts have been made in this chapter to quantify the effects of specific climatic variables on the energy budget of the red deer. Predicted effects on the energy budget are then related to observed behaviour and distribution patterns.

## 6.2 Method

Five weather stations were established on different parts of the study area before fieldwork began in winter. The sites for the weather stations, see Fig. 6.1, were selected to cover a range of conditions experienced in the area under observation. Each station consisted of a Munro Mk. IV cup-counter anemometer, mounted on a tripod, and a thermohygrograph (Casella & Co. Ltd.) housed within a well-ventilated white-painted metal screen, mounted on a metal stand. The metal screen is illustrated in Fig. 6.2. The instruments were erected to record at one metre above ground level, in order to approximate to the thermal environment of a standing adult red deer. The bi-metallic thermographs were calibrated, initially, in-doors under controlled temperature conditions. In the field calibration was maintained by checking the observed instrument reading against permanently installed mercury thermometers, which had been checked for accuracy, and read to within ± 0.5°C of each other. Any necessary adjustments were carried out each time the charts were

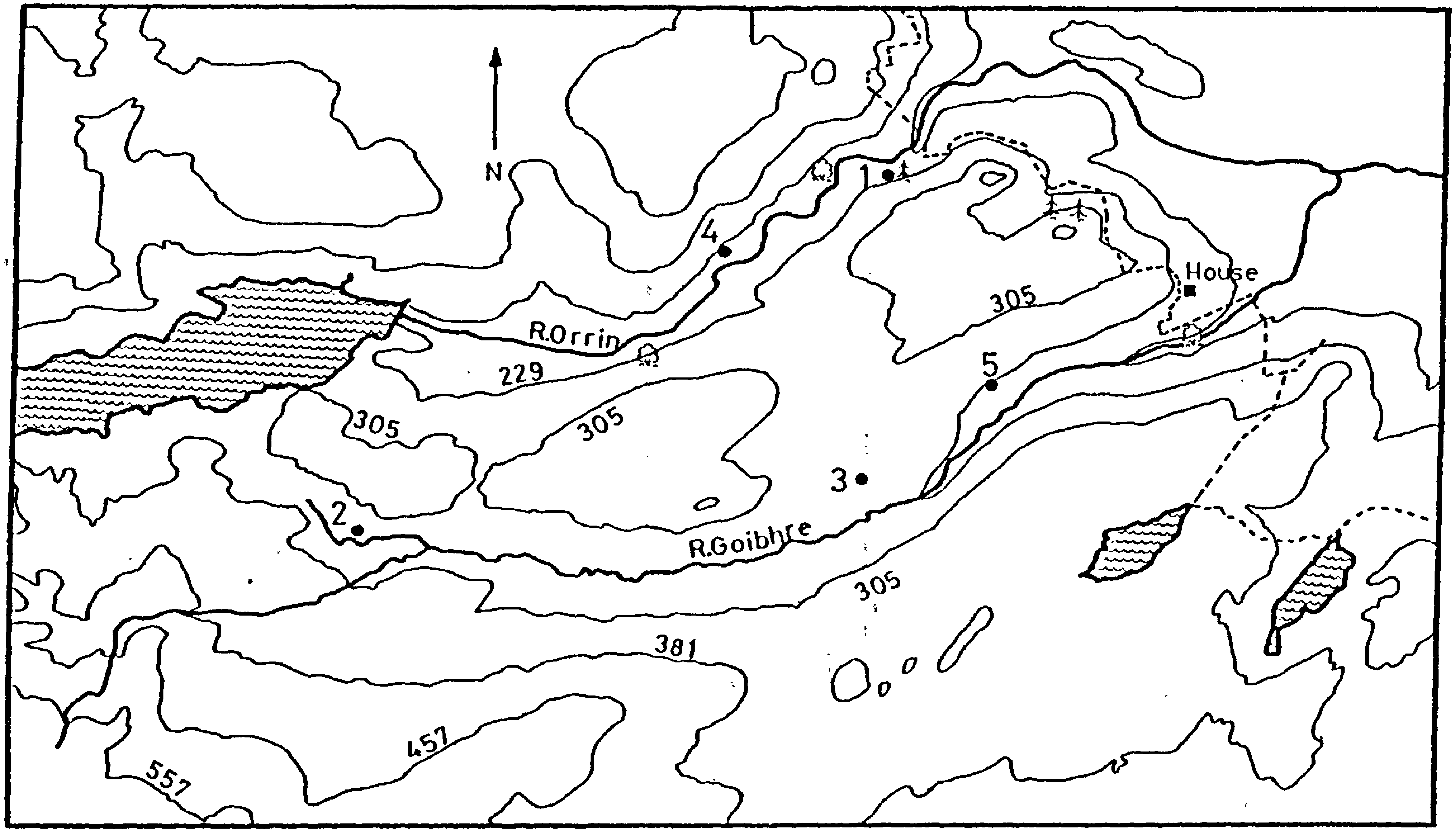
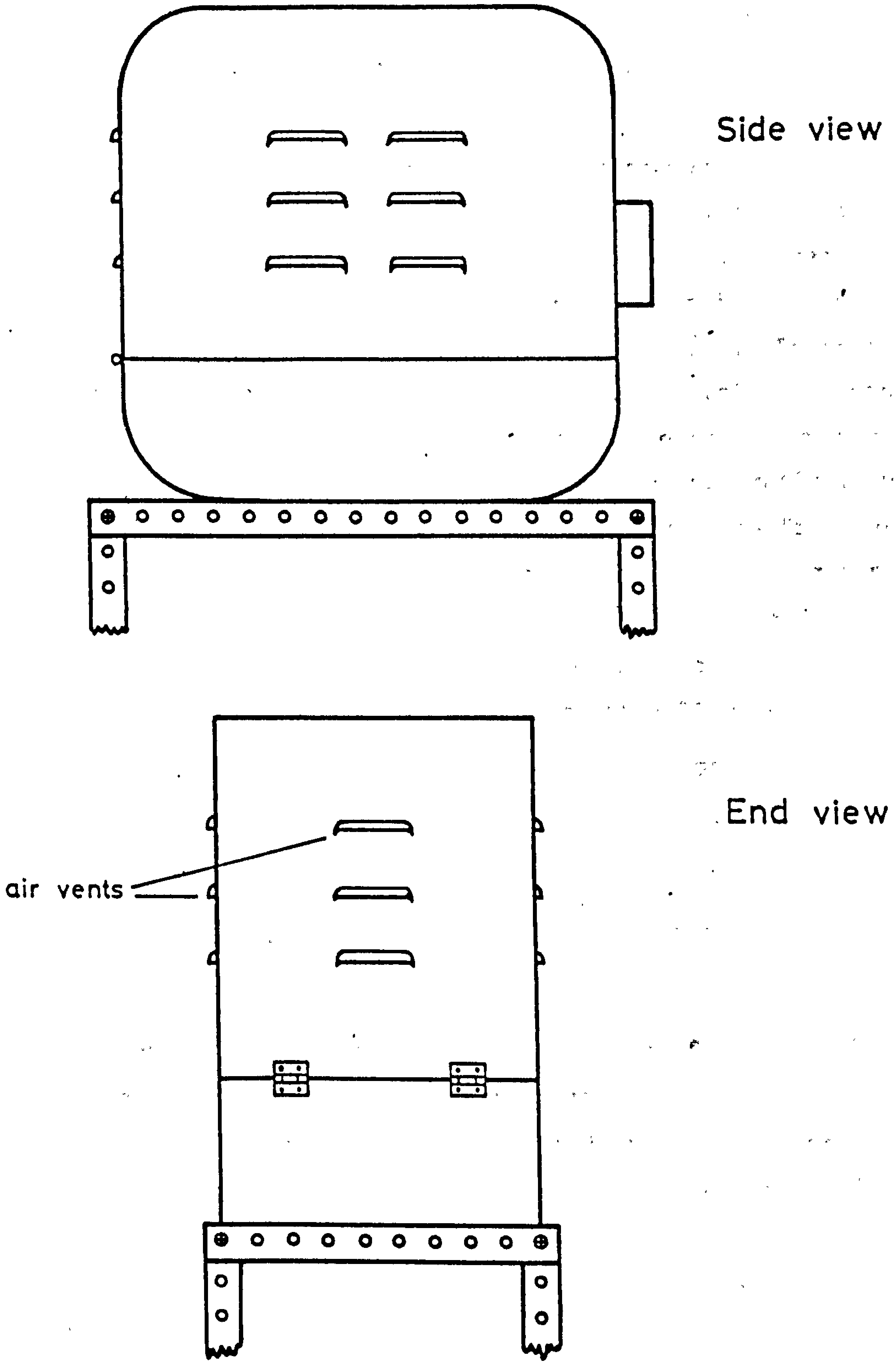


Figure 6·1 The location of the weather stations

Figure 6.2 The metal screen containing the thermograph



changed. The hygrograph elements of the instruments were fitted with new hairs and calibrated in-doors against an Assman psychrometer, under steady conditions in a large room. Calibration in the field was attempted against a whirling psychrometer, but large discrepancies were found between the two instruments, such that the accuracy of the hygrograph was in considerable doubt. As a result records of relative humidity were discontinued.

A continuous recording anemometer although constructed for the purpose of this study, failed to operate successfully when exposed in the field. Estimates of wind speed were made in the field using the Beaufort scale, as detailed in the Meteorological Office Observer's Handbook (H.M.S.O. 1969). Later in this section Beaufort values are converted to values of wind speed in metres per second at one metre above ground surface. The values obtained are of course only an approximation, but may be adequate to demonstrate potential heat loss from deer. Tables of equivalent wind speeds ($ms^{-1}$) at 10m above ground level for given Beaufort values are presented in the Observer's Handbook (see: Table 2.1). Values for 1m above the ground are calculated using a simplified form of Hellman's formula:

$$Vh/V_{10} = 0.233 + 0.656 \log_{10} (h + 4.75)$$

Where Vh = wind speed at height h (metres)

$V_{10}$ = speed at 10m.

### 6.2.1 Description of the weather station sites - see Fig. 6.1

Station 1

Glen Orrin, within a small plantation of European Larch and Scots Pine, which was open to deer. The trees ranged from 10-20 m in height and were spaced from 2-5 m apart. The ground flora consisted of *Calluna* and *Agrostis* species. This site had a north-westerly aspect and was situated at a height of 183 m, on a steep slope (approx. 19°).

Station 2

Western part of Glen Goibhre, on open ground. A level site with only gently sloping ground on all sides. The vegetation was short (10-15 cm) *Trichophoreto-Eriophoretum*, giving way to areas of vegetation dominated by *Calluna*, on the drier slopes. This site was at a height of 282 m.

Station 3 - see Plate 6.1

An exposed hill-top above Glen Goibhre, at a height of 305 m. This site overlay short wind-clipped *Calluna*. It dropped away 40 m into Glen Goibhre to the south, and to the north onto an open area between the two glens.

Station 4

Glen Orrin, situated on the south-east facing slope at a height of 244 m. This site, on a gently sloping terrace, was sheltered from the north and had micro-topographic features within 100 m of the station, which offered some shelter. The site overlay *Trichophoreto*-*Callunetum*, of about 15 cm in height, which gave way to *Calluna* on the drier hummocks nearby.

Station 5 - see Plate 6.2

Glen Goibhre, an open site with a southerly aspect, and ground sloping upwards to the north. The instruments were sited on a small knoll at 229 m, supporting a short-grazed turf of *Agrostis*-*Fescue*, with dead bracken. The site was surrounded with vigorous *Calluna* up to 40 cm in height.

Before commencing fieldwork each day, windrun was recorded over a five minute period at the house, using a cup-counter anemometer, also erected at one metre above ground-level. Wind direction was also recorded using a vane or smoke from the chimney of the house. Any changes in wind direction during the day were noted when observations of the deer were made.

### 6.2.2 Classification of Shelter

When field observations were made, a simple index of shelter, consisting of three categories (Table 6.1), was assigned to locations where deer were seen. The value of the shelter index depended on the available topographic and micro-topographic shelter in relation to the wind direction at the time of observation. On days with no detectable wind, an extremely rare occurrence, topographic features alone were considered.

Plate 6.1 Weather station No. 3

Plate 6.2 Weather station No. 5

Table 6.1 The Classification of Shelter

| Shelter Class Number | Description |
|---|---|
| 1 | Fully exposed eg. ridge tops |
| 2 | Topographic and micro-topographic features offering some shelter |
| 3 | Topographic and micro-topographic features offering good shelter |

Observations of the deer stock, described already (Chap. 2), were used in this section and related to the weather records.

## 6.3 Statistical Methods

### 6.3.1 Discriminant Analysis

This technique results from the wish to distinguish statistically between two or more groups of cases (see: Klecka 1975). In order to distinguish between groups, a collection of discriminating variables are selected, that measure certain characteristics on which the groups are expected to differ. Discriminating variables are weighted and linearly combined in such a fashion that the groups are forced to be as statistically distinct as possible. The 'discriminant functions' take the following form:

$$D_i = d_{i1}Z_1 + d_{i2}Z_2 + \ldots\ldots\ldots\ldots + d_{ip}Z_p$$

where $D_i$ is the score on the discriminant function i, the d's are weighting coefficients and the Z's are the standardised values of the p discriminating variables used in the analysis. The functions are formed in such a way as to maximise the separation of groups.

## 6.4 Results

### 6.4.1 Wind

Records of windrun and direction during fieldwork are presented in Fig. 6.3. Stations 3 and 1 are consistently the most exposed and sheltered sites respectively, which is to be expected from their locations. Stations 2, 4 and 5 experienced similar wind speeds. The variability between these stations can be accounted for in part, by examining the wind roses in Fig. 6.3. The relative exposure of sites 2, 4 and 5 is a function of the surrounding topography and the prevalent wind direction over a particular sampling period.

### 6.4.2 Temperature

Daily minimum and maximum temperatures during fieldwork for each of the weather stations are presented in Fig. 6.4. Breaks in the records are the result of instrument malfunction and my occasional absence from the area.

Fig. 6.3 Wind records during winter 1976/7

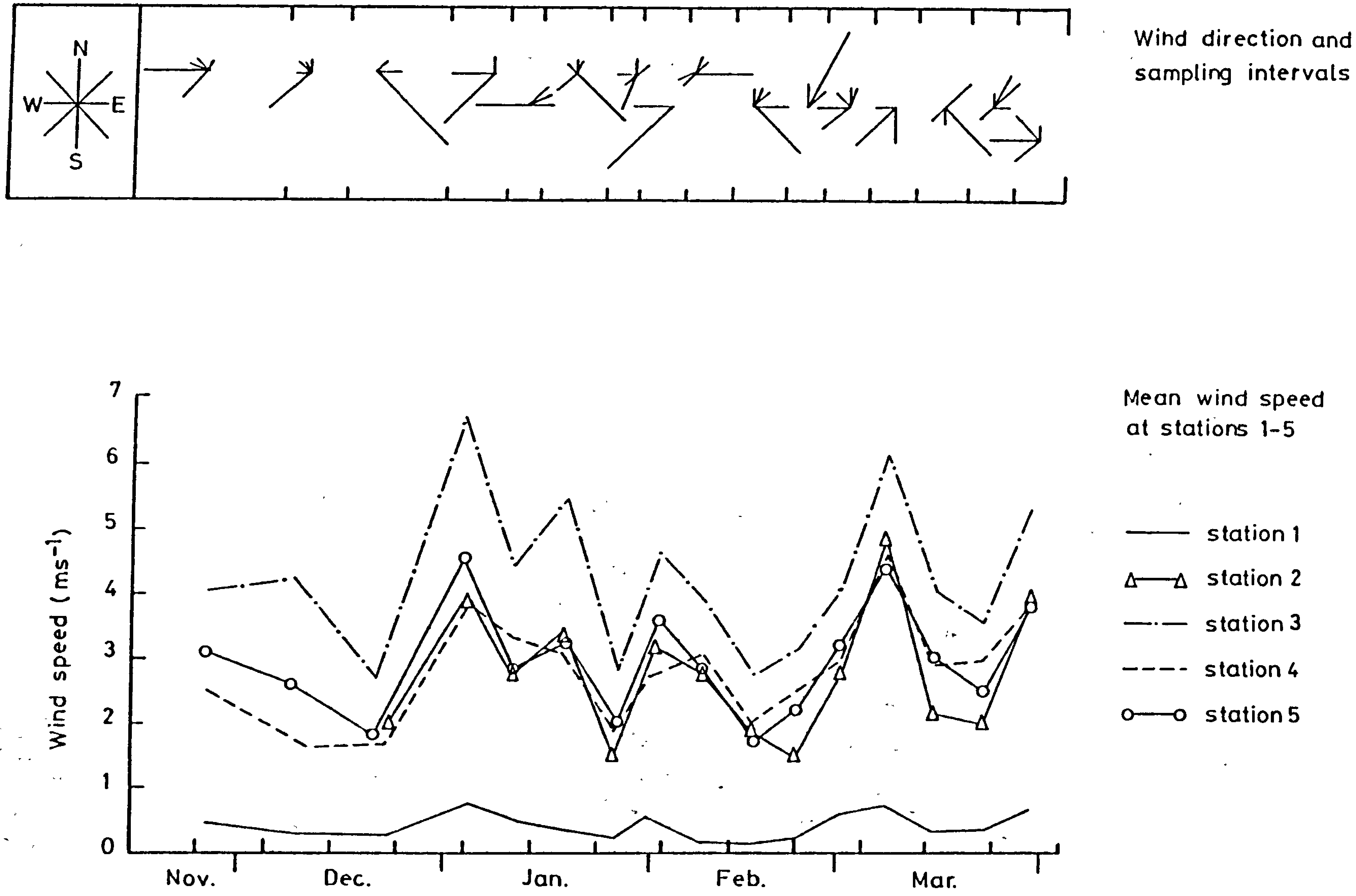
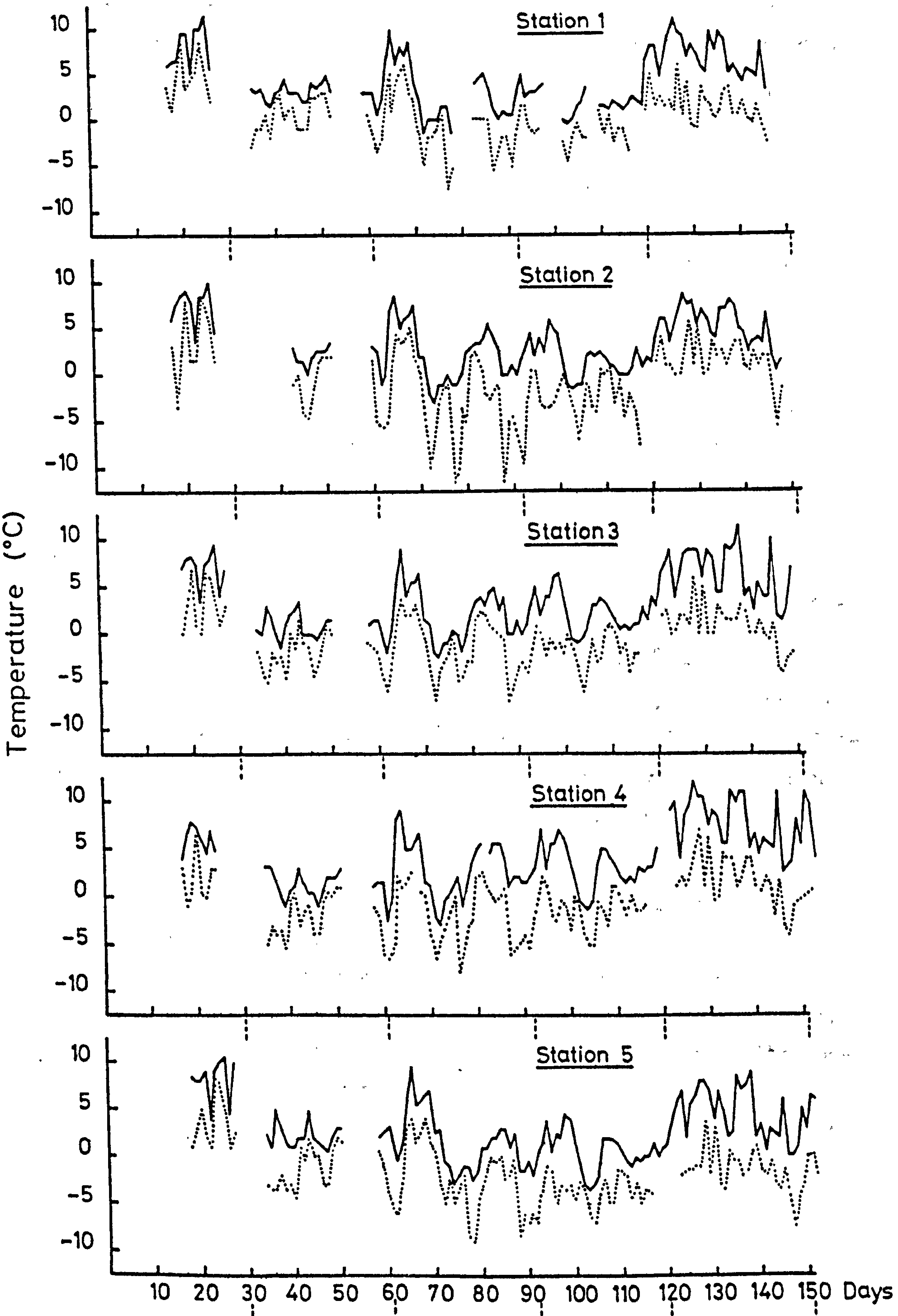


Figure 6.4 Daily minimum and maximum air temperatures recorded during winter 1976/7

(Daily minima are represented by the broken lines)



The variation between sites in daily minima and maxima, reflects certain characteristics of the weather station sites. Daily maxima will be influenced by a number of factors including the amounts of insolation received and the degree of turbulence and mixing of air masses by winds. At night, when daily minima usually occurred, the position of the site on slopes relative to the movement and settling of cold air masses may be important.

The variation in both air temperature and wind speed that occurs throughout the study area can influence the thermal environment and may therefore affect deer distribution.

### 6.4.3 The influence of temperature on the selection of shelter

The range of temperature recorded during winter (266-282$^{o}$K) was divided into three approximately equal classes (in terms of $^{o}$K). The crosstabulation of site shelter with temperature class is presented in Table 6.2 (a). There is no apparent relationship between the selection of potential shelter by deer and air temperature ($\chi^2_{[4]} = 5.96$, $P = 0.2022$). This result may be a consequence of the relatively small differences in temperature that exist between sheltered and more exposed areas. Such differences in air temperature, in isolation, may have a relatively minor influence on the energy exchange of red deer.

### 6.4.4 The influence of wind on the selection of shelter

To test for the avoidance of wind by deer, site data were assigned as lee or windward, according to Fig. 6.5. The selection of lee or windward sites in relation to wind speed is not significant at the 5% level ($\chi^2_{[2]} = 4.67$, $P = 0.0975$), see: Table 6.2 (b).

Intuitively one might expect the relationship to be stronger than this, if the hypothesis that deer select shelter under conditions of energy stress is to be sustained. The classification of sites to a particular aspect, in this case, cannot take into account adjacent landforms. It is quite possible, therefore, for sites classed as windward from their aspect, and a knowledge of wind direction when the observation was made, to be sheltered due to the nature of the surrounding topography.

Table 6.2 Site selection in relation to temperature and wind speed. The numbers in the tables refer to the raw observations of deer groups; those within parenthesis are the percentage of the column total accounted for by the raw observation values.

(a) Air temperature and the selection of potential shelter

| | Shelter Index | | | |
|---|---|---|---|---|
| Temperature($^{o}$K) | EXPOSED | INTERMEDIATE | SHELTERED | Total |
| 266.0-271.0 | 6<br>(12.0%) | 39<br>(16.0%) | 59<br>(20.7%) | 104<br>(18.0%) |
| 271.5-276.5 | 35<br>(70.0%) | 161<br>(66.0%) | 191<br>(67.0%) | 387<br>(66.8%) |
| 277.0-282.0 | 9<br>(18.0%) | 44<br>(18.0%) | 35<br>(12.3%) | 88<br>(15.2%) |
| Total | 50 | 244 | 285 | 579 |

Null Hypothesis : Ho = shelter selected is independent of air temperature

Chi Square = 5.96, 4 degrees of freedom

Significance, P = 0.2022

(b) The use of lee and windward sites in relation to wind speed

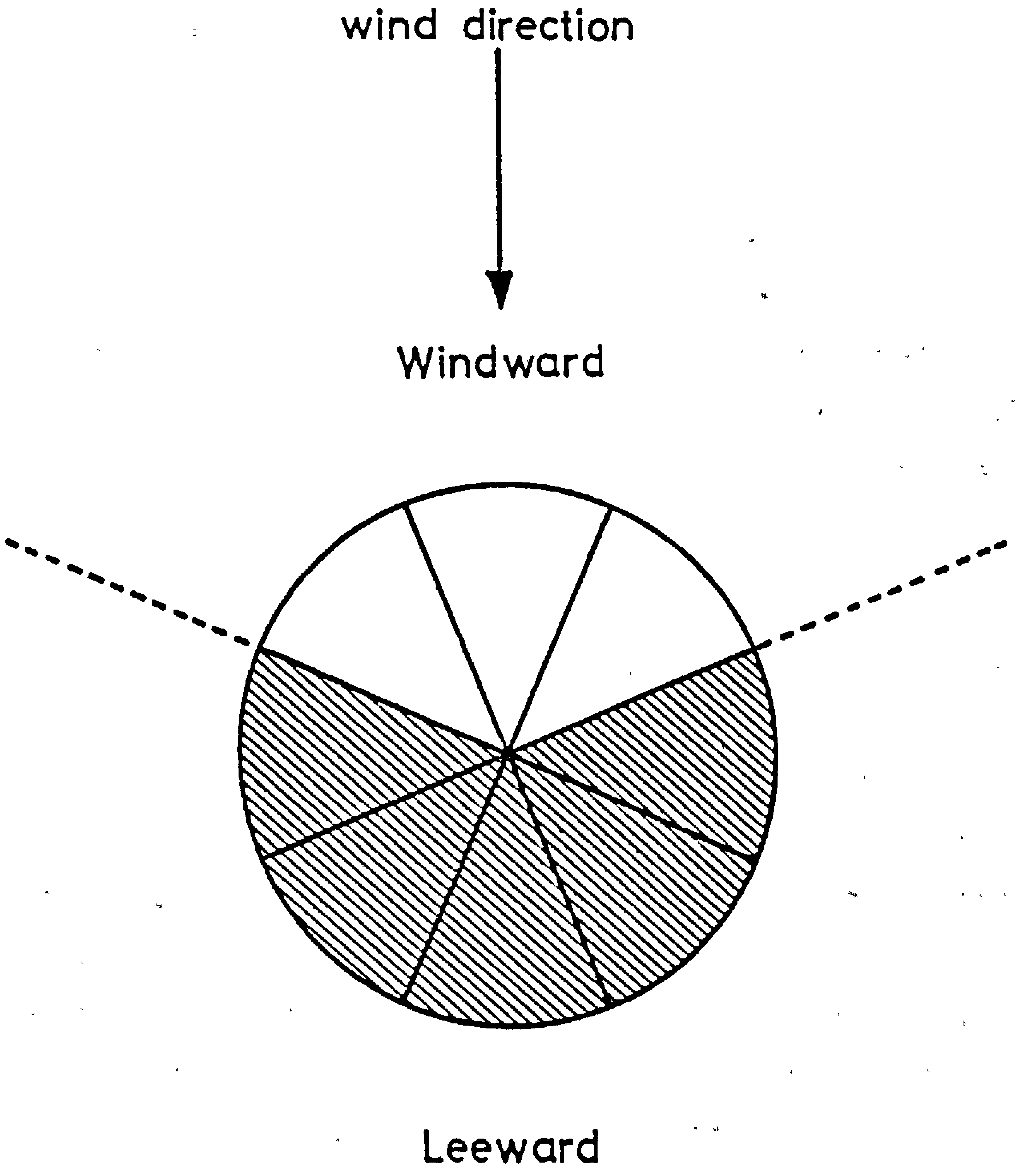
| | Wind speed (Beaufort Scale) | | | |
|---|---|---|---|---|
| Aspect | 1-2 | 3-5 | 6-8 | Total |
| LEE | 87<br>(64.4%) | 260<br>(67.9%) | 33<br>(82.5%) | 380<br>(68.1%) |
| WINDWARD | 48<br>(35.6%) | 123<br>(32.1%) | 7<br>(17.5%) | 178<br>(31.9%) |
| Total | 135 | 383 | 40 | 558 |

Null Hypothesis : Ho = selection of lee and windward sites is independent of wind speed

Chi Square = 4.67, 2 degrees of freedom

Significance, P = 0.0975

Figure 6.5 Site classification with respect to wind direction (8 cardinal compass points)



Despite the complications arising from attempts to assign sites to wind or leeward in areas with complex topography, it is clear that windward sites are avoided by deer during winter. There is a range of available aspects for deer to make use of on the study area (see: Fig. 2.13), but more deer were observed on lee sites than windward during winter ($\chi^2_{[1]} = 8.29$, $P < 0.01$), (see: Table 6.3 (a)).

### 6.4.5 The influence of wind speed on the selection of shelter

Deer sought better shelter as wind speed increased, with a greater proportion of animals in better shelter at the highest wind speeds ($\chi^2_{[4]} = 19.02$, $P = 0.0008$), see Table 6.3 (b). Exposed locations were completely avoided by deer when winds were high (Force 6-8), being occupied to the greatest extent when winds were lowest (Force 1-2).

### 6.4.6 The combination of wind speed and air temperature as an influence on the selection of shelter

The effects of temperature and wind speed on the distribution of red deer have been considered separately in the previous sections. However these two variables do not operate in isolation, in terms of the energy exchange of homeotherms. It is desirable therefore to combine the influences of both temperature and wind speed into a single variable (termed 'cold stress'), and examine its influence on deer distribution.

#### (i) A simple linear combination of temperature and wind speed

A convenient way of combining the influence of these two variables is with the use of discriminant analysis. Temperature and wind speed are considered as the discriminating variables, with which the groups (shelter classes) are expected to differ. Although discriminant analysis can be used for more than two groups of cases, the outcome becomes more difficult to understand, and there is the additional statistical problem of deciding how many discriminant functions to derive (Klecka 1975). Thus, in the present case, where there are three shelter classes (or groups), shelter class one (SC1) and shelter class three (SC3) are considered as the two groups which are to be distinguished between.

Table 6.3 Site selection in relation to wind.

(a) The use of lee and windward sites by deer during winter

(Figures in parenthesis are expected frequencies)

| Lee | WINDWARD | Total |
|---|---|---|
| 380<br>(348.75) | 178<br>(209.25) | 558 |

Null Hypothesis : Ho = no difference in the use of lee and windward sites

Chi Square = 8.29, 1 degree of freedom

Significance, P = $< 0.01$

(b) The influence of wind speed on site utilisation with respect to shelter

Wind speed (Beaufort Scale)

| Shelter | 1-2 | 3-5 | 6-8 | Total |
|---|---|---|---|---|
| EXPOSED | 22<br>(15.6%) | 28<br>(7.1%) | 0<br>(0.0%) | 50<br>(8.6%) |
| INTERMEDIATE | 62<br>(44.0%) | 168<br>(42.5%) | 14<br>(32.6%) | 244<br>(42.1%) |
| SHELTERED | 57<br>(40.4%) | 199<br>(50.4%) | 29<br>(67.4%) | 285<br>(49.2%) |
| Total | 141 | 395 | 43 | 579 |

Null Hypothesis : Ho = Shelter selected is independent of wind speed

Chi Square = 19.02, 4 degrees of freedom

Significance, P = 0.0008

Temperature and wind speed data, collected in the field when observations of deer were made, were tested and found to be approximately normally distributed. However the assumptions underlying the use of this test, that the discriminating variables have a multivariate normal distribution and equal variance-covariance matrices within each group, need not be strongly adhered to, since the technique is very robust (see: Klecka 1975). The data were evaluated using the sub-program DISCRIMINANT of S.P.S.S. (Nie et al. 1975). The scores on the discriminant function in SC1 are then compared with those in SC3. The rational behind this comparison being, that as cold stress increases deer are expected to seek better shelter. Cold stress values should therefore be higher for those observations associated with SC3.

Values of cold stress are significantly higher when deer were observed to be utilising SC3 ($t_{[49]} = 5.99$, $P < 0.001$, one-tailed test). Similarly, further comparisons were made with temperature and wind speed values alone. The observed use of SC3 was not associated with low temperatures alone ($t_{[70]} = -2.25$, N.S., one-tailed test). However the use of SC3 was associated with higher wind speeds ($t_{[333]} = 4.43$, $P<0.001$, one-tailed test).

The results indicate the power of the two variables, in isolation, to account for the observed use of shelter by deer on the study area. Although the combination of wind speed and temperature apparently provides the best relationship with the observed use of shelter, wind speed alone also has a considerable influence.

### (ii) A theoretical model to predict cold stress for red deer

Previously Grace & Easterbee (1979) described a simple model which estimates heat loss (Watts) from a standing adult red deer, when exposed to different combinations of temperature and wind speed, at night (see: Appendix 6.1). Such a model may also be able to account for the observed use of shelter on the basis of heat loss under given weather conditions. For the purpose of the present discussion, the model mentioned above has been modified, to estimate the energy exchange of a deer during day time, and to find the calculated heat loss, to provide values of cold stress. Full details of the amended model can be found in Appendix 6.2

Values of cold stress were obtained from the evaluation of the weather data collected in the field, by the use of the theoretical model. To facilitate a comparison with the results obtained above, a similar procedure was adopted; cold stress was significantly higher when deer were utilising SC3 ($t_{[64]} = 4.80$, $P < 0.001$, one-tailed test). The results of the analyses are summarised in Table 6.4.

The theoretical model despite its considerable sophistication does not produce a 'better' result than the simple linear combination of wind speed and temperature. However, discriminant analysis (linear combination of wind speed and temperature) automatically finds the 'best' values for the parameters, whereas in the theoretical model estimates are provided for the parameters (except surface temperature). Output from the theoretical model is, therefore, being subjected to more rigorous testing. There is a distinct advantage in the use of the model rather than the linear combination of variables, in that the latter method provides an index of stress, the absolute values of which have no physiological meaning. The cold stress index generated by the theoretical model is based on a fundamental consideration of the mechanisms of heat loss from a deer. The theoretical model can, therefore, be used to provide data with which inference can be made, based on physiological grounds. Such an ability is implicit in the approach adopted to the consideration of deer distribution in this section.

### 6.4.7 Heat loss from a deer, predicted by the theoretical model

The theoretical model may be used to demonstrate the influence of temperature and wind speed on the potential heat loss from a deer. Calculated heat loss (Watts) for a 60 kg adult red deer is illustrated for three temperatures, over a

Table 6.4 Summary of results of the utilisation of shelter

| Variable | Variable | Test | Significance |
|---|---|---|---|
| Shelter | Temperature (3 classes) | Chi-square | N.S. |
| " | Wind speed (3 classes) | " | $P = 0.008$ |
| Shelter (SC1 cf. SC3) | Temperature | t-test (one-tailed) | N.S. |
| " | Wind speed | " | $P < 0.001$ |
| " | Cold stress (linear combination) | " | $P < 0.001$ |
| " | Cold stress (theoretical model) | " | $P < 0.001$ |

range of wind speeds (1-14 m $s^{-1}$), and at a fixed level of radiation, in Fig. 6.6. Considerable increases in heat loss result from a decrease in ambient temperatures or an increase in wind speed. As expected, greatest potential heat loss occurs when the lowest temperature is combined with the highest wind speed.

The total daily energy requirement of an animal may be expressed as follows:

$$Q_{me} = Q_{mb} + Q_{ma} + Q_{mp} + Q_{mh}$$

where $Q_{me}$ is the total daily energy requirement, $Q_{mb}$ is the basal metabolic energy expenditure, $Q_{ma}$ is the activity expenditure, $Q_{mp}$ is the production expenditure and $Q_{mh}$ is the additional energy cost to maintain homeothermy.

The additional cost to maintain homeothermy is only part of the total energy requirement when the sum of the heat production resulting from the first three items ($Q_{mb} + Q_{ma} + Q_{mp}$) is less than the total heat loss of the animal (Moen 1973). Productive processes can be ignored for adult red deer during winter in upland Scotland, since even the demands of pregnancy are low for the first two thirds of the term (see: Anderson 1978). Details of two contrasting activity regimes ($Q_{mb} + Q_{ma}$), based on information for a 60 kg white-tailed deer (Moen 1976) are presented in Table 6.5. The 24-hour heat production levels for the two activity regimes are illustrated by hatched lines in Fig. 6.6. Total heat loss under simulated winter weather exceeds heat production from metabolism and activity under relatively modest conditions of cold stress. For much of the winter, therefore, red deer, on the basis of the output of the model, would need to devote considerable amounts of energy to maintain body temperature.

Geist (1974) has quoted from studies of domestic herbivores, which have shown that on a diet of good to medium hay, the animals can ingest only about 14,500 KJ of metabolisable energy per day. Even if red deer could obtain the estimated maximum daily energy intake (equivalent to 168 W), which is

Figure 6.6 The influence of wind speed and temperature on the estimated heat loss of a 60 kg adult red deer, during daytime (early January, 4/8 cloud)

Levels of energy expenditure indicated are based on calculations by Moen (1976)

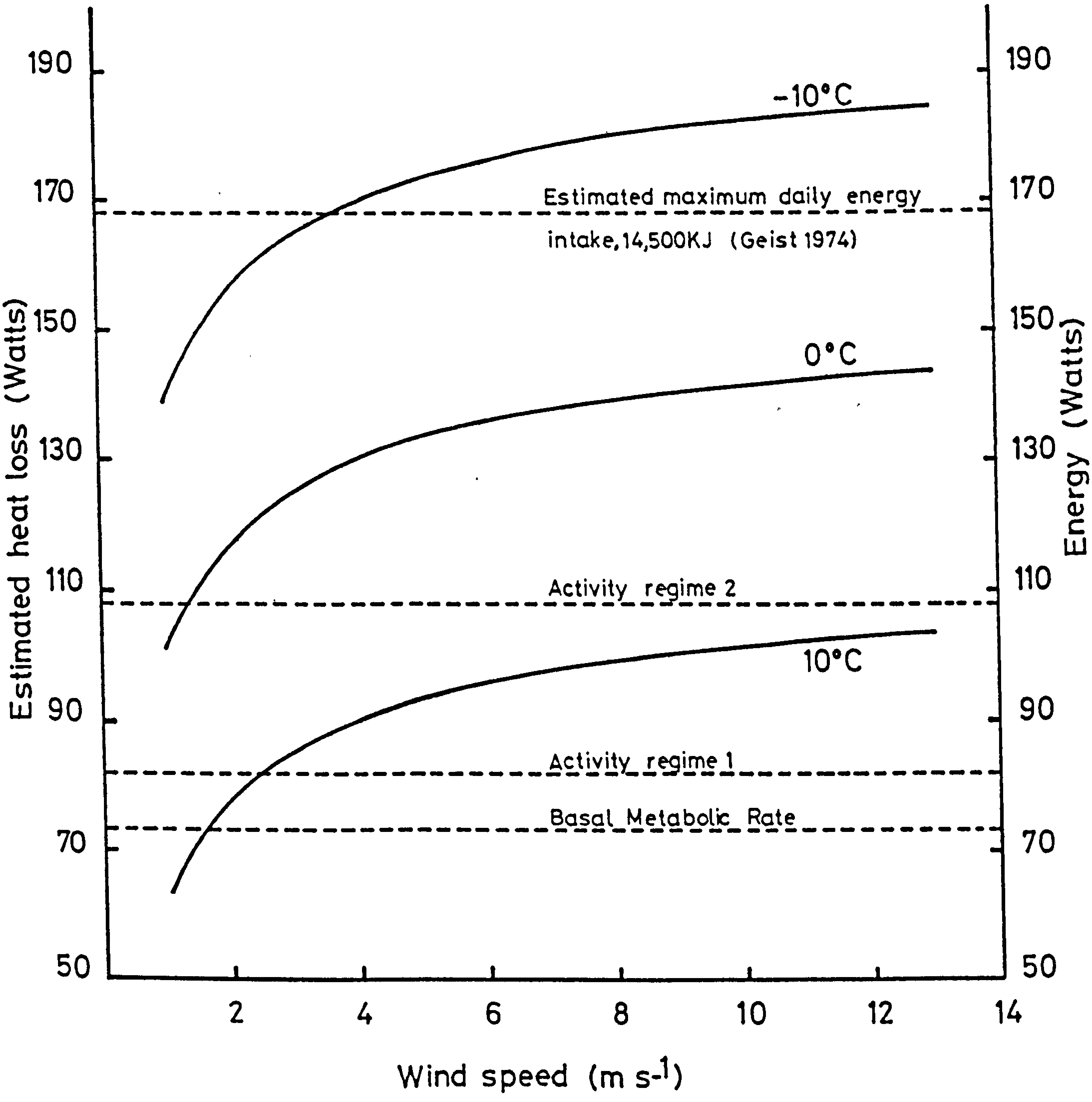


Table 6.5 Details of the activity regimes used in Figure 6.6 (Based on values calculated by Moen (1976) for a 60 kg white-tailed deer)

Regime 1

| Activity | % of time | 24-hour energy cost (Watts) |
|---|---|---|
| Bedded | 75 | 55 |
| Standing | 10 | 8 |
| Running | 0 | 0 |
| Foraging | 10 | 12 |
| Walking | 5 | 7 |
| Total | | 82 |

Regime 2

| Activity | % of time | 24-hour energy cost (Watts) |
|---|---|---|
| Bedded | 25 | 18 |
| Standing | 30 | 24 |
| Running | 3 | 13 |
| Foraging | 30 | 36 |
| Walking | 12 | 17 |
| Total | | 108 |

unlikely in winter in upland Scotland, weather conditions can quite easily result in the heat loss of the animal exceeding potential energy input. It should be noted that Fig. 6.6 refers to conditions during daylight, which are generally more favourable, in terms of energy balance, than at night, when radiative losses may increase considerably.

### 6.4.8 Comparisons of stags and hinds

#### (i) Activity in relation to cold stress

The data for cold stress produced by the theoretical model were used in the comparison of stag and hind groups with respect to activity. There was no difference in the proportions of hind groups bedded or grazing under different conditions of cold stress ($\chi^2_{[2]} = 0.56$, $P = 0.7573$); nor was there any difference for stag groups ($\chi^2_{[2]} = 2.23$, $P = 0.3287$), see Table 6.6 Comparison of equivalent column percentages in the two tables reveals, however, that a greater proportion of stags is apparently bedded under high cold stress conditions, compared with hinds. A comparison was made between the proportions of hind and stag groups grazing or bedded under conditions of high cold stress. There is a considerable difference between the sexes in the activity observed under these circumstances ($\chi^2_{[1]} = 8.37$, $P < 0.01$) see Table 6.7, with a greater proportion of hind groups observed grazing.

#### (ii) Activity in relation to shelter

Activity of hind and stag groups with respect to the selection of the three classes of shelter was examined. The proportions of hind and stag groups grazing on sites with different potential shelter are similar ($\chi^2_{[2]} = 3.98$, $P \doteq 0.1367$), see Table 6.8(a). There are few records of deer on exposed sites during winter as a whole. Proportions of hind and stag groups observed bedding under different conditions of shelter were also similar ($\chi^2_{[2]} = 1.78$, $P = 0.4105$), Table 6.8(b). Most deer of either sex were observed to be bedded in the most sheltered locations ( 60% of observations of both sexes).

Table 6.6 The activity of red deer in relation to cold stress

(a) Hinds

| Cold Stress | Grazing | Bedded | Total |
|---|---|---|---|
| LOW | 58<br>(17.6%) | 2<br>(11.1%) | 60<br>(17.3%) |
| MODERATE | 145<br>(44.1%) | 9<br>(50.0%) | 154<br>(44.4%) |
| HIGH | 126<br>(38.3%) | 7<br>(38.9%) | 133<br>(38.3%) |
| Total | 329 | 18 | 347 |

Null Hypothesis : Ho = proportion of animals grazing or bedded is independent of cold stress

Chi Square = 0.56, 2 degrees of freedom

Significance, P = 0.7573

(b) Stags

| Cold Stress | Grazing | Bedded | Total |
|---|---|---|---|
| LOW | 17<br>(10.0%) | 2<br>(7.7%) | 19<br>(9.7%) |
| MODERATE | 75<br>(44.1%) | 8<br>(30.8%) | 83<br>(42.3%) |
| HIGH | 78<br>(45.9%) | 16<br>(61.5%) | 94<br>(48.0%) |
| Total | 170 | 26 | 196 |

Null Hypothesis : Ho = proportion of animals grazing or bedded is independent of cold stress

Chi Square = 2.23, 2 degrees of freedom

Significance, P = 0.3237

Table 6.7 The comparison of the activity of stag and hind groups under conditions of high cold stress.

(Expected frequencies in parenthesis)

|  | Activity |  |  |
|---|---|---|---|
| Sex | Grazing | Bedded | Total |
| Male groups | 78<br>(84.48) | 16<br>(9.52) | 94 |
| Female groups | 126<br>(119.52) | 7<br>(13.48) | 133 |
| Total | 204 | 23 | 227 |

Null Hypothesis: Ho = no difference in proportions of male and female groups grazing or bedded

Chi Square = 8.37, 1 degree of freedom

Significance, P = < 0.01

Table 6.8 Activity of deer in relation to shelter.

(a) Grazing

| Shelter | HINDS | STAGS | Total |
|---|---|---|---|
| EXPOSED | 22<br>(6.7%) | 16<br>(9.4%) | 38<br>(7.6%) |
| INTERMEDIATE | 151<br>(45.9%) | 63<br>(37.1%) | 214<br>(42.9%) |
| SHELTERED | 156<br>(47.4%) | 91<br>(53.5%) | 247<br>(49.5%) |
| Total | 329 | 170 | 499 |

Null Hypothesis : Ho = no difference between proportion of hind and stag groups grazing in relation to site shelter

Chi Square = 3.98, 2 degrees of freedom

Significance, P = 0.1367

(b) Bedded

| Shelter | HINDS | STAGS | Total |
|---|---|---|---|
| EXPOSED | 1<br>(5.6%) | 4<br>(15.4%) | 5<br>(11.4%) |
| INTERMEDIATE | 6<br>(33.3%) | 5<br>(19.2%) | 11<br>(25.0%) |
| SHELTERED | 11<br>(61.1%) | 17<br>(65.4%) | 28<br>(63.6%) |
| Total | 18 | 26 | 44 |

Null Hypothesis : Ho = no difference between proportion of hind and stag groups bedded in relation to site shelter

Chi Square = 1.78, 2 degrees of freedom

Significance, P = 0.4105

These results may reflect the amount of sites which are exposed or, alternatively, that deer are avoiding such areas. The proportion of the study area which could be classed as exposed will, in many cases, vary with respect to the wind direction; some sites such as the higher ridge tops will, however, be consistently exposed. It is not possible to state what proportion of the area is exposed, but since a range of aspects are represented on the study area, it is probable that the availability of more exposed sites is not a limiting factor in this case, and that it is the avoidance of such sites by deer which is contributing to the low levels of use recorded.

## 6.5 Discussion

### 6.5.1 Temperature and wind speed

The use of a theoretical model has provided estimates of heat loss from a deer under specified weather conditions, and indicates the considerable energy loss that deer in the Scottish uplands may experience during winter. The energy loss resulting from the maintenance of homeothermy, under conditions of poor nutrition, leads to acute weight loss in deer over the winter (see: Mitchell, McCowan & Nicholson 1976 and Anderson 1978). Use of shelter is essential therefore to spare the limited supplies of energy derived from food and reserves stored within the body and thus prevent excessive catabolism, which may lead to impaired performance and, ultimately, to the death of the animal. The sheltering behaviour of deer, which evidently plays a major role in determining winter distribution in upland areas of Scotland, can be seen in perspective when the energy exchange of the animal is considered in relation to prevailing weather.

Temperature and wind speed have previously both been shown to significantly affect the energy loss of homeotherms, and both variables may, therefore, influence deer distribution in winter. The results reveal that in relation to the recorded range for each variable, wind speed has a greater influence on shelter-seeking than temperature, when either variable is considered in isolation; this is in accordance with suggestions from other studies (eg. Staines 1976b). There are reasonable grounds for this suggestion, since the reduction in wind speed from the use of shelter may be considerable (Grace & Easterbee 1979), whereas the selection of sites with a more favourable temperature regime may be more difficult to achieve. Staines (1976b) recorded little difference in temperature between sites occupied by red deer, and unoccupied, exposed sites nearby. There were occasions however, when deer appeared to react to low temperatures. In late afternoons, in cold still weather, when temperature inversions occurred, animals were observed to move uphill away from low-lying areas, where cold air would tend to accumulate. Differences between the high level weather station (no. 3), compared with those in the two glens, were up to 6-7°C on such occasions.

Although either temperature or wind speed may individually influence heat loss from deer, it is the combination of these two variables which is of greatest significance. This combination, referred to as 'cold stress', had most effect on deer distribution during winter, and better shelter was sought as conditions of cold stress increased. Staines (1976b) has reported a similar reaction by red deer in the Eastern Highlands.

### 6.5.2 Precipitation

A further influence on the energy budget of the animal may be that of precipitation, since the wetting of fur or hair coats can markedly increase heat loss (see: Lentz & Hart 1960). But in common with reports by Staines (1970), deer were not observed to seek shelter from rain. However, effective shelter from rain is not generally available to Scottish red deer, and the avoidance of strong winds is probably of most importance, since heat loss from wetted pelts will rise with increasing wind speed. Furthermore, rain is more likely to penetrate the animal's coat, thereby promoting heat loss, when driven by strong winds.

When there was little wind, or when in good shelter, deer did not appear to react to falling snow. Deer remained bedded while snow accumulated on their bodies. Snow-lie did modify grazing behaviour, and has been documented elsewhere (Chap. 4). Heavy snow falls did cause major movements of deer, and previously established social factors appeared to break down, with large groups of deer of both sexes gathering in the lower, eastern parts of the glens (see also: Darling 1937).

Dispersal and the re-establishment of hind and stag range occurred with the onset of improved weather.

### 6.5.3 Energy exchange and the activity of red deer

Taking into account potential losses in relation to available energy, the red deer may optimise foraging time so that maximum gain of energy is achieved, while losses due to exposure and activity are kept to a minimum. Even discounting losses due to cold weather, the energy cost of foraging is approximately 1.7 times more than that of bedding (Table 6.5). It has been shown (Fig. 6.6) that even on a theoretically optimum energy input (derived from hay), energy loss under moderate conditions of cold stress can exceed input. Under such circumstances it may be most expedient for deer to remain bedded, rather than forage and expose a greater proportion of body area to the cold environment (see: Mautz 1978). Examples of behaviour supporting this view have been documented for white-tailed deer by Severinghaus & Cheatum (1956) and Verme (1965), and for red deer stags by Cooper (1971). Stags were also observed to limit grazing activity during conditions when cold stress was high, in the present study. This tendency did not however appear to apply to hinds to the same extent. Jackes (1974) has similarly reported that stags tended to remain bedded for most of the day when strong winds were blowing, but hinds seemed to be less affected by these conditions. It has been shown in Chap. 2 that hinds had a greater proportion of better quality grazings available to them, and they were also more frequently observed to be grazing during daylight hours than stags. When weather conditions are unfavourable, in terms of energy loss, it will be advantageous for deer to expend energy in foraging, only if returns from this activity are greater than the costs. If hinds are able to exploit areas of better quality forage, then they may be able to continue to graze longer, or after conditions have made the situation unprofitable (ie. energy loss exceeds gains) for stags. This may explain why stags appear more prone to limit grazing activity than hinds, during conditions of high cold stress. It would be interesting to be able to compare relative amounts of grazing activity during night-time, when cold stress may be greatest.

Despite the differences between the sexes in the relative amount of time that grazing was observed, the overall use of shelter by hinds and stags was similar. Energy conservation is important to both sexes, and although hinds may be on a somewhat higher plane of nutrition than stags (Chap. 2), shelter is necessary so that any benefits accruing are not entirely expended in increased costs to maintain homeothermy. Such considerations may be of particular significance to hinds with a calf 'at foot'. Deer calves lose more heat per unit area than adult animals simply as a result of their small physical size, and hence greater surface area to volume ratio. Problems of maintaining homeothermy are, on theoretical grounds, more acute for calves with their small body size and low energy reserves, amounting to only some 1-4% of liveweight, in comparison with 16-19% for lambs and 10-16% for young cattle (Simpson et al. 1978). Simpson et al (1978) report that red deer are probably exposed to cold stress almost continuously throughout their first winter of life in the Scottish Highlands. Considering the investment that the female deer devotes to the production of young, it appears most unlikely that hinds with calves would not exploit available shelter in an optimal manner. Jackes (1974), however, was of the opinion that stags required better shelter than hinds during winter. Such a conclusion may have resulted from observing stags bedded when hinds were grazing which, it has been suggested above, may be related to the quality and quantity of available grazings and considerations of energy exchange, rather than a specific requirement for shelter. When bedded, hinds used areas of better shelter as much as stags did, while both sexes, although tolerating less shelter when grazing, avoided areas where heat loss would be high.

The ingress of red deer into forest plantations has been mentioned previously. Coniferous trees can provide effective shelter both from convective and radiative heat loss (Grace & Easterbee 1979) and this may be one of the reasons which makes these areas attractive to deer. As well as potential shelter, forests will also contain food sources. Despite their external appearance, man-made forests are rarely uniform and some open areas invariably remain, which together with fire-breaks, rides and roadsides, will support vegetation that deer can exploit. Deer that enter afforested areas will not be exposed to the same degree of cold stress as experienced by animals on the open hill. It may be expected that if suggestions presented in this chapter are valid, then deer utilising forest plantations may show signs of improved productivity over those on nearby open hills, the nutritive value of respective grazings being equal. Food quality within forest areas may be of higher quality which will also contribute to improvements in productivity. The results from investigations currently in progress, which are examining the productivity of red deer in forests, should be of considerable interest in relation to the present work.

## 6.6 Summary

(1) The importance of shelter to red deer during winter was established from considerations of the energy budget in relation to weather and nutrition.

(2) Field observations when related to weather conditions, indicated that wind speed apparently influenced sheltering by deer. Temperature alone did not appear to influence sheltering by deer under most circumstances.

(3) Temperature and wind speed were combined to produce a single variable, cold stress. Cold stress had the strongest influence on sheltering by deer of the variables examined. A greater degree of shelter was selected as conditions of cold stress increased.

(4) A theoretical model was developed to estimate the heat loss from deer under specified weather conditions. Output from this model also reveals the selection of superior shelter when cold stress was high. The importance of shelter to the red deer in relation to winter weather and potential food supply was demonstrated.

(5) Observed differences in the behaviour of hinds and stags during winter are considered in relation to energy exchange and the characteristics of the respective home ranges. It was concluded that the greater observed activity of hinds may be the result of the availability of more nutritious food plants on hind home range.

(6) The activity of both sexes in relation to shelter was similar. Exposed areas were avoided during grazing; when bedding, deer selected more sheltered areas.

# Chapter 7 Discussion and Conclusions

## 7.1 Discussion

During winter, hinds and stags, although tending to occupy separate areas for much of the time, behaved in a similar fashion, and there were no major differences in behaviour. Shelter was used extensively by both sexes; areas offering better potential shelter were selected as weather conditions promoting heat loss increased. On the study area deer were wary of man, and it is possible that site selection is a compromise between available shelter and the ability to detect danger. However the effects of disturbance were not investigated.

The occupation of different areas of range by hinds and stags resulted in greater use being made of areas of better quality grassland by hinds. The presence of a larger area of superior grazings on hind ranges, or at least being available to hinds, may result in females receiving a superior diet. I have suggested that this could account for the observation that hinds spent more time grazing over the winter than stags.

The use of faecal analysis revealed the importance of Calluna in the diet of the red deer on the study area; Calluna occurred with the greatest frequency of any single species in the diets. Better quality grasses accounted for up to 40% of the diet of stags and hinds, and the significance of sites supporting these species, in the nutrition of ruminants in the uplands, must surely outweigh their total area. Unfortunately it did not prove possible to state whether hinds were selecting a superior diet to stags on the basis of the analysis. Recent work (Staines & Crisp 1978) suggests that the chemical analysis of rumen contents may reveal differences in quality between stag and hind diets, which on the basis of species composition are apparently similar.

Chemical analysis of Calluna revealed that deer were not selecting for any particular attribute for which tests were carried out. However, for much of the winter only the current year's growth was selected, which includes the most nutritious part of the plant. Selection became less intensive when snow-lie and ice made other food plants less available. Much of the herbage above four years of age is of similar food value, and the main benefit of muirburn may be the establishment of areas of building-mature Calluna, offering maximum productivity of current year's growth. Hewson (1976) found that during winter building and mature stands were most heavily used, and there was a positive correlation between the height of heather and dung deposition. Stands of this type may minimise grazing times because of maximum productivity, and also provide good bedding sites, offering both insulation from wet and cold ground, and shelter from the wind. The intensive use of certain areas of pioneer Calluna was thought to be related to the presence of invading graminids subsequent to burning, and in other cases to the proximity to areas of good grassland.

The use of pellet-group counts to provide an index of deer use on a range of sites on the study area provides additional support to the findings in other chapters. Although it proved difficult to separate the influences of food quality and shelter as independent variables influencing site utilisation, overall, shelter from the prevailing wind was considered to be the major influence on deer distribution during winter.

Having established that shelter was influencing deer distribution in winter, the effects of weather were then examined. While wind speed in isolation had a strong influence on sheltering by deer, temperature alone did not appear to be a significant factor. Heat loss however, will vary with both temperature and wind speed, and it was shown that the combination of these two variables was of greatest significance in promoting shelter seeking by red deer. The value of sheltering to deer, in terms of the energy budget, was put into perspective with the development of a theoretical model, which provides an estimate of heat loss (Watts) from an adult red deer under varying weather conditions. Output from this model suggests that the avoidance of energy loss, and hence shelter seeking, is of critical importance to red deer in the uplands of Scotland during winter. Although deer may be optimising their diets in relation to the available vegetation on the home range, intake of food is not sufficient to meet the increased energy losses caused by winter weather.

The fat cycle in deer (Mautz 1978) is part of the physiological adaptation for survival during unfavourable periods of the year, when food shortages are experienced. Fat reserves available to deer during winter are obviously influenced by the quality and quantity of forage during the previous summer and autumn. It has been argued that this period of the year, rather than winter, is most critical, since the ability of deer to gain sufficient energy in excess of maintenance requirements, in order to lay down fat reserves, depends on summer weather, both in terms of plant productivity and the ability of deer to freely range and adequately exploit optimum food resources. While the ability to lay down fat reserves is important, and will exert a major influence on condition and survival during winter, this does not diminish the need for deer, under normal circumstances, to conserve energy. Potential energy loss as a result of cold weather may completely deplete the energy reserves of the animal. In reality it is best not to consider either winter or summer in isolation; both seasons are important to deer in northern latitudes.

A point of considerable interest that has not been discussed so far, is that of the segregation of hinds and stags in relation to the availability and utilisation of vegetation. Why, it may be asked, don't stags which are bigger and stronger than hinds, with the additional possible advantage of being antlered during winter, displace hinds from areas of better grazing? Hinds were present on the study area throughout the year, although their numbers increased during winter. Stags arrived on the study area in numbers in early winter, and they occupied peripheral areas to what was considered to be hind home range, and shared certain areas with hinds. There was no sign of any displacement of hinds, and when grazing on "communal" areas, groups of stags and hinds avoided each other, and a high degree of segregation of the sexes was observed. Both sexes used shelter to a similar extent, and I do not believe either hinds or stags significantly differ in their sheltering requirements, for reasons previously advanced. Apart from occasional innate dispersion, most deer do not move far from their place of birth (see: Mitchell, Staines & Welch 1977). Stags may maximise their reproductive fitness by the avoidance of competition with hinds with which they have mated, and are either pregnant or have a calf at foot. A proportion of hinds may in any case be genetically related to stags wintering on adjacent range. The prevention of competition by stags may result from the complete avoidance of certain areas of better grazing, and differential selection on areas of shared range; this may impart an energetic advantage to those hinds which are pregnant, have a calf at foot, or may be potential mothers in the future.

A similar argument has previously been advanced to account for the segregation of the sexes in bighorn sheep by Geist & Petocz (1977), and may also serve to explain the use of female range by young stags. Geist & Petocz argue that young rams which associate with maternal female groups in winter are unlikely to mate with them, and, at that age, have only a slight chance of impairing the reproductive potential of females that will be the eventual mothers of their offspring. They suggest, therefore, that there is no particular reason for young rams to segregate from females. This hypothesis may account for the observed behaviour of the different sex and age classes in red deer, as it does in bighorn sheep.

## 7.2 Conclusions

The distribution of red deer during winter was principally governed by the pattern of micro-climate in relation to food supply.

During winter hinds and stags tended to occupy separate areas of range, with some ground used communally. Minor differences in behaviour between the sexes may be related to the relative quality of available vegetation on male and female home ranges.

Although vegetation had a strong influence on deer use of the study area, and areas dominated by Calluna and better quality grassland were of obvious importance, the most significant factor influencing distribution in winter was the availability of shelter.

The availability of shelter was important to both hinds and stags. Areas offering potentially better shelter were selected as conditions promoting heat loss increased.

## 7.3 Suggestions for further research

A greater insight into the interaction of the red deer with its environment could be achieved with the use of more sophisticated equipment than was available in the present study. There have been major advances in the micro-electronics industry in the past few years, and comprehensive monitoring of the weather can be achieved with relatively compact and hence portable equipment, which is now highly reliable and requires less frequent servicing. Data-logging facilities are available which enable large amounts of information to be stored in the field on magnetic-tape cassettes or solid-state memory. The transference of large bodies of data to a computer is therefore greatly simplified.

A radio-telemetric study of red deer would enable the monitoring of distribution, activity and metabolic rate of those animals carrying transmitters. Valuable information could be obtained on the behaviour and physiological status of deer under a variety of environmental conditions during day and night, complementing observational studies.

Equipment costs in the proposals above are likely to be high, and it is unlikely that work of a more esoteric nature such as this, would be financed under present economic conditions. Further progress may be made without incurring great expense by the development of theoretical models to estimate heat loss, since at present there are a number of assumptions which have to be made if such an exercise is to be attempted. There are two areas which may supply information useful for the development of a more realistic model of energy exchange in the red deer: i) the development and use of deer simulators, subjected to a range of conditions experienced in the field, would yield further information on energy exchange; ii) the use of semi-domesticated red deer on farms, for monitoring energy exchange may prove of value, and further necessary information on coat and tissue resistances could be obtained.

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# Appendix 4. Laboratory Procedures

## A 4.1 The Determination of Ethanol Soluble Carbohydrates

### Reagents

i) Dissolve 0.250 g D-glucose (Analar), dried to a constant weight at 80°C (Yemm & Willis 1954), in distilled water; dilute to 1 litre in a volumetric flask. Autoclaved distilled water is used in the dilution, as an added precaution against the proliferation of micro-organisms within the stock solution. The stock solution is refrigerated when not in use.

Standard Solutions are prepared daily. A range of Standards is prepared such that on dilution 2 ml of each constitute part of a range from 0 to 0.20 mg glucose.

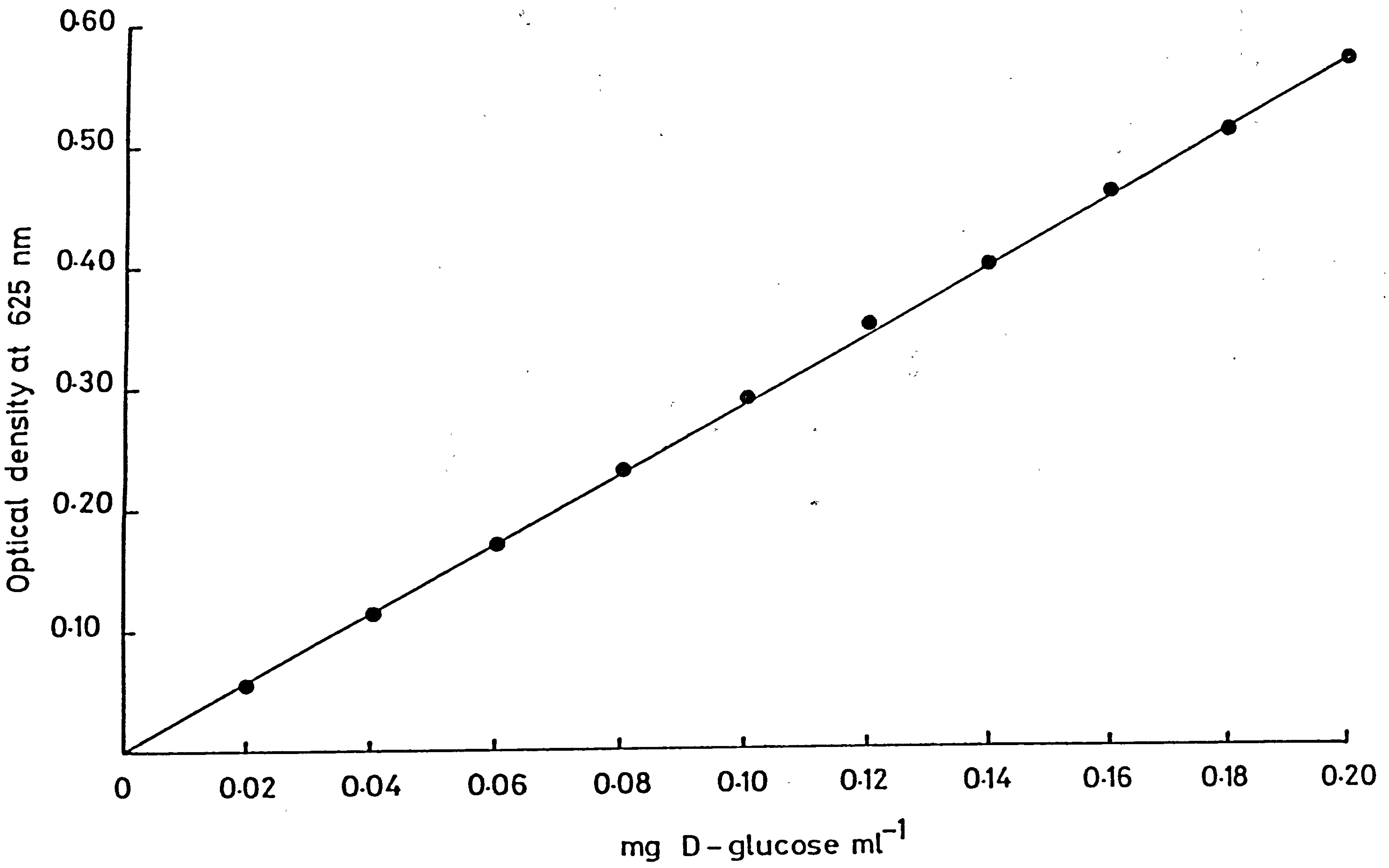
ii) Add carefully 760 ml concentrated sulphuric acid to 330 ml of water in a boiling flask immersed in an ice-water bath. Add 1 g of thiourea and dissolve completely, using a magnetic stirrer, before adding 1 g of anthrone and dissolving (I Lamb pers. comm.). After preparation the reagent is transferred to a darkened bottle and left overnight in a refrigerator. Store in a refrigerator when not in use.

### Procedure

Colour Development

Pipette 2 ml of each Standard into a set of boiling tubes. Pipette 2 ml of distilled water into a further set of tubes, and add 50 $\mu$l of ethanol extracts to the tubes, except for one which serves as a blank. Place tubes in a purpose built basket, and place in an ice-water bath. Add 10 ml of chilled anthrone with an automatic dispenser. Place marbles in the top of each tube, to act as condensers, and incubate tubes in a vigorously boiling water bath, in a darkened fume cupboard, for precisely 10 minutes. Promptly remove the tubes and allow to cool in an ice-water bath, in the dark. After cooling, allow the tubes to come to room temperature and read the optical absorptivity at 625 nm, using the water blank as a reference. Prepare a calibration graph from the standards and use it to obtain mg glucose in the sample aliquot (see: Fig. A4.1).

Figure A4·1 Standard curve for the determination of ethanol-soluble carbohydrate in _Calluna_ samples



### Calculation

X = mg glucose in sample as read from calibration graph

% ethanol soluble carbohydrate in sample =

$$\left( \frac{X \times \text{Extract Vol.}}{\text{Aliquot Vol.}} \right) / \text{Sample Weight} \times 100$$

## A 4.2 Colorometric Methods for the Determination of both Nitrogen and Phosphorus using a Micro Digestion Technique

### (i) Digestion

#### (a) Reagents

1. Dissolve 0.1 g Selenium in 100 mls conc. Sulphuric Acid (Analar) by heating, with a bunsen, until the solution becomes colourless. Cool and store in a glass-stoppered bottle.
2. 100 volume Hydrogen Peroxide.

#### (b) Apparatus

1. Heating block to accommodate 30 Pyrex 150 mm x 16 mm medium walled tubes.
2. Volumetric glassware.
3. Visible Range Spectrometer.

### Procedure

Grind oven dry samples to pass through a 0.5 mm screen. Weigh accurately approximately 0.1 g of the sample into the Pyrex tube. Add 2 ceramic beads to each test-tube followed by 2 mls of the digestion mixture. Shake the tube thoroughly to mix sample and acid and carefully add 1 ml hydrogen peroxide slowly. After the initial vigorous reaction has subsided place the tube into the heating block at room temperature and heat to 340°C. After clearing (approximately 1½ hours) heat for a further 30 minutes. Remove from block and when cool make the samples up to a volume of 50 ml.

### Notes

1. Extreme care should be exercised when handling selenium and when adding hydrogen peroxide to the digestion mixture.

2. If the sample does not clear after the addition of the hydrogen peroxide, a further 1 ml may be added.

3. The resulting digest cannot be used for the determination of potassium as the selenium interferes. However, the digestion can take place using only sulphuric acid but the digestion time is increased to approximately 5 hours.

(ii) Determination of $NH_4$ - H (Based on the method of Crooke & Simpson 1971)

Reagents

1. 8.5% (w/v) Sodium Salicylate
0.06% (w/v) Sodium Nitroprusside

Dissolve 85 g Sodium Salicylate and 0.6 g Sodium Nitroprusside in 500 mls deionised water and dilute to 1000 mls with deionised water.

2. 0.25% Sodium Dichloroisocyanurate in 0.6 N NaOH

Dissolve 0.625 g Sodium Dichloroisocyanurate and 6 g Sodium Hydroxide in 100 mls deionised water and dilute to 250 mls with deionised water.

Store reagents (1) and (2) in a refrigerator.

Standards

1. Stock Solution

Dissolve 0.4715 g $(NH_4)_2SO_4$ in deionised water and dilute to 1000 mls with deionised water.

Dilute stock standard to give 250 mls of a solution of concentration 2 mg N $l^{-1}$ and one of 1 mg N $l^{-1}$.

2. Working Standards

To each 50 ml flask add 0.1 mls of the digestion mixture.

| | | | |
|---|---|---|---|
| 0.1 | mg N $l^{-1}$ | 5 | mls of 1 mg N $l^{-1}$ solution to 50 mls (deionised water) |
| 0.2 | do. | 10 | do. |
| 0.4 | do. | 20 | do. |
| 0.6 | do. | 30 | do. |
| 0.8 | do. | 40 | do. |

|  |  |  |  |
|---|---|---|---|
| 1.0 | mg N $l^{-1}$ | 25 | mls of 2 mg N $l^{-1}$ solution to 50 mls (deionised water) |
| 1.2 | do. | 30 | do. |
| 1.4 | do. | 35 | do. |
| 1.6 | do. | 40 | do. |
| 1.8 | do. | 45 | do. |

## Procedure

### 1. Standards

To a 10 ml volumetric flask, add 5 ml of the standard 2 ml of reagent (1) followed by 2 ml of reagent (2). Shake the solution and place in a water bath (37°C) for 10 minutes until the emerald green colour develops. Cool to room temperature and dilute to the mark with deionised water.

The standards now have a value of half their original value, ie. 0.05 mg N $l^{-1}$ to 0.9 mg N $l^{-1}$.

Shake and read the absorbance, against a blank, at 667$\mu$m, narrow slit, with the Beckman D.B. Spectrophotometer.

A plot of the concentration against absorbance should give a straight line.

### 2. Samples

After digestion and the samples have been made up to 50 ml, dilute a 10 ml aliquot to 100 mls. To a 10 ml volumetric flask add 3 ml deionised water, 2 ml sample and 2 ml of each reagent in the order previously mentioned. The procedure is now the same as for the standards. From the graph the amount of Nitrogen can be found.

## Notes

1. The method employed is similar to that used for neutral solution, the difference being the increase in the strength of Sodium Hydroxide. Due to the high hydrogen ion concentration, two problems arise: (a) the salicylate ion precipitates out as salicylic acid. To overcome this problem water is first added to the flask to reduce the $H^+$ concentration, and (b) the pH of the resulting solution is lowered to approximately pH8. For the reaction to reach completion the pH of solution

must be in the region of pH 14. By increasing the strength of the Sodium Hydroxide this problem is overcome.

2. Reagents are stable for approximately two days.

3. Calculation

$$\% N = \frac{\text{Graph Reading} \times 25 \times 10^{-2}}{\text{Sample weight}}$$

### (iii) Determination of Phosphorus (Based on procedures described by Murphy & Riley 1962)

Reagents

1. 2.5% Ammonium Molybdate (in 10 N Sulphuric Acid)

Dissolve 25 g Analar Ammonium Molybdate in 100 mls water.

Carefully and slowly add 275 mls of concentrated sulphuric acid, with constant stirring, to 600 mls of water. Cool to room temperature. Add the Ammonium Molybdate solution to the acid solution and make up to 1000 mls with distilled water.

Store in an amber bottle. Solution keeps indefinitely.

2. 1% Stannous Chloride (in 1 N Hydrochloric Acid)

Dissolve 0.5 g Stannous Chloride in 50 mls 1N Hydrochloric Acid.

Prepare fresh daily.

Standards

1. Stock Phosphorus Solution: 100 mg P $l^{-1}$

Dilute 0.4393 g Potassium Dihydrogen Phosphate, dried in a desiccator to 1000 mls in a volumetric flask with distilled water.

2. Working Standards

Dilute the stock solution 1/10 to give 10 mg P $l^{-1}$.

Procedure

Standards

Using 100 mls flasks take the relevant aliquotes to give final concentrations in the range 0.1 mg P $l^{-1}$ - 0.9 mg P $l^{-1}$.

To each flask then add 4 mls of the Ammonium Molybdate solution, 80 mls of water (thoroughly shake the flask) and finally 1 ml of the Stannous Chloride. Make up to the mark with water, shake, leave 5 minutes for the blue colour to develop and read at 667$\mu$ m, narrow slit on Beckman D.B. Spectrophotometer before 30 minutes has elapsed. A plot of concentration against absorbance should give a straight line.

Samples

After the digest has been made up to 50 mls, take a 10 ml aliquot and add to a 100 ml flask and proceed as described above for the standards. From the graph the amount of phosphorus can be found.

Notes

1. Always add the Sulphuric Acid to water.
2. The blue colour is only stable for a period not exceeding 30 minutes.
3. Calculation

$$\% \text{ P} = \frac{\text{Graph reading x 0.05}}{\text{Sample weight}}$$

### A 4.3 The determination of Neutral Detergent Fibre (N.D.F.)

The method for the determination of Neutral Detergent Fibre (N.D.F.) was developed by Van Soest & Wine (1967). Waldern (1971) developed a method based on that of Van Soest & Wine on a much smaller scale, permitting savings in time when dealing with large numbers of samples, and economy in the use of equipment and reagents. Because of the small size of the *Calluna* samples available for this determination, Waldern's method was scaled down.

Micro-Method

Reagents

Reagents were prepared as in Van Soest & Wine(1967)

(i) Neutral Detergent Solution

30 g of sodium lauryl sulphate are added to 1 litre of distilled water. The following are added: 18.61 g

disodium dihydrogen ethylene-diamine tetracetic dihydrate; 6.81 g sodium borate decahydrate; 4.56 g disodium hydrogen phosphate and 10 ml 2-ethoxy-ethanol. Agitate to dissolve. Check pH to range from 6.9 - 7.1.

(ii) Decahydronaphthalene (Decalin).

(iii) Acetone - Analar.

(iv) Sodium sulphite - anhydrous.

Apparatus

(i) Refluxing apparatus - micro-Kjeldahl flasks are fitted with large marbles (approx. 2 cm diameter). Dampened collars of absorbent material also aid condensation.

(ii) Sintered glass crucibles - coarse porosity.

Procedure

Air dried samples are ground to pass a 0.5 mm screen. Weigh accurately about 0.1 g of the sample into a micro-Kjeldahl flask. Carefully add 10 ml of cold neutral detergent solution to avoid splashing any of the sample high up onto the walls of the flask. Add 0.1 g of sodium sulphite and 1 ml of decalin. Slowly bring flasks to the boil (10 minutes) to avoid foaming. Adjust heat for gentle boiling to prevent particles being pushed up onto the walls of the flask. Particles can be washed back down into the boiling reagent with hot neutral detergent solution if necessary, using a pasteur pipette. A constant level of digesta is maintained by adding appropriate volumes of hot neutral detergent solution, to ensure a minimum of variation in digestion between samples. Boiling is continued for one hour. Transfer the contents of the flasks to previously tared sintered glass crucibles, and wash any remaining particles from the flasks with hot distilled water. Apply vacuum to the crucibles to achieve filtration. Wash samples in the crucibles with a minimum of hot water. Remove vacuum and rewash samples with hot water and re-apply vacuum. Wash samples twice with acetone in the same manner and suck dry. Dry crucibles at 100° C for 8 hours or overnight. Cool in an efficient desiccator and weigh. The difference in weight of the crucible is cell wall constituents.

## Calculation

$$\%\ \text{cell wall constituents of sample} = \frac{\text{weight of cell wall constituents} \times 100}{\text{Sample weight}}$$

## Comparison of Methods

To assess the value of the method a trial was conducted in which three replicates of 10 Calluna samples were evaluated for N.D.F., using the micro-method as outlined above, and both Waldern's and Van Soest & Wine's methods. The results of this trial are reported in Table A 4.1. An analysis of variance was performed upon those data using the subprogram ANOVAR of S.P.S.S., and the results reported in Table A 4.2. The lack of significance in the F-ratio signifies the comparability of the methods. I therefore considered that the micro-method was appropriate for use in this case, particularly since I was concerned with differences between samples rather than absolute values of N.D.F.

Table A 4.1 Results of the trial comparing methods for the estimation of cell wall constituents

| Sample Number | Van Soest & Wine % c.w.c. | Waldern, % c.w.c. | micro, % c.w.c. |
|---|---|---|---|
| 1 | 27.19 | 27.89 | 28.98 |
| 2 | 29.21 | 29.58 | 28.48 |
| 3 | 31.24 | 32.38 | 32.12 |
| 4 | 29.20 | 28.62 | 30.37 |
| 5 | 29.33 | 29.70 | 30.24 |
| 6 | 29.25 | 29.30 | 30.51 |
| 7 | 32.43 | 33.88 | 33.10 |
| 8 | 25.63 | 26.25 | 26.81 |
| 9 | 29.27 | 30.10 | 30.28 |
| 10 | 29.81 | 29.37 | 29.93 |

Table A 4.2 Analysis of Variance of cell wall constituents results using different methods

Variate - cell wall constituents (N.D.F.)

| Source of variation | D.F. | Sums of Squares | Mean Square | F-Ratio |
|---|---|---|---|---|
| Methods | 2 | 3.4212 | 1.7106 | 0.456 N.S. |
| Error | 27 | 101.2890 | 3.7514 | |
| Total | 29 | 104.7102 | | |

N.S. - not significant at 5% level.

F-Ratio is not significant at 5% level, and thus null hypothesis, Ho, of no significant differences between methods is accepted.

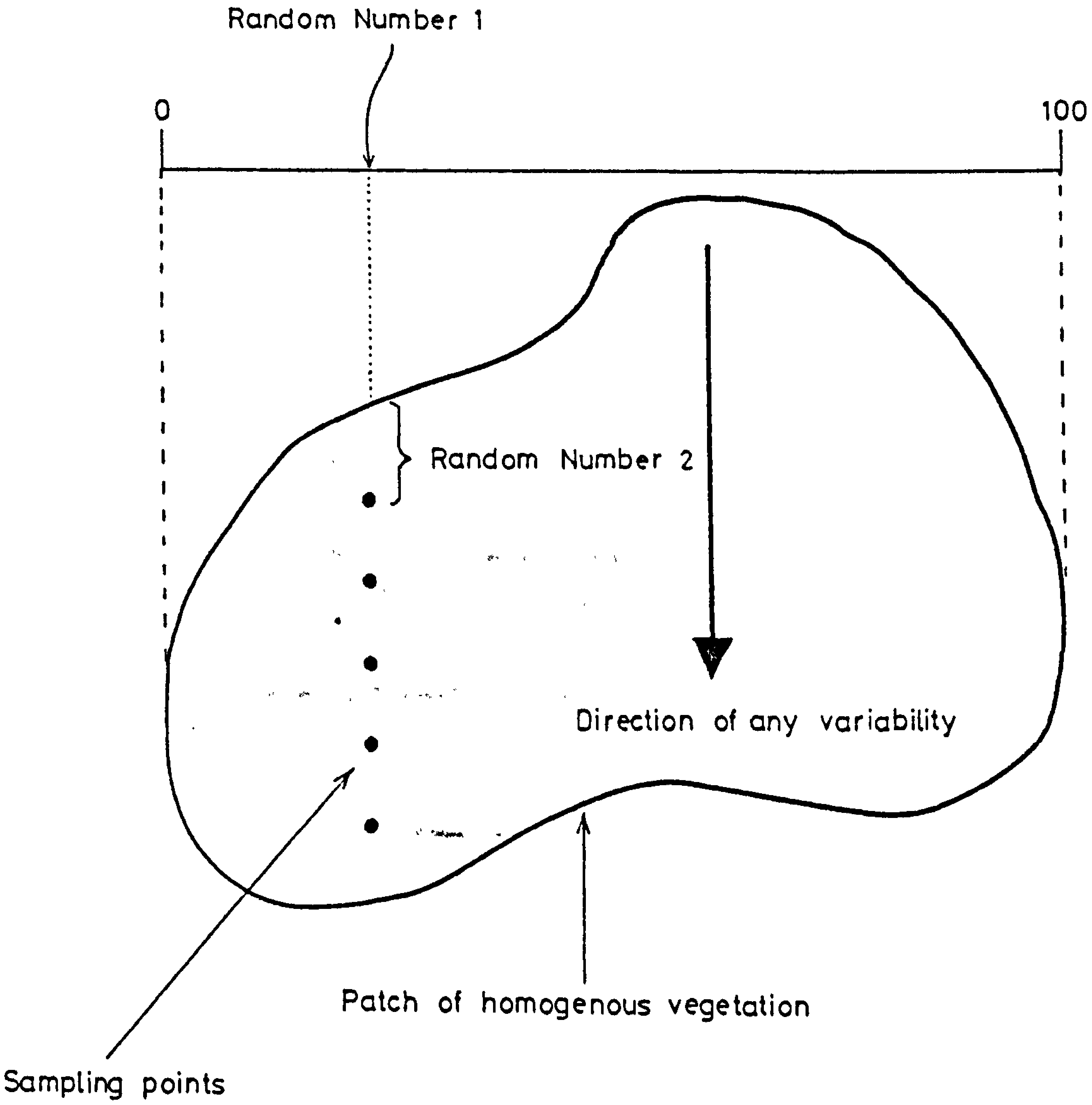
## Appendix 5. The Sampling Method for the Ground Survey

The sampling scheme was based on the recognition of patches of homogenous vegetation. The approximate limits of such a patch of vegetation were determined either by pacing, or with the use of a range-finder. The direction of maximum change in variability within the site, if detectable was noted; the object being to establish an imaginary baseline, the dimension of the plot, at right-angles to the line of maximum variability. If no obvious sign of variability existed within the plot, the base-line was established wherever was most convenient for sampling purposes. The base-line, see Fig. A 5.1, was divided into 100 equal units and by the use of a set of random numbers, the point of commencement of the first transect was determined. Random numbers were produced by means of a computer program which selected n numbers between one and one hundred, where n is the number of transects. These numbers were ranked in ascending order, and the difference between them produced as the distance along the base-line of the first and subsequent transects. A further set of random numbers between one and ten was produced in the same manner, to determine the first sampling point along a transect. Subsequent sampling points were determined on a regular basis: the inter-sampling point distance being calculated from the plot dimension, along the transect course, divided by five; five sampling points per transect being evaluated. At each sampling point a circular area one metre in diameter was scanned (approx. $0.8m^2$), and the index of utilisation recorded.

In this scheme the individual sampling unit was the transect. Thus the sequence of events described aimed to sample a site in a random fashion, to cover within-transect variability and minimise between transect variability. In this way individual transects were comparable for subsequent statistical analysis.

Fig. A5·1

The Schematic Representation of the Method For Ground Survey



Appendix 6.1

Grace, J. and Easterbee, N. (1979)

The natural shelter for red deer (*Cervus elaphus*)
in a Scottish glen

Journal of Applied Ecology, 16, 37-48

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# THE NATURAL SHELTER FOR RED DEER (*CERVUS ELAPHUS*) IN A SCOTTISH GLEN

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## SUMMARY

(1) The shelter afforded by the topography and vegetation of a Scottish glen was measured. The reduction of wind speed in the glen overall was as high as 42%. No single part was most sheltered, the ranking of sites depending on wind direction. Small-scale undulations in topography and a small area of woodland reduced wind speed by up to about 95%. The shelter value of dwarf shrub and herbaceous vegetation could be estimated from its height.

(2) The influence of shelter on heat loss from deer was calculated, using established theory and published data. The extreme conditions, in the woodland and on the exposed hillside, were compared. It was estimated that nearly twice as much heat would be lost in the exposed position. Woodland reduced convective heat losses and radiative exchange with the cold sky.

## INTRODUCTION

The original habitat of the red deer (*Cervus elaphus* L.) is considered to be open woodland and forest margins. In Scotland, because of climatic change and the destruction of this habitat in historic times, the animal lives in a different environment of open moors and exposed mountains where the species does not attain its full size. In contrast, much larger specimens occur in parts of Europe, in New Zealand where Scottish deer have been introduced, and in Scotland when deer are experimentally fed (Ritchie 1920; Blaxter *et al.* 1974).

Many authors suppose that nutrition is responsible for the poor productivity of red deer in Scotland, so much attention has been paid to the diet (see Mitchell, Staines & Welch 1977). A few authors have remarked on the 'value of shelter' (Flerov 1952; Dzieciolowski 1969), but there have been only partial attempts so far to assess its role. The present paper examines the hypothesis that shelter may be of great importance, both in explaining the poor performance of the animal in Scotland, and in accounting for 'sheltering behaviour' in relation to topography, which has been observed (Jackes 1974; Staines 1976). Attention is given to the winter environment, as it is known that the animals lose weight at this time when demands for homeothermy are greatest, and when approximately 70% of the hinds are pregnant. Wind was measured at different places in the study area, and established theory is used to explore the significance of the results for heat loss from deer.

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## STUDY AREA

The study area covered Glen Goibhre and the eastern part of Glen Orrin. Both are part of the catchment of the River Conon, and lie approximately 34 km NW of Inverness (Grid Reference NH 43 49).

The floors of the glens are approximately 210–250 m above m.s.l., separated by a central ridge rising to 370 m. The land rises to 580 m to the south, and 450 m to the north. To the west the Western Highlands exceed 1080 m.

The dominant vegetation is a heather bog resembling the Tricophoreto-callunetum of McVean and Ratcliffe (1962). There are small areas of mixed deciduous woodland in Glen Orrin and at the eastern end of Glen Goibhre. A small area of coniferous woodland is open to deer at the eastern end of the study area.

Deer always frequent the area, and in the winter there are about 0·13 $ha^{-1}$.

## MATERIALS AND METHODS

### (*a*) *Macrotopographic shelter*

The position of five meteorological stations is shown in Fig. 1. The anemometers (Munro cup-counter Mk IV) were 1 m above the ground, and mean wind speeds were calculated from readings taken approximately every 7 days from November 1976–April 1977. On three occasions the recording was postponed due to stalking activities. Wind direction was recorded daily at the house except during periods of absence (Fig. 1), when missing data were replaced by Meteorological Office records from Strathconon and Dalcross 13 and 35 km respectively from the study area.

### (*b*) *Microtopographic shelter*

Microtopographic shelter was investigated during July 1977. A modified Sheppard cup anemometer, with a digital L.E.D. counter unit, was erected 1 m above ground level in an open reference site near the top of the north facing slope of Glen Goibhre. Another was erected successively at 90 m intervals along transect A–B in order to traverse the glen completely, crossing areas of different microtopography (Fig. 1). Wind run at 1 m was recorded simultaneously at the reference and at each sampling site for periods of 5 minutes. Simultaneous sampling was achieved by shortwave radios. Wind direction was also recorded. The anemometers were calibrated in laminar air flow in a wind tunnel over a range of wind speeds.

### (*c*) *The wind profile over vegetation*

Wind profiles were measured over different vegetation associations in the study area using a portable 4 m mast, with 4 aneometers as in (*b*) above. The aneometers were attached to the mast at 3·97 m, 2·44 m, 1·22 m and 0·50 m above ground level. Wind run was recorded for three consecutive 5 minute periods and the results plotted as the average wind speed over 15 minutes. The weather during the period was cloudy and windy, corresponding to near-neutral stability.

Sampling sites were selected to give wind profiles over a representative range of vegetation heights. Five consecutive sites along a transect were sampled and then surveyed to determine microtopographic relief. Two further sites were sampled on level ground, with fetch of approximately 200 m and 80 m. To estimate the aerodynamic

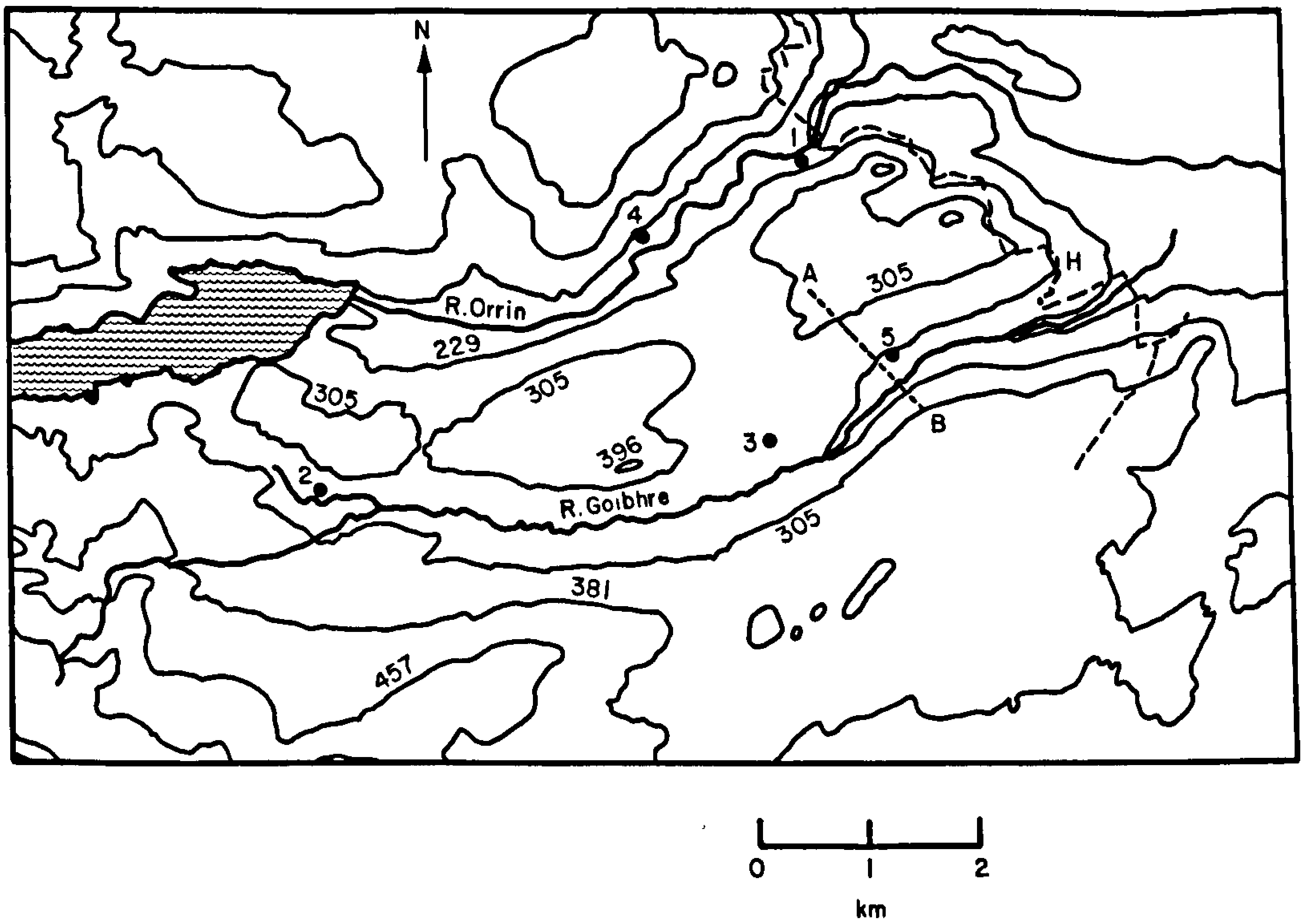

FIG. 1. Map of the study area, showing the house (H), positions and numbers of the meteorological stations (●) and the transect (A-B) referred to in the text.

roughness of the vegetation, and hence its shelter effect, the usual logarithmic plot was made:

$$u(z) = \frac{u^*}{k} \frac{\ln(z - d)}{z_0}$$

where $u(z)$ is the mean wind speed at height $z$, $d$ is the zero plane displacement of 0·63 × the height of the vegetation, $u^*$ is the friction velocity, $k$ is von Karman's constant of 0·41, and $z_0$ is the roughness length. By plotting $\ln(z - d)$ against wind speed, $z_0$ was obtained from the intercept on the $y$ axis (Monteith 1973).

### (*d*) *Energy balance*

The energy balance of an animal can be expressed as follows:

$$M = C + E + G + R + J$$

where $M$ is the net gain of heat from metabolism; and $C$, $E$, $G$, $R$ are the net losses of heat by convection, evaporation, conduction and radiation. $J$ is the rate of change of stored heat.

A main effect of shelter is to reduce the wind speed, and hence reduce the heat loss by forced convection. This component may be calculated from established theory, using the non-dimensional Nusselt number Nu:

$$C = \rho c_P(T_s - T)\frac{\kappa \mathrm{Nu}}{d}$$

where $\rho$ is the density of air (1·29 kg $m^{-3}$), $c_P$ is the specific heat of air at constant pressure (1010 J $kg^{-1}$ °$C^{-1}$), $T_s$ is the average surface temperature, $T$ is the air temperature, $\kappa$ is the thermal diffusivity of air (0·189 $cm^2$ $s^{-1}$) and $d$ is the characteristic dimension of the body (see Monteith 1973). To obtain a value for $d$, a deer is assumed to be a horizontal cylinder of diameter $d$ set perpendicular to the wind direction. In the calculation of $C$ it was assumed that $d = 0{\cdot}45$ m. The Nusselt number was calculated from the Reynolds number ($\mathrm{Re} = u \times d/\nu$) using the relationship

$$\mathrm{Nu} = x\,\mathrm{Re}^y$$

where $u$ is the wind speed, $\nu$ is kinematic viscosity of air (0·133 $cm^2$ $s^{-1}$) and $x$ and $y$ are empirical coefficients which have been established for heated cylinders exposed in wind-tunnels (values were taken from the appendix in Monteith 1973).

It is beyond the scope of the present paper to establish a complete energy balance. However, some discussion of radiative shelter is required. The radiative heat loss can be estimated from the animal surface temperature ($T_s$) and the temperature of the surrounding surface ($T_{\mathrm{surrounds}}$)

$$R = \epsilon\sigma(T_s^4 - T_{\mathrm{surrounds}}^4)$$

where $\epsilon$ is the emissivity, previously found to be 0·95 – 1·0 for mammalian coats (Moen 1973), and assumed here to be 1·0; and $\sigma$ is the Stefan-Boltzmann constant ($5{\cdot}67 \times 10^{-8}$ W $m^{-2}$ $K^{-4}$).

## RESULTS

### (*a*) *Macrotopographic shelter*

Figure 2 shows the mean wind speed at the five meteorological stations over the study period. Station 3 on an open ridge-top was the most exposed, and station 1 in open coniferous woodland was the most sheltered. Wind directions, also shown in Fig. 2, account for the variability between stations 2, 4 and 5. The relative exposure of these sites is a function of the surrounding topography and the prevalent wind direction over a particular sampling period.

### (*b*) *Microtopographic shelter*

Figure 3 indicates the results from the transect across Glen Goibhre (see Fig. 1 for location). The most exposed site relative to the reference site (No. 1) was at the lowest altitude (No. 9). This is attributed to the funnelling action of the steep-sided glen at this point whereas the sides of the glen were not affected by this phenomenon (compare sites 9 and 10). Site 13 was in a shallow gully, which accounts for its greater shelter compared with sites immediately above and below.

### (*c*) *Wind profiles*

Figure 4 shows another transect and part of the wind profile data. The effect of microtopographic shelter is again demonstrated by comparing the profiles at sampling points 3, 4 and 5. A scale drawing of a deer is shown in this diagram, so that the effect of bedding as opposed to standing may be assessed in relation to the vertical wind profiles. The wind profiles are 15-minute averages, measured over vegetation of different height. The vertical scale has been exaggerated to facilitate the graphical representation of the profile data. The two other profiles determined were at level sites: a *Juncus*-dominated

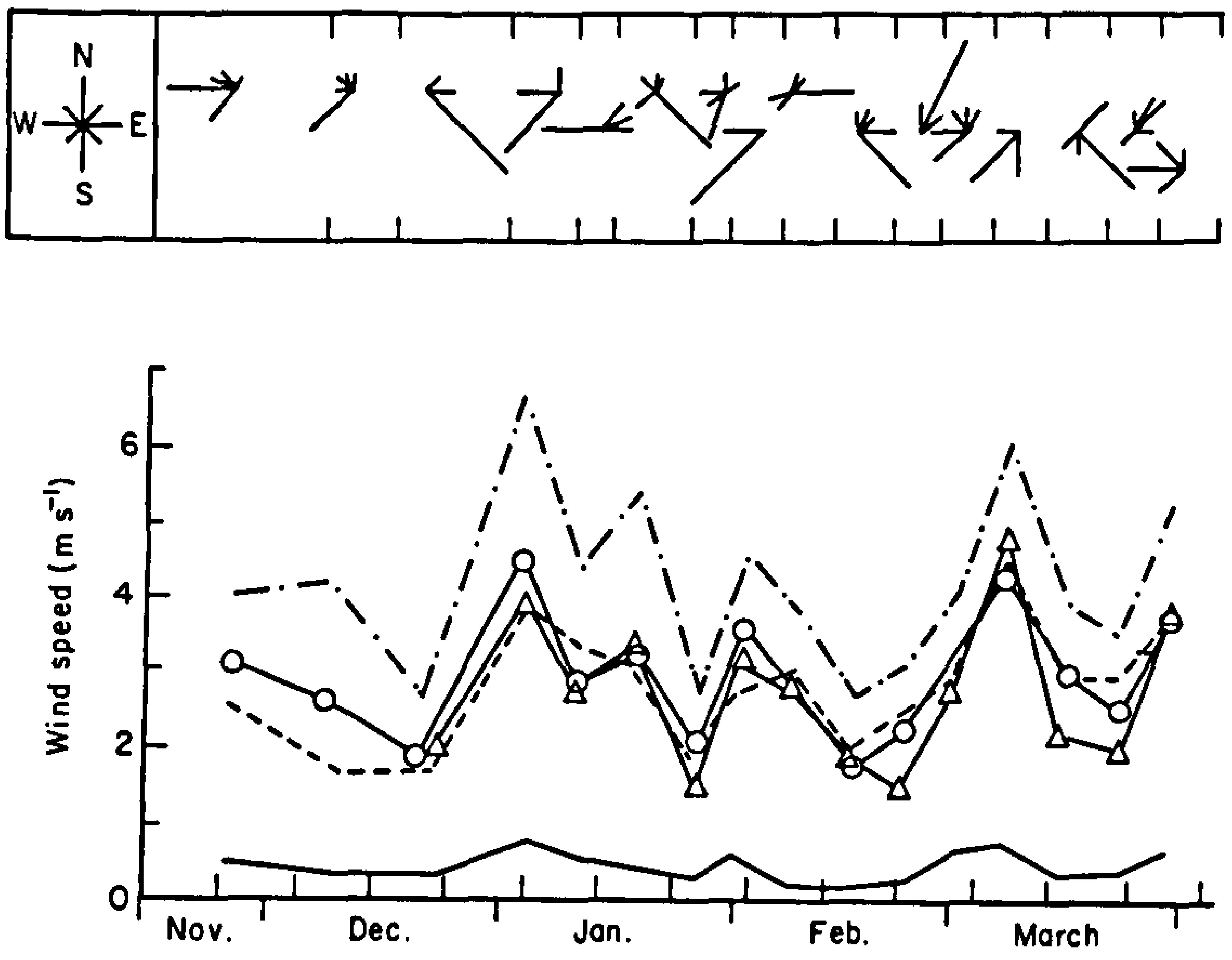

FIG. 2. Wind recordings for winter 1976/77. The top diagram shows the wind direction at the house and the sampling intervals. The lower diagram shows the mean wind speed at stations 1–5 (depicted in Fig. 1). —— station 1; △—△ station 2; –·–· station 3; – – – station 4; ○—○ station 5.

vegetation where the fetch was 80 m and a nearby *Erica tetralix* bog where the fetch was 200 m.

Good determinations of $z_0$ are to be expected only where the fetch is considerable and the ground is level (see Bradley 1968). These criteria were properly fulfilled for the *Juncus* and *Erica tetralix* sites. At other sites the ground was undulating and up-wind roughness variable. Nevertheless, the relationship between $\ln(z - d)$ and wind speed was nearly

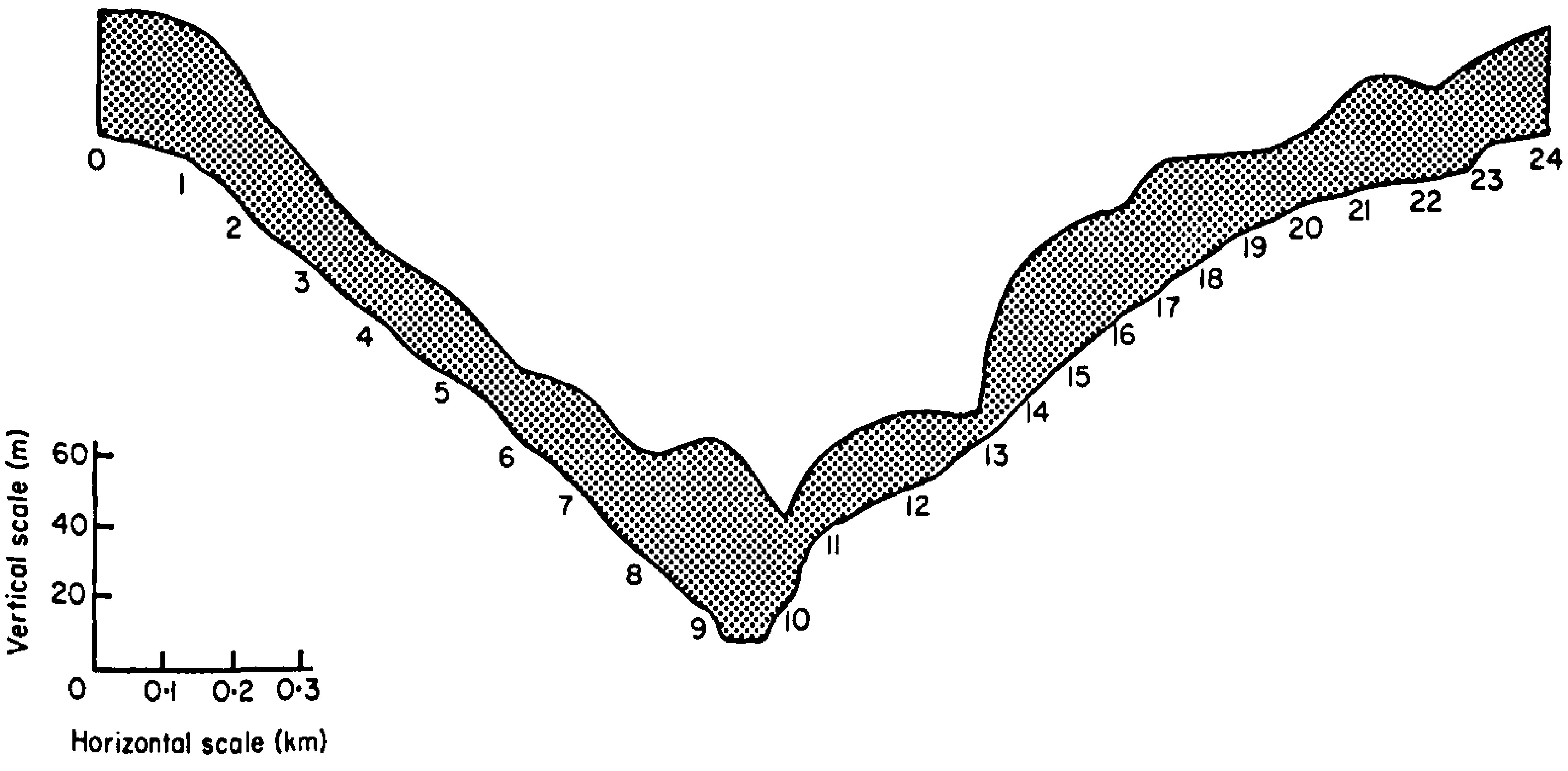

FIG. 3. Wind speed at twenty-five points along the transect A-B (depicted in Fig. 1). Note that the vertical scale is exaggerated × 5. The wind speed is expressed as a fraction of the value at the reference point 0, and illustrated as stipple.

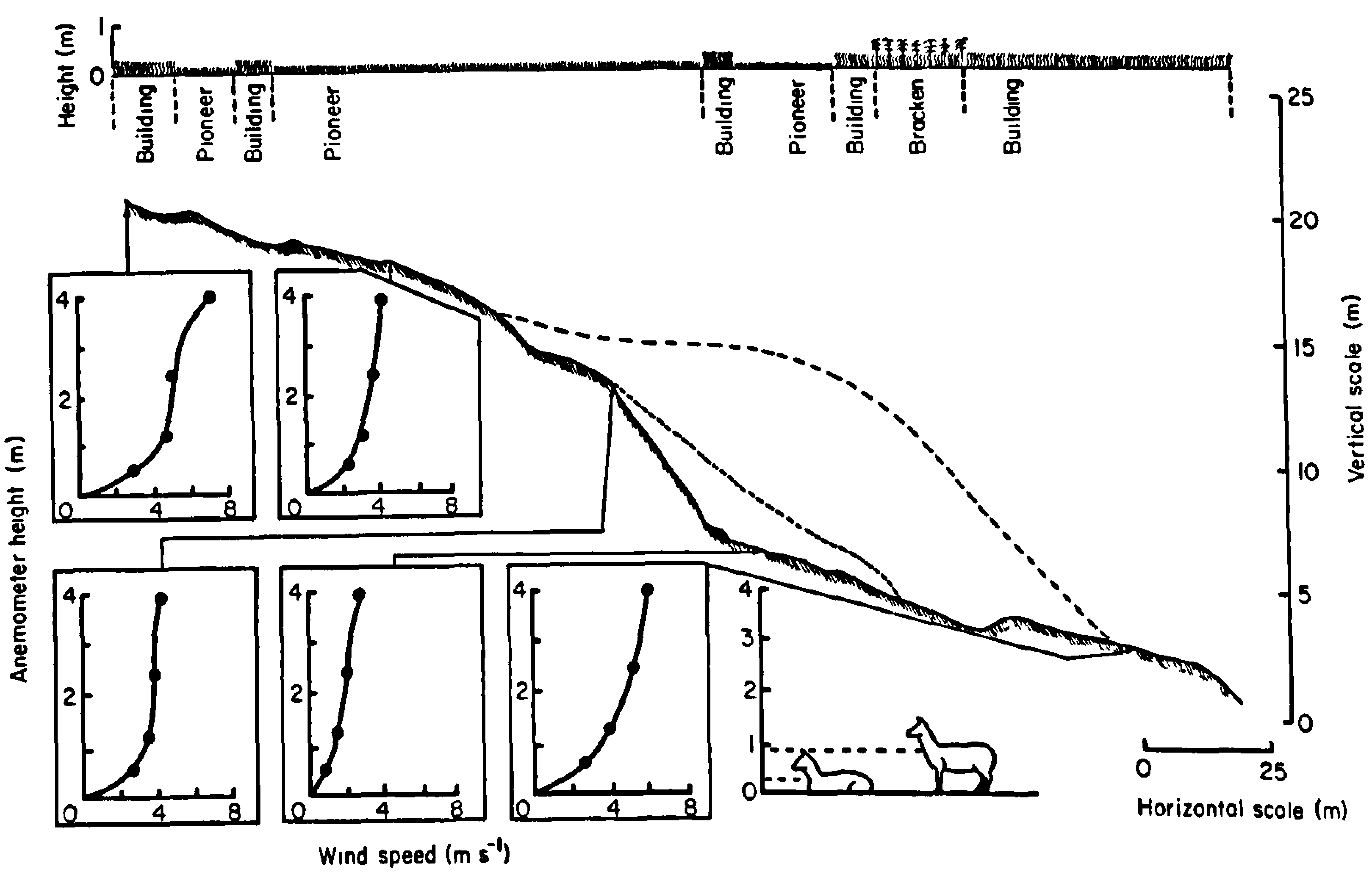

FIG. 4. The shelter of a small gully. Wind speed profiles measured at five places along a NE–SW transect passing through a small gully (the banks of which are shown by broken lines). The wind direction was WSE. 'Building' and 'pioneer' refer to the age class of the heather.

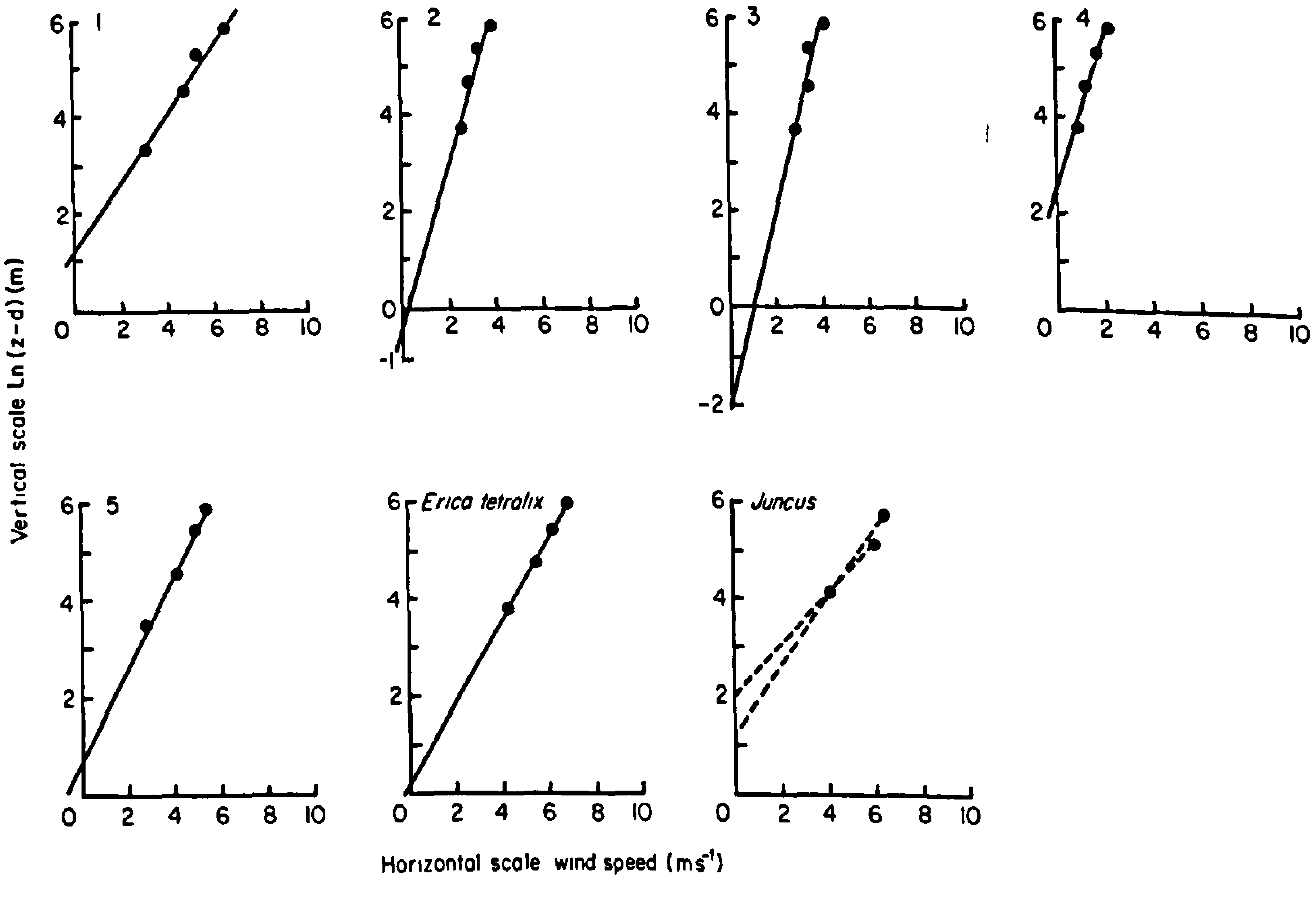

FIG. 5. Wind speed profiles from Fig. 4, and two others in which the fetch was considerable, drawn as logarithmic plots (see text). The numbers 1–5 refer in sequence to the profiles in Fig. 4, commencing at the top of the slope.

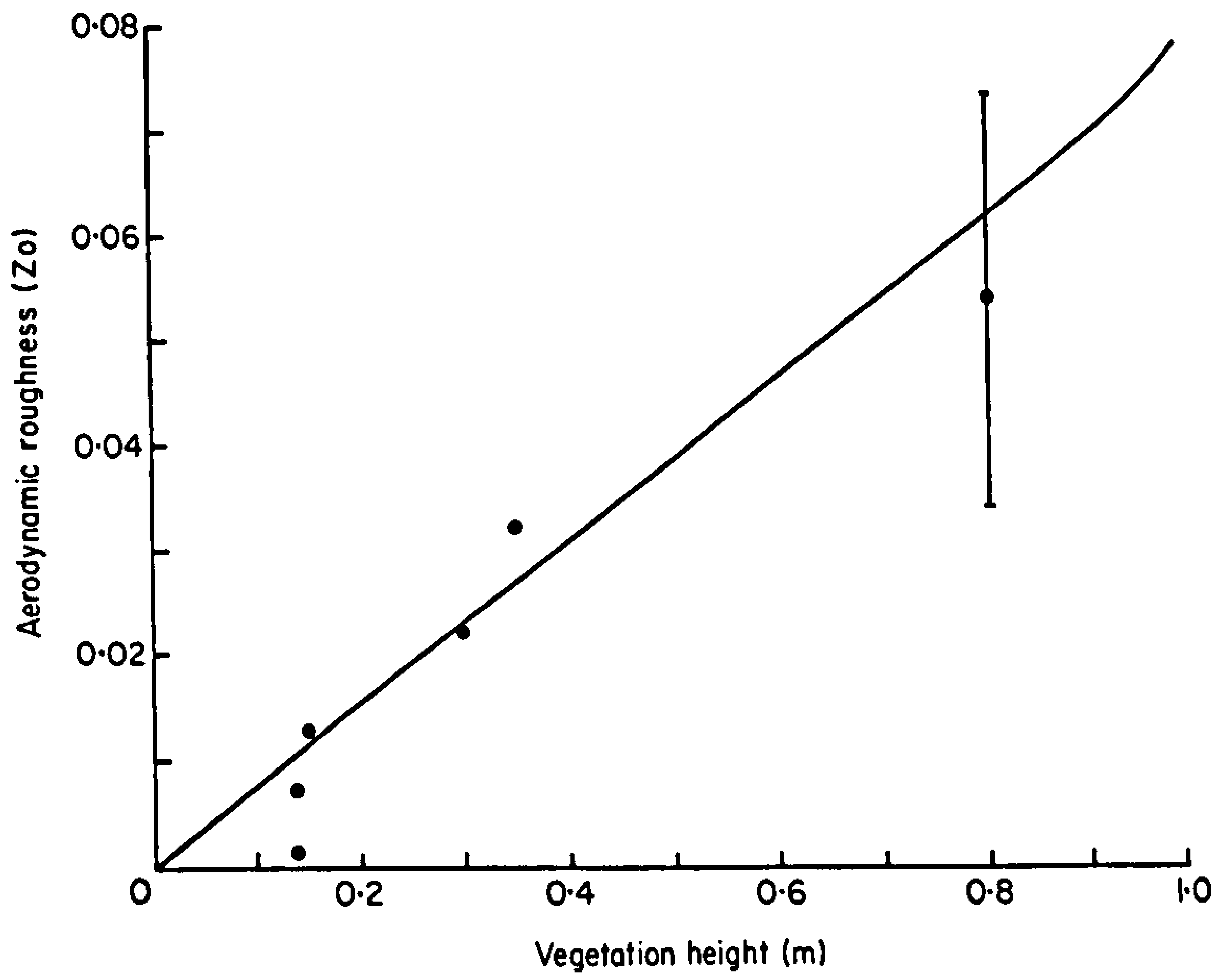

FIG. 6. The relationship between vegetation height and the aerodynamic roughness $z_0$. Obtained from the data of Fig. 5.

linear (Fig. 5), suggesting that the wind speed at deer-height could be estimated from a knowledge of the wind speed at a single reference height above the ground and the height of the vegetation. The relationship between vegetation height and $z_0$ (obtained as the intercepts in Fig. 5), is shown in Fig. 6: $z_0$ is rather less than 0·1 of the vegetation height. Fig. 7 facilitates assessment of the shelter-effect of vegetation over the height-range 0·1–1.0 m, calculated at three different ambient wind speeds, corresponding on the Beaufort scale to a gale, fresh breeze and a gentle breeze.

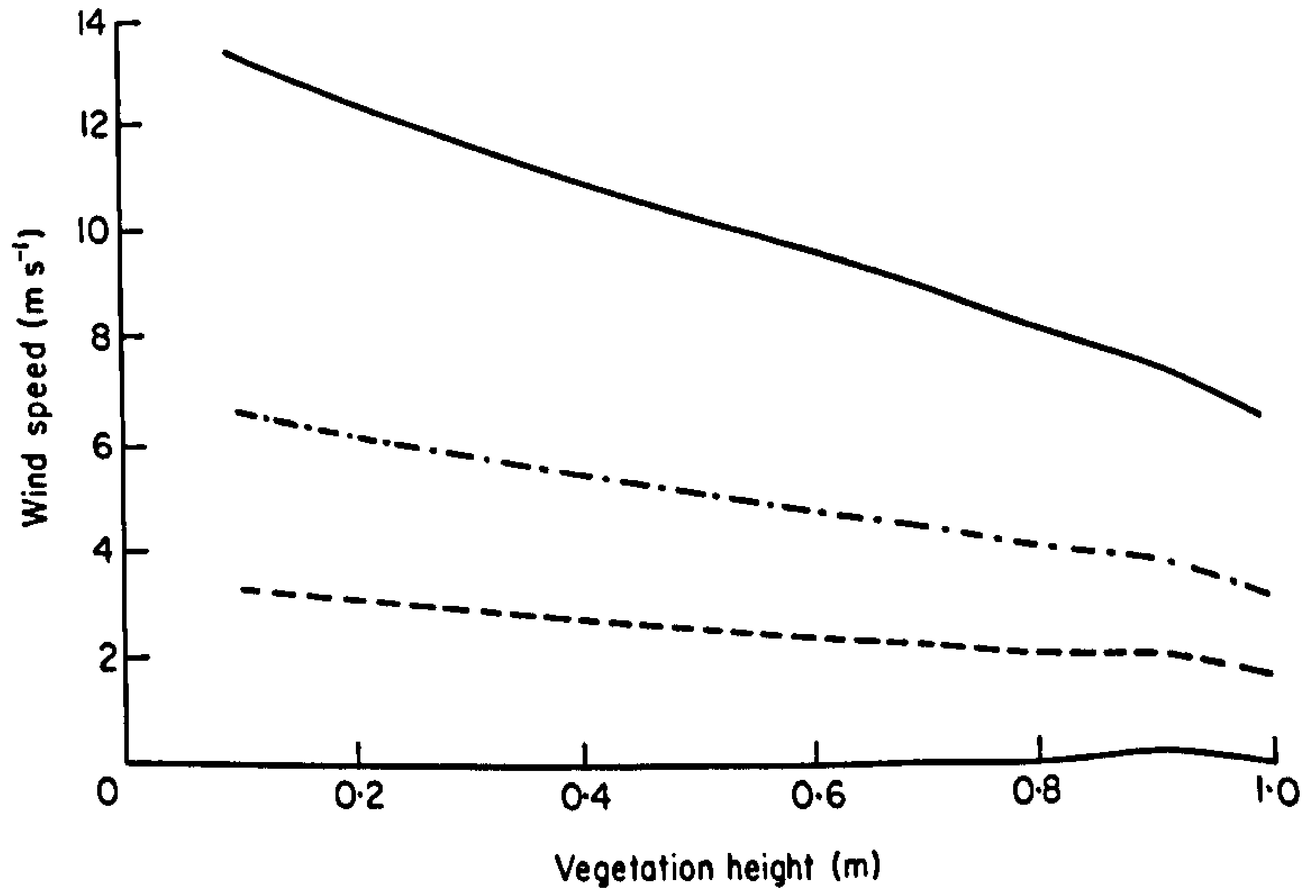

FIG. 7. The influence of vegetation height on the wind speed at deer height (1·0 m). The three curves are calculated assuming standard wind speeds at 10 m, corresponding to gale (—), fresh breeze (-·-·), and gentle breeze (····).

where $T_{\mathrm{surrounds}}$ is the mean temperature of the sky, ground, and other surfaces to which the animal surface is exposed.

$G'$, $C$ and $R$ are all expressed relative to the appropriate surface area of the animal, and related to each other as follows:

$$G' = C + R$$

If $T$, $T_{\mathrm{surrounds}}$ and the values of the resistances are known, it is therefore possible to solve the equations by finding the value of $T_s$ at which $G' = C + R$. This may be done by devising a computer program to make a large number of trials, varying $T_s$ until the right value is found.

Estimates of the resistances can be obtained from the literature as follows: Blaxter's (1967) table of skin resistances for five mammals suggests that the difference between species may not be very great. We have excluded his value for young pigs (which seems exceptional) in estimating a vasoconstricted skin resistance of 1·0 s $\mathrm{cm}^{-1}$. The coat resistance can be estimated from its thickness, and using information from the white-tailed deer by Moote (1955): for a 2·5 cm thick coat the resistance is likely to be 8 s $\mathrm{cm}^{-1}$ although this might be reduced to 4·5 s $\mathrm{cm}^{-1}$ in strong wind as the coat is distorted (Moen 1973; Monteith 1973 and personal communication). The aerodynamic resistance $r_a$ is related to the Nusselt number, viz. $r_a = d/\mathrm{Nu}^{K}$. For the standard deer ($d$ = 0·45 m) the values of $r_a$ corresponding to various wind speeds are shown in Fig. 8: even at the lowest wind speeds, $r_a$ is small compared with $r_c$. We have taken 'sheltered' and 'exposed' wind speeds from Fig. 2 and interpolated on Fig. 8 to obtain estimates of $r_a$ as 4·7 and 0·7 s $\mathrm{cm}^{-1}$ corresponding to a sheltered woodland and an exposed hillside, respectively.

To make the calculations, information on radiative geometry is needed. Although the entire 2·2 $\mathrm{m}^2$ of body surface is an appropriate value to take in the calculation of convective losses, the effective radiative surface is much less, as many parts of the deer surface can 'see' other deer surface (at $T_s$) instead of the much colder sky or the ground. Blaxter *et al.* (1959) working with sheep, recommend a value of 0·7, which we have also used, as the proportion of the area which is fully exposed.

### (*f*) *The extremes compared*

Calculated heat losses of a 60 kg deer standing at an exposed site under a clear sky were compared with those obtained at a sheltered woodland site. The assumptions made were: in the sheltered condition; the air, ground and canopy temperature is 0 °C, $r_s$ = 1·0 s $\mathrm{cm}^{-1}$, $r_c$ = 8·0 s $\mathrm{cm}^{-1}$, $r_a$ = 4·7 s $\mathrm{cm}^{-1}$. In the exposed condition, the surface temperature of the sky and ground (constituting the surrounds) is −10 °C, though the air temperature is kept at 0 °C, $r_s$ = 1·0 s $\mathrm{cm}^{-1}$, $r_c$ = 4·5 s $\mathrm{cm}^{-1}$, $r_a$ = 0·7 s $\mathrm{cm}^{-1}$. Body temperature $T_c$ is taken as 38 °C. In both cases it is assumed to be night, so solar radiation is zero.

Table 1 shows that at the sheltered site the heat loss of the standard deer is 108 W, while 163 W are lost at the exposed site. The basal metabolic rate ($M$) for a deer of weight $w$ may be calculated as $M = A_w{}^n$ where $n$ = 0·75 and $A$ = 3·4 watts per $\mathrm{kg}^{0.75}$ (Monteith 1973). Our 60 kg animal may thus be expected to show a basal metabolic rate of 73 W (though the actual metabolic rate for a walking animal might be much more). The calculated heat losses (Table 1) are higher than this, and suggest a considerable extra demand on energy resources when the resting or grazing animal is in the exposed condition.

TABLE 1. Calculated surface temperatures and heat losses for a 60 kg deer in sheltered or exposed conditions at night (see text for details) Units = W per deer

| | $T_s$ (°C) | Total heat loss | Convective heat loss | Radiative heat loss |
|---|---|---|---|---|
| Sheltered | 7·2 | 98 | 44 | 53 |
| Exposed | 2·4 | 184 | 100 | 84 |

The calculated surface temperatures (Table 1) are in the same range as the measured surface temperatures mentioned above. This is encouraging and serves as a rough check on the method.

In the preliminary trials it was found that the ratio of convection to radiation was very sensitive to assumptions made about the effective surface area for radiation. Our results (using a value of 0·7 $m^2$ of radiative surface per $m^2$ of convective surface) suggest that radiation is a much more important factor than thought by Moen (1973).

## DISCUSSION

The shelter from topography can be considerable. Our results agree with those of Rutter (1968), Nageli (1971) and Roberts (1972), which showed that it was not uncommon to record wind reductions of up to 50% on lee slopes. This variation is considerable in terms of shelter created by man-made wind breaks and shelter belts (Jensen 1954; Caborn 1957) and large in relation to the variation in mean wind speed over the British Isles (see Gloyne 1964).

The reduction of wind speed in the glen as a whole, excluding the forested part, was as high as 42%. No single part may be regarded as the most sheltered, as the ranking of sites changed from week to week according to the wind direction (Fig. 2). Superimposed on this, are the effects of small-scale undulations in the topography such as in the gully where reductions as high as 92% were recorded (such extremes of topographic shelter are unlikely where deer are kept in fields on farms).

The variation in shelter is augmented by the heterogeneity of the vegetation: the wind speed over tall vegetation (1 m) is half that over short vegetation (0·1 m) (Fig. 7). Tall vegetation may have the added advantage of forming a good insulative layer on which the animal can bed down; as Gatenby (1977) has shown for sheep that the heat losses to the ground from animals bedded on short grass are extremely high. Reduction in radiative heat loss could also be expected when the animal beds in tall vegetation, through reduction in exposure to a cold sky.

Completely open topography is particularly unfavourable, as wind speeds are much higher and radiative losses maximal. Topographic shelter may be partly effective in reducing the exposure of animal surface to the sky, but dense coniferous canopy is obviously far more effective. Whereas the radiative temperature of a cloudless sky is often 20° lower than the ambient air (Moen 1973), tree canopies in the winter are seldom more than a few degrees different from the ambient air temperature. A quantitative estimate of the effect of woodland shelter is given in Table 1, in which radiative shelter is shown to be as important as shelter from wind in reducing heat loss. However, this is an estimate pending more reliable data on resistances and radiative geometry.

There is much evidence from other work that winter conditions have considerable impact on the weight, behaviour and survival of deer. Anderson (1972) dealing with the comprehensive data from the Isle of Rhum, found that the severity of winter weather and deaths of deer were highly correlated, and concluded that winter weather, particularly temperature, is of overwhelming importance. However, only records of wind speed in excess of Force 8 Beaufort Scale ('Gale') were available for his study. Verme (1968) reported that most heat was lost from white-tailed deer when low temperatures and high winds occurred simultaneously. Staines (1976) reported that resting deer were found in proportionally more shelter as 'chilling' conditions increased.

During conditions when convective and radiative energy loss are high it is important for red deer to seek shelter, unless their plane of nutrition is sufficient to meet the increased demand for homeothermy. The winter diet of red deer in much of Scotland is poor, and Mitchell, McCowan and Nicholson (1976) demonstrate the deterioration in weight and body condition that occurs between September and April. Much of the local distribution of red deer during winter may thus be related to the pattern of shelter, as outlined. This suggestion is in accordance with the observations of Staines (1976), who reports that shelter was the limiting factor affecting distribution during winter in NE Scotland.

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## Appendix 6.2 The Estimation of Heat-loss

The model described by Grace & Easterbee (1979) is used as the basis for the estimation of energy exchange between the animal and its surroundings. However, since it was desirable to calculate a figure for estimated energy exchange during daytime, when observations of deer were made, the basic model, which estimates energy exchange at night, requires further development.

### A 6.2.1 Radiative Exchange

The radiative exchange component of the model was subsequently estimated as follows:

$$Rn = (1-\rho 3)\ (1+\rho 1)\ St^* + Ld + Le - Ts^4$$

where: Rn is Net Radiation, $\rho 3$ is the reflectance of the deer (estimated on the basis of values for other species at 0.30) to short-wave radiation (0.35-3.0$\mu$m), $\rho 1$ is the reflectance of Calluna (0.14, Monteith 1973), St* is the mean total solar irradiance, Ld is the mean flux of atmospheric radiation, Le is the longwave environmental radiation, and Ts is the mean surface temperature of the deer.

Total solar radiation St (diffuse and direct components) is estimated from a knowledge of the solar constant, the solar elevation and the cloud cover. The intensity of solar radiation, G, is directly related to the solar elevation, ho, at midday:

$$G = lo \sin ho$$

where lo is the solar constant (1360 W $m^{-2}$), ho varies from a minimum in mid-winter to a maximum in mid-summer:

$$ho = (90-L) + \delta$$

where L is the latitude of the study area ($57^\circ$ 30' N) and $\delta$ is the sun's declination, values for which can be obtained from List (1958).

Attenuation of solar radiation occurs within the atmosphere, due to the presence of gases, aerosols, water droplets and ice particles in clouds. The degree of attenuation of solar radiation was estimated from records of cloud cover and weather conditions during days when observations were made, using information from a study by Lamb (1964). A value for maximum solar radiation at noon, Stm, was subsequently calculated:

$$Stm = G \times F$$

where F is the fraction of solar radiation reaching the earth's surface.

Daily insolation, DI, was calculated as follows:

$$DI = (2N/\pi) \times Stm$$

where N is the daylength in hours, which can be obtained from List (1958).

A mean figure for solar irradiance, St*, for each particular observation day was calculated from the value of DI:

$$St^* = DI/N \quad (W\ m^{-2})$$

The mean flux of atmospheric radiation is calculated as follows:

$$Ld = (1-c)\,\varepsilon a(0)\sigma Ta^4 + c \quad (\ Ta^4)-9$$

where c is the fraction of the sky covered in cloud (the mean value for a day's observation period was used), $\varepsilon a(0)$ is the emissivity of clear sky ($1.20-171/Ta^4$), $\sigma$ is the Stefan-Boltzmann constant ($5.67 \times 10^{-8}\ W\ m^{-2}K^{-4}$) and Ta is air temperature.

Longwave environmental radiation is calculated as follows:

$$Le = T_1^{\,4}$$

where $T_1$ is the temperature of the terrestrial surfaces surrounding the deer, assumed to be $2^oK$ colder than the air.

To estimate the amount of radiation intercepted by the surface of the deer, the horizontal irradiance must be multiplied by a shape factor, which depends on the geometry of the surface and the directional properties of the radiation. The mean value of solar irradiance St* was divided into direct and diffuse components. Diffuse solar radiation was estimated as St* x 0.7, which is the mean for the months of fieldwork, estimated from data for Eskdalemuir observatory presented by Chandler & Gregory (1976). The direct solar radiation component is therefore St* - St* x 0.7.

## Interception of direct solar radiation

The amount of direct solar radiation intercepted by the model deer is estimated as follows:

$$\bar{S}b = (Ah/A)\ Sb \times 1-\rho 3 \quad (\mathrm{W\ m^{-2}})$$

where $\bar{S}$b is the mean flux intercepted by a cylinder, Sb is the horizontal flux, Ah is the area of shadow cast on a horizontal surface and A is the surface area of the model deer, $\rho 3$ is the reflectivity of red deer fur, assumed here to be 0.30, which is an estimate based on values for a range of species given by Monteith (1973).

For a horizontal cylinder of radius r (0.5 x d, the characteristic dimension) = 0.225m, and length h = 1.33m, Ah depends on solar azimuth and elevation. The mean solar elevation, $\beta$, during the study period was 17.5°, and solar azimuth, $\theta$, is taken to be 45°.

$$Ah/A = \frac{\operatorname{cosec}\beta\ 2\pi^{-1} X(1-\cos^2\beta\ \cos^2\theta)^{0.5} + \cos\beta\ \cos\theta}{2(X+1)}$$

where X is the ratio h/r.

## Interception of diffuse radiation

The diffuse radiation intercepted by the deer is made up of both short and long wave components. The short wave components are the diffuse solar radiation from sky and clouds, Sd, and the reflected short wave radiation $\rho$St*; where $\rho$ is the reflectivity of the terrestrial surfaces, taken to be Calluna, with a reflectivity of 0.14 (Monteith 1973). The longwave components are: Ld, the atmospheric radiation, and Le which is the environmental radiation from terrestrial sources. If the radiation is assumed to be isotropic, ie. the intensities of the diffuse fluxes are independent of the angle between source and object, and the area of shadow is ignored, then the sum of the components is:

| | short wave | long wave |
|---|---|---|
| upper half surface | $0.82Sd+0.18\ St$ | $0.82Ld+0.18Le$ |
| lower half surface | $0.18Sd+0.82\ St$ | $0.18Ld+0.82Le$ |

## The emission of long wave radiation

The long wave radiation emitted from the deer is simply:

$$\sigma Ts^4 \quad (W\ m^2)$$

where Ts is the surface temperature of the deer and $\sigma$ is the Stefan Boltzmann constant.

A positive net radiation, Rn, results in a gain of energy from the environment by the deer. Conduction of heat from the body core to the dry surface, G', must be equal to the heat loss by convection, C, and radiation, $R_{out}$, as follows:

$$G' = C + R_{out}$$

$$Rn = R_{in} - R_{out}$$

Positive net radiation during daylight hours results in a positive increment of energy to the animal, resulting in less energy derived from metabolism, being expended to maintain a constant body core temperature.

$$G' = C + R_{out} - R_{in}$$

and consequently:

$$G' = C - Rn$$

The values of G' and C' are calculated as by Grace & Easterbee (1979). The estimate of coat resistance, $r_c$, is an average figure based on a range of values obtained from information from the white-tailed deer (Moote 1955) and adjusted for the affects of wind speed according to the results of Lentz & Hart (1960), who worked on young caribou. For the estimates of $r_c$, the deer is assumed to be head into the wind so that the coat is not ruffled.