THE BEHAVIOUR OF WILD REINDEER IN NORWAY

Brian R. Thomson

Ph.D.

University of Edinburgh

1977

This thesis presents the results of my investigations into behaviour and activity in the course of team research on the ecology of reindeer under the International Biological Programme "Tundra Project" (Norway IBP,PT/UM). Where relevant, the contribution of research colleagues is made clear in the body of the thesis.

Some aspects required to be reported before publication of this thesis, in particular activity, leadership and caribou-insect relationships. These are presented in an Appendix. Both the thesis and the Appendix have been composed by myself.

Brian R. Thomson,
14th August, 1977,
Edinburgh.

CONTENTS

PREFACE 6

ACKNOWLEDGEMENTS 7

Ch.1. INTRODUCTION 9
1.1. Objectives 10
1.2. Field Work and Methods 13
1.3. The Approach to Behaviour Study 17

Ch.2. STUDY AREAS 23
2.1. Reindeer Ranges in South Norway 24
2.2. Hardangervidda 28
2.2.1. Situation and Topography 28
2.2.2. Climate 32
2.2.3. Geology and Soils 32
2.2.4. Plants 36
2.2.5. Animals 39
2.2.6. Human Influence 44

Ch.3. STUDY POPULATIONS 46
3.1. Snøhetta 52
3.2. North Ottadalen 56
3.3. Forelhogna 62
3.4. Hardangervidda 64
3.4.1. History 64
3.4.2. Population Size 65
3.4.3. Population Composition 69
3.4.4. Calf Production 71
3.4.5. Sex Ratio 77
3.4.6. Future Management Policy 79

Ch.4. LIFE CYCLE 81
4.1. Morphological Characteristics 82
4.2. Seasonal Ecology 86
4.2.1. Winter 86
4.2.2. Calving 91
4.2.3. Summer 94
4.2.4. Rut 97

PHOTOGRAPHS 101

Ch.5. INDIVIDUAL BEHAVIOUR PATTERNS 118
5.1. Maintenance Behaviour 119
5.1.1. Ingestion 119
a) Feeding 120
b) Antler-chewing 126
c) Drinking and Eating Snow 130
d) Rumination 131
e) Urination and Defecation 133
5.1.2. Locomotion 136
a) Walking, Trotting and Running 136
b) Swimming 140
5.1.3. Comfort Behaviour 141
a) Stretching & Shaking 142
b) Contact Grooming 144
c) Velvet-cleaning 146
d) Sneezing and Coughing 148

Ch.5.2. Antagonistic Behaviour 151
5.2.1. Threat Types 154
5.2.2. Frequency of Antagonism 159
5.2.3. Antagonism at Calving 161
5.2.4. Antagonism in Summer 165
5.2.5. Antagonism in the Rut 168
5.2.6. Antagonism in Winter 169
5.3. Sexual Behaviour 171
5.3.1. Rutting Behaviour 173
a) Standing Posture 173
b) Head-swinging and Driving 173
c) Hunching and Urinating 176
d) Muzzling and Pawing 178
e) Antler Clashes and Fights 183
f) Bush Thrashing 187
g) Female Chases 190
h) Mounting and Copulation 192
5.3.2. Sequence of Rutting Patterns 194
5.3.3. Sex Behaviour in Winter 198
5.4. Mother-Infant Behaviour 205
5.4.1. Pre-Calving Behaviour 206
5.4.2. Parturition 208
5.4.3. Maternal Care 215
5.4.4. Suckling 217
5.4.5. Defence of Calf 227
5.4.6. Mother-Infant Bond 231

Ch.6. SOCIAL BEHAVIOUR 237
6.1. Communication 239
6.1.1. Visual 241
6.1.2. Tactile 249
6.1.3. Acoustic 250
6.1.4. Olfactory 253
6.2. Gregariousness 260
6.2.1. Searching Behaviour 263
6.2.2. Social Facilitation 264
6.3. Leadership and Social Responsibility 266
6.4. Play 268
6.4.1. Calf Play 269
6.4.2. Adult Play 273
6.4.3. Play Situations 276

Ch.7. SOCIAL ORGANISATION AND THE ENVIRONMENT 280
7.1. Social Structure 281
7.1.1. Group Movement and Distribution 282
7.1.2. Group Size and Individual Distance 285
7.1.3. Group Composition and Segregation 290
7.1.4. Group Activity 295
7.2. Social Hierarchy and Winter Grazing 297
7.3. Winter Winds and Heat Loss 314
7.4. Migration to Calving Grounds 333
7.5. Calving: A Time and Place 342
7.6. Post-Calving Aggregation and Movement 352
7.7. Insect Harassment 358
7.8. The Rut 364
7.9. Disturbance from Predators and Hunt 373

Ch.8. ACTIVITY AND ENERGY EXPENDITURE 383

Ch.9. COMPARISON WITH OTHER RANGIFER POPULATIONS 394
9.1. Wild Reindeer Populations in South Norway 398
9.2. Wild and Domestic Reindeer 400
9.3. Mountain, Tundra and Woodland Reindeer 402
9.4. Reindeer and Caribou 405

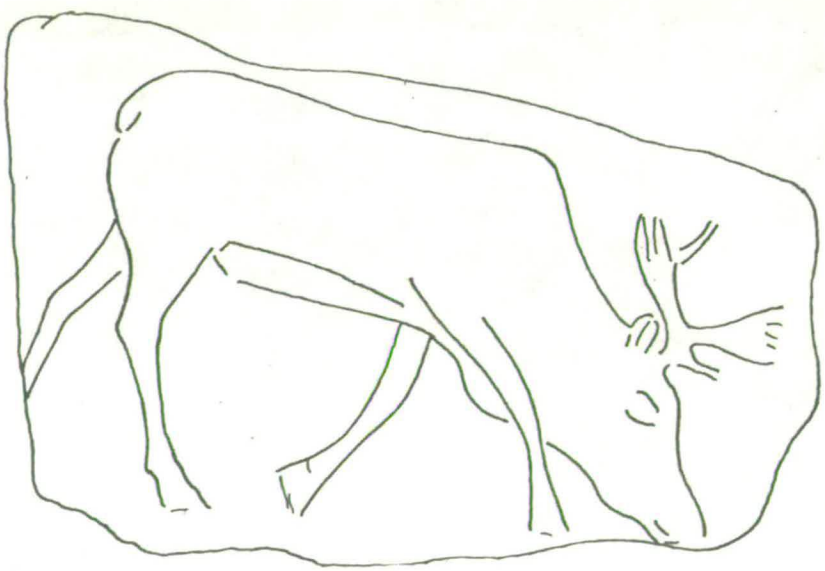
REFERENCES 414

APPENDIX
1. Wild reindeer activity, Hardangervidda, Jan.-June 1970.
2. Wild reindeer activity, Hardangervidda, July-Dec. 1970
3. Wild reindeer activity, Hardangervidda, 1971.
4. Reindeer activity on Hardangervidda.
5. Reindeer disturbance.
6. Leadership in wild reindeer in Norway.
7. The behaviour and activity of caribou at Prudhoe Bay, Alaska.

PREFACE

"Usually entirely alone I have wandered through the country, going quietly that I might see the animals undisturbed and free from fear of man, and, as I have not used or carried fire-arms while on these trips, exceptionally good opportunities have been offered for observation. For hours at a time I have crawled among the unsuspicious Caribou, watching their behaviour while they slept, fed, and in other ways led their natural life without the sound of rifle to fill them with fear. This work has supplied me with much material....."

From A. Radclyffe Dugmore, 1913, "The Romance of the Newfoundland Caribou".



Late Palaeolithic engraving on stone of a reindeer grazing, from La Madeleine, Dordogne, France (from Graziosi, 1960).

ACKNOWLEDGEMENTS

Field work was begun in Norway in September 1969, financed by an 8-month scholarship from the British Council. Thereafter until systematic observations ended in September 1971 the study was financed by the Norwegian International Biological Programme "Tundra Project" with support from the Direktoratet for vilt og ferskvannsfiske in Trondheim (the Norwegian Directorate for Game and Freshwater Fisheries). From October 1971 to October 1973 the analysis of field data was done under a grant from the University of Edinburgh at the Department of Forestry and Natural Resources. I am grateful to all these organisations for their financial support of this study.

I would especially like to thank the Reindeer Project leader, Dr. E. Gaare of Viltforskningen (Norwegian State Game Research Institute), and Wildlife Supervisor, Dr. J.D. Lockie of Edinburgh University, for their unfailing support and guidance at all stages of the work. Reindeer research colleagues in Norway were of notable help in the field, namely Eigil Reimers, Eldar Gaare, Gøsta Hansson, and particularly Terje Skogland, with whom I shared several field trips, including the one to Alaska. In this connection I should perhaps acknowledge the writer in a Norwegian newspaper who maintained that Skogland and myself should be considered for honorary membership of the Hardangervidda Herd! I am also indebted to Anne Jackes of the University of Edinburgh, Department of Forestry and Natural Resources, who acted as my Field Assistant throughout summer and autumn 1970, and whose many useful observations are incorporated in this thesis. Local knowledge was helpful before moving into the mountains and I would particularly single out for mention Ole Skarpaas at Hardangervidda, Olav Heitkøtter at North Ottadalen, and the late Per Holaker at Snøhetta.

In summer 1972 I was invited by the Institute of Arctic Biology in Fairbanks, Alaska, with funds from the I.B.P. Tundra Program of the U.S.A. to make comparative behaviour observations of caribou on Arctic tundra at the Prudhoe Bay Oil Extraction Site, North Slope. My thanks to Dr. Robert White and Dr. /

Dr. Jack Luick of the I.A.B. for making this trip possible, and for the opportunity it afforded to present a paper at the First International Reindeer/Caribou Symposium at Fairbanks.

I am also grateful to Dr. Ethel Lindgren and Mr. Mikel Utsi of the Reindeer Council of U.K. for their hospitality in the course of visits to their Reindeer Herd at Glenmore, Cairngorms.

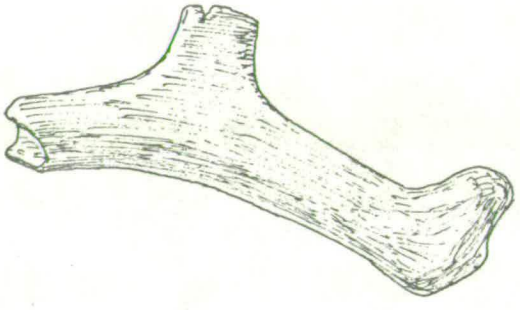
The writing of the thesis was largely achieved in 1975, and completed in 1976 and 1977. This would not have been possible without the willingness of my ex-employers, the Scottish Landowners' Federation, to grant me leave to return to Norway in November 1973 for an International Reindeer Modelling Seminar, and again for a further three-month study in autumn 1975. Miss Patricia Johnston of the S.L.F. and Mrs. Catriona Scott typed an excellent draft and final copy of the manuscript. Sections of the thesis were read and many helpful suggestions for improvement were made by Drs. J.D. Lockie, E. Gaare, and R.G. White. My sincere thanks to all the above-mentioned.

Finally, congratulations must go to my non-Rangifer relatives and friends for tolerating my often obsessive interest with reindeer behaviour and ecology for long periods over the last eight years.

CHAPTER ONE INTRODUCTION

"My worthy friend the late Dr. Ramsay, Professor of Natural History in Edinburgh, assured me that the horns of this species were found fossil in 1775 in a marl pit, five feet below the surface, near Craigton, in the shire of Linlithgow."

From Pennant's'History of Quadrupeds', 1781.



Remains of reindeer antler found at Raesgill, Lanarkshire, in 1849 (from Smith, 1869).

CHAPTER ONE INTRODUCTION

Over much of the tundra, mountains and taiga woodland of Scandinavia, reindeer (Rangifer tarandus) are semi-domesticated and managed as free-ranging herds. In the Northern Tundra, thousands of Lapp families rely on reindeer herding as their traditional and sometimes only life source. The only wild reindeer remaining in Scandinavia are found on various mountain ranges in Southern Norway. Some of these wild reindeer populations have no history of ownership of semi-domestication, while others have an ancestry of once-managed deer which have been allowed to revert to the wild state following the economic failure of a reindeer husbandry project.

In 1969 I was awarded a British Council Scholarship for wildlife studies in Norway. Having studied the effects on forest trees of browsing and fraying by roe deer (Capreolus capreolus) (Thomson, 1966), and with some experience of mountain red deer (Cervus elaphus) in Scotland, I was interested in pursuing a behaviour-related study on Norwegian wild reindeer in their mountain habitat.

1.1. OBJECTIVES

The precise objectives of the behaviour study were influenced by the particular aims of two organisations: Viltforskningen, earlier Statens Viltundersøkelser (The Norwegian State Game Research Institute), and their efforts in relation to wild reindeer research and management; and the Norwegian I.B.P./

I.B.P. Tundra Biome Project which in 1969 had begun its five year programme of research into tundra-type ecosystems.

Earlier research by Viltforskningen had shown that with an insufficient annual cull a wild reindeer population would expand to the extent that severe over-grazing of the range would occur, particularly on the lichens of the wintering areas (Gaare, 1968). This in turn would result in deteriorating physical condition of the animals, as evidenced from reduced carcase weights and jawbone lengths (Reimers, in prep.). Viltforskningen were therefore concerned to promote further research on the question of suitable carrying capacities for different reindeer ranges. A clearer understanding of the behaviour and social structure of reindeer herds in their natural habitats was considered essential in evaluating the impact of management policies on the populations and furthering understanding of reindeer ecology generally.

The Norwegian I.B.P. began studies in 1969 to investigate the production and energy flow of tundra ecosystems. The Hardangervidda mountain plateau was chosen as representative of arctic-alpine tundra and the wild reindeer population there was recognised as being the probable major component in the secondary production process, and therefore in need of investigation.

Cand. real. Eldar Gaare led and co-ordinated the research team study on the ecology of wild reindeer on Hardangervidda. Reindeer food selection, food intake and use of plant communities was a principal arm of the research, with most of this field work by /

Terje Skogland. Gøsta Hansson undertook most laboratory analysis of rumen samples from culled wild reindeer, and oesphageal fistula samples of experimental tame reindeer taken out into the field. To integrate with these animal-plant relationships being investigated, my study included systematic recording of activity, to determine the time spent on grazing and other activities at different months of the year. The results of these investigations have been reported in Gaare, Skogland & Thomson (1970); Gaare & Skogland (1971); Thomson (1971, 1973); Skogland (1974); Gaare, Thomson & Kjos-Hanssen (1975); Gaare & Skogland (1975); and Østbye et. al. (1975). (See Appendices 1, 2, 3 & 4). Study on the physical condition of reindeer from samples collected on Hardangervidda was held in abeyance while Cand. real. Eigil Reimers was in Alaska, and will shortly be reported (Reimers, in prep.). In the course of my fieldwork, group composition counts were made to assist management policies for hunting, associated with annual air census by Arne Krafft, Research Leader in Viltforskningen.

It is generally felt that individual responsibility within a team framework was a successful approach in terms of research results, development of new perspectives, and international co-operation in research. Following an international modelling workshop on Rangifer in Trondheim in 1973, a practical computer model to handle population parameters is now at the stage of management application, and can be adapted for other Cervid populations (information from Cand. real. E. Gaare, Viltforskningen, Elgester gt. 10., 7000 Trondheim). The activity /

activity times and feed intake data from Hardangervidda have become the essential inputs in investigating the relationships of energy balance through modelling (information from Dr. R.G. White, Institute of Arctic Biology, Fairbanks, Alaska). Comparative field work in 1972 at Prudhoe Bay, Alaska, on caribou by White, Thomson, Skogland and others (White et.al. 1975) has formed the basis for experimenting with activity and grazing models (further information from Dr. F. Bunnell, University of British Columbia, Vancouver).

1.2. FIELD WORK AND METHODS

Behaviour study through naturalistic observations of animals in the field works on the simple but effective principle of locating, following, and recording the behaviour of undisturbed animals over as long a period as possible. At all times of the year 10 x 50 binoculars assisted in the locating of reindeer herds and groups, while concentrated observation and recording was made with a prismatic spottingscope (x 25 to x 40) mounted on a tripod (Plate 1.). Selective use was made of a 35mm camera with telelens and a super-8mm x 10 movie camera.

At 15-minute intervals I made counts of the number of deer in a herd variously involved in grazing, lying, standing, walking, trotting, and running. Between these regular activity counts I recorded group sizes and composition as well as individual and social behaviour patterns. A field thermometer and hand anemometer measured ambient air temperatures and wind-speeds, with subjective assessment made of other /

other aspects of weather and the environment. Notebook recording was found to be more reliable than use of a portable casette tape recorder, because the batteries would tend to freeze.

I travelled on skis in winter in the course of observations, and often used a snow-scooter to set up a base camp in a suitably situated hytte (mountain cabin). A white camouflage suit over the outer layer of clothing was used in winter to allow a closer undetected approach towards herds. Observations at calving time corresponded with the major period of spring thaw, so that with deep "rotten" snow, snow-shoes were used as an alternative to travel by skis and on foot. In the snow-free period from June to mid-October herds travelling 15 - 20 km daily were followed on foot. Often on pitching tent in the evening the deer would subsequently graze and move around the camp area.

From the onset of study I intended to spend ten days per month in the field for intensive observations. The extent to which this was achieved is shown in Table 1.1. In summer with easier access to supplies it was possible to spend even longer per field trip. Over the two years of systematic study in Norway, 200 observation days allowed over 800 hours of actual observation of wild reindeer, and some 2,400 regular 15-minute activity counts. This prolonged observation time was possibly due to a combination of favourable circumstances:

(1) A social species such as reindeer living in an open treeless /

Table I.I Systematic field observations of the behaviour and activity of wild reindeer in Norway.

Mountain Range	Main Location	Dates of reindeer observation (incl.)	Season	*
North Ottadalen	Lordalen	September 16-27,1969	Rut	R
Snøhetta	Reindøl	October 15-22, 1969	Rut	R
Snøhetta-Knutshø	Hjerkinnhoi	November 21-29,1969	Early Winter	
Hardangervidda	Smaaroi	January 22-29, 1970	Early Winter	GSH
Forelhogna	Sandfjell	February 28-March 5,1970	Mid-Winter	H
Hardangervidda	Krossvassh'd	April 11-19, 1970	Late Winter	GSH
North Ottadalen	Asbjørndalen	May 9-14, 1970	Calving	
Hardangervidda	Olavsdalen	May 23-27, 1970	Calving	S
Hardangervidda	Central	July 6-17, 1970	Early Summer	
Hardangervidda	Central	August 2-30, 1970	Summer	J
Hardangervidda	Central	September 1-8, 1970	Hunt	J
North Ottadalen	Lordalen	September 16-27, 1970	Rut	J
Hardangervidda	Halstjørn	October 14-18, 1970	Rut	S
Hardangervidda	Halstjørn	December 1-9, 1970	Early Winter	GS
Hardangervidda	Sønstevatn	January 20-27, 1971	Early Winter	S
Hardangervidda	Sønstevatn	March 2-8, 1971	Mid-Winter	H
North Ottadalen	Asbjørndalen	May 5-9, 1971	Calving	
Hardangervidda	Olavsdalen - Haarteigen	May 23-June 1, 1971	Calving	S
Hardangervidda	Central	July 1-29, 1971	Early Summer - Summer	S

* Observations assisted by Anne Jackes (J).

Complementary field studies by T. Skogland (S), G. Hansson (H), E. Gaare (G), and E. Reimers (R).

Comparative observations:

Prudhoe Bay, North Slope, Alaska.(Caribou)	June 25 - August 2, 1972.
Glenmore, Cairngorm, Scotland.(Domestic Reindeer)	July 23, 1969.
" " "	February 9-13, 1972.
" " "	May 29 - June 5, 1972.
" " "	September 28 - October 3,1972.
Reindøl, Snøhetta, Norway.	December 1-4, 1975.

less habitat allows ready contact with, and continuous observation of large numbers of animals. Herds of several thousands, hundreds, and individuals or groups of less than ten, were variously observed for long periods. The total number of reindeer observed on each field trip varied, but was never less than 10% of the population, and as high as 80%.

(2) Because of differences in the timing of the breeding cycle of Norwegian wild reindeer on different ranges, it was possible to observe 4 rutting seasons and 4 calving seasons in the course of the study period (Table 1.1.).

(3) Comprehensive additional observations on activity and behaviour for the 1970 summer, hunt and rut, were made by field assistant, Anne Jackes. Gøsta Hansson also assisted me in the recording of activity on some winter trips (Table 1.1.).

(4) Close liaison with Eldar Gaare and Terje Skogland studying range ecology and animal-plant relationships, allowed a sharing of facilities and equipment on many trips.

In 1972, at the invitation of the Institute of Arctic Biology, Fairbanks, Alaska, with funds from the I.B.P. Tundra Biome of the U.S.A., I made comparative observations of the summer behaviour and activity of caribou on the North Slope at Prudhoe Bay (White et. al. 1975, and Appendix 7). In the 40 days of observation in summer 1972 caribou were observed for some 130 hours with 450 15-minute activity counts.

Also, with the approval of the Reindeer Council of the U.K., visits /

visits were made to the Scottish tame reindeer herd at Glenmore, Cairngorms, during winter, calving, and the rut (Table 1.1.). As this thesis relates to the behaviour of wild reindeer in Norway these additional observations in Alaska and Scotland are not incorporated, but are specifically referred to, notably in Chapter 9.

Wherever valid, quantitive data has been tested for statistical significance.

1.3. THE APPROACH TO BEHAVIOUR STUDY

Behaviour studies on mammals have often utilised concepts borrowed from the analysis of behaviour patterns of invertebrates, or "lower vertebrates" such as fish and bird species. For example, it has often been tacitly assumed that behaviour is a relatively fixed and species-specific characteristic, which can therefore be tested and analysed through a variety of experiments on caged or penned animals. However, when knowledge of the performance of such an animal as part of a population in its natural environment is scanty or lacking, ethological "conclusions" on the instinctiveness of behaviour or "intelligence" of the animal, can be misleading. With the state of knowledge of reindeer in their natural habitats in 1969, this was not therefore considered a satisfactory approach.

From evolutionary theory, it follows that the performance of an animal is the response to its social and physical environment which is tending to maximise its chances of survival for breeding. Through natural selection, non-adaptive behaviour /

behaviour should have gradually been eliminated. The behaviour of an animal will be partly determined by a learned response to influences in its natural environment and partly through innate patterns which may be considered as "evolutionary learning". In reindeer, as in many other mammals, the behaviour associated with courtship is displayed as relatively fixed patterns, so that the rut appears as a heavily ritualised performance, and to a large extent independent of environment. In many other social situations, such as when a herd is moving away from a potential predator, reindeer show a flexible response as an adult animal emerging as leader makes instant decisions which effectively increases the herd's chances of survival. While it will be seen that a few individual behaviour patterns may appear as characteristic of the species as for example is a morphological characteristic, flexibility in behaviour appears as a general response to a varied and changing social and physical environment. This also means that differences in social relationships and group responses may be expected in populations of the same species living in different environments.

In this study, analysis of activity at different seasons indicated that in common with other ruminant populations, wild reindeer showed a short-term rhythm of alternating grazing and lying periods based on the feeding-rumination cycle, and at certain times of the year a long term 24-hour rhythm with activity synchronised to changing light conditions (Thomson, 1973). Superimposed on this basic activity pattern are changes dependent on seasonal changes in the deers' /

deers' biology, food supply, cover in the habitat, the weather, and other animals. It was concluded that for a population in a different area the activity pattern would be similar only in so far as environmental influences afforded similar pressures (Thomson, op. cit.). The evidence for a similar flexibility in social organisation and social relationships in response to the environment is considerable and is mainly presented in Chapter 7.

At the start of this study in autumn 1969, knowledge of the behaviour of the wild reindeer was restricted to incidental observation by biologists in the course of other studies, and anecdotal reports from local people and hunters. With his long experience of reindeer, Veterinarian Sven Skjenneberg had included many behavioural aspects in his book on domestic reindeer husbandry (Skjenneberg & Slagsvold, 1968). However, it was uncertain the extent to which wild reindeer differed in their behaviour. In Sweden, behavioural studies on semi-domesticated woodland reindeer were being undertaken by Espmark (1964a, b; 1968). In North America, aspects of caribou behaviour had been studied by Banfield (1954), Pruitt (1959, 1960, 1966), Lent (1965a, b; 1966), de Vos (1960), and Henshaw (1968a), while monographs on the ecology of caribou by Kelsall (1968), Skoog (1968), and Bergerud (1971) had included much information on behaviour. Although caribou and reindeer had by this time been classed as the same species (Rangifer tarandus) by Banfield (1961), Pruitt (1960) had warned against interpreting reindeer and caribou behaviour within the same frame of reference.

From /

From this background I hoped to observe and record as much of the behavioural repertoire of Norwegian mountain reindeer as possible in the course of study, and relate it to these earlier studies on caribou and domestic reindeer as well as the original objectives of study. I was aware that much could be learned from field observation of ungulates in open habitats as evidenced, for example, from the pioneer studies of red deer in the Scottish Highlands by Darling (1937), and elk in Wyoming by Altmann (1952).

Within the period of study and up to the present time knowledge on Rangifer behaviour in particular, and ungulate behaviour in general, has increased considerably. In particular, English translations of earlier Russian work have become available. Baskin (1970) reports on the behaviour, and Zhigunov (1968) and Egorov (1965) on the ecology of reindeer populations in the U.S.S.R., with some reference to wild as well as domestic reindeer. In Sweden, Espmark (1971a, b, c; 1975) has published his detailed studies on mother-young relationships and acoustic communication. Further caribou behaviour studies have been reported by Bergerud (1974a, b), Child (1973), Miller et.al. (1972, 1975), Ericson (1975) and Bubenik (1975b). Aspects of the behaviour of wild reindeer have been included in reports by myself (Appendices 1, 2, 3, 5 & 6) and Skogland (1974, 1975). Since 1971 Skogland re-arranged his study of reindeer-plant relationships on Hardangervidda to incorporate recording of behaviour and activity, so that over the next 2½ years further behaviour observations were made (Skogland, 1974; and in prep.). The main focus for behavioural field work has now switched to the /

the Snøhetta range, where it is hoped to mark individual reindeer and follow their movements (Skogland, pers. comm.).

Two international symposiums, "The Behaviour of Ungulates and its Relation to Management" at the University of Calgary, Alberta, Canada, in 1971 (proceedings published 1974), and the First International Reindeer/Caribou Symposium at the University of Fairbanks, Alaska, 1972 (proceedings published 1975), have stressed and illuminated the importance of ecological studies of behaviour in relation to wildlife management.

Since this work may be the first comprehensive behaviour study of wild reindeer, I have designed it to catalogue all aspects of behaviour, but have laid particular emphasis on those aspects which have not so far been fully recorded or recognised. As well as complying with the specific objectives of study, I hope it may act as a source material for management of the wild reindeer populations in Norway, and form the basis for a comparison with reindeer and caribou populations in other environments and with other ungulates in general, particularly populations in open tree-less habitats.

Except where otherwise specified, the results and their interpretation are my own. Chapters 2 and 3 introduce the study areas and populations; Chapter 4 presents a broad picture of the wild reindeer's life cycle and behaviour; Chapters 5 and 6 detail the various individual and social behaviour patterns; Chapter 7 considers the influence of environmental influences on social behaviour and organisation; Chapter 8 considers activity /

activity as related to energy expenditure; and Chapter 9 discusses similarities and differences in behaviour between different Rangifer populations.

CHAPTER TWO STUDY AREAS

"Remains of reindeer antlers in Scotland have been found in several localities in Ross-shire, Sutherland, Caithness, Orkney, Perthshire, Dumbartonshire, Lanarkshire, Linlithgowshire (West Lothian), Ayrshire, and Dumfriesshire."

From J.A. Smith's 'Notice of remains of the rein-deer (Cervus tarandus) found in Ross-shire, Sutherland and Caithness, with notes of its occurrence throughout Scotland'. The Proc. Soc. Antiq. Scotland 8, 1868-69.

Reindeer antler found in a Pictish broch at Keiss, Caithness, around 1865.(from Smith, 1869).

CHAPTER TWO STUDY AREAS

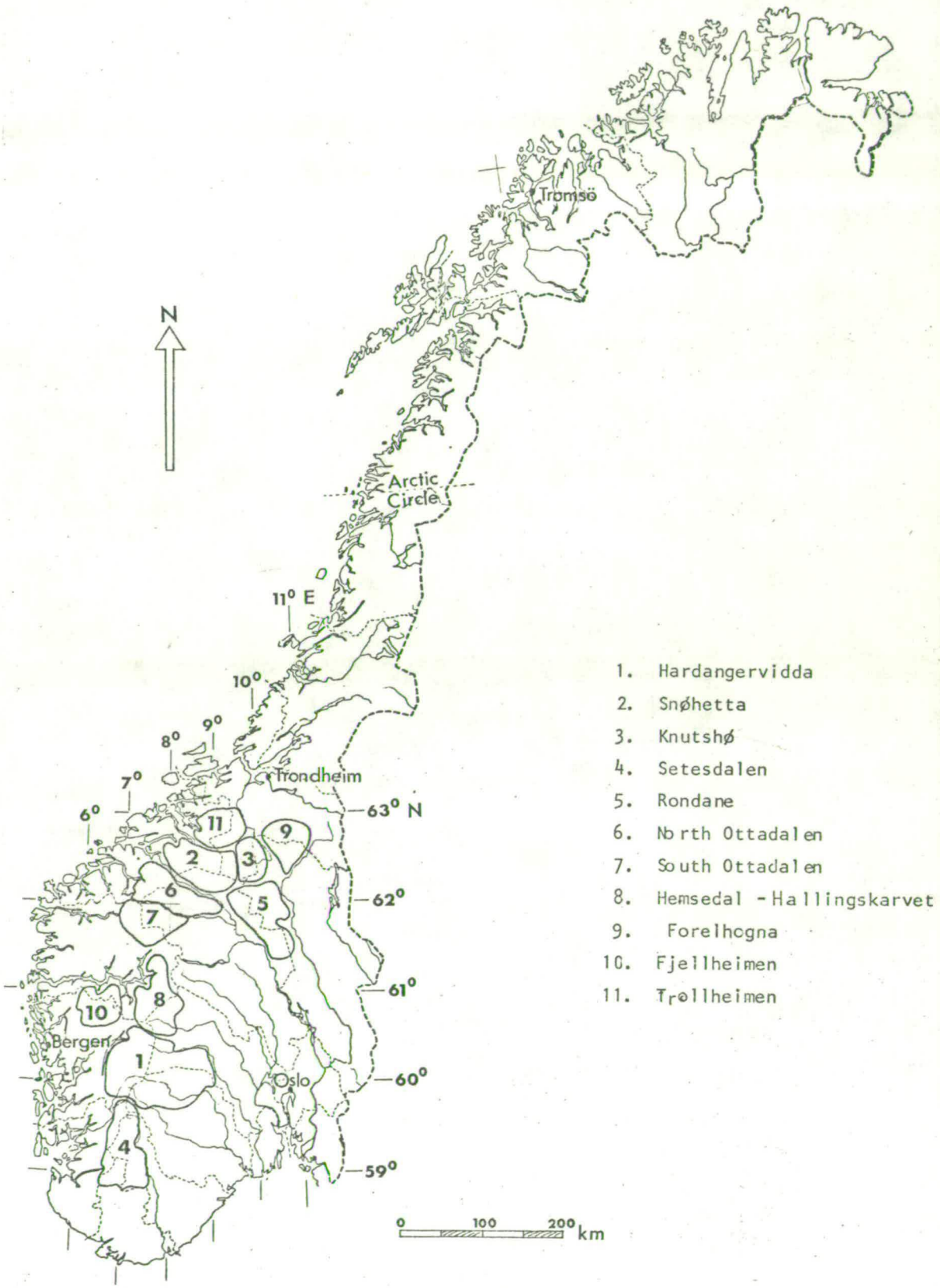
2.1. REINDEER RANGES IN SOUTH NORWAY

Apart from a small herd of woodland reindeer on the Finland-U.S.S.R. border (Rangifer tarandus fennicus), the only wild reindeer remaining in Scandinavia live on mountain ranges in Southern Norway (Rangifer tarandus tarandus) (Map, Fig.2.1.). The vegetation of this mountain environment has been described as Arctic-Alpine "tundra", since at these northern latitudes, 59°N to 63°N, land above 1,000 m gives rise to plant communities closely akin to those of the Arctic tundra north of 66°32'N.

Tundra-type flora and fauna are adapted to surviving long cold winters with relatively rapid growth and reproduction in the short summer season. The tundra zone is clearly at the cold and dry end of climatic range (see Fig. 2.2.). The characteristic determinants of the ecosystem are not only low temperatures and drought stress, but also the extreme fluctuation in seasonal photoperiod, the prevailing radiation regime, and the availability of nutrients (U.S. Tundra Biome, 1971). The distribution of tundra-type environments in the Arctic and Sub-Arctic regions of the world is shown in Fig. 2.3.

The mountainous area of South Norway is dissected and divided into separate ranges by wide glaciated valleys, fjord cliffs, glaciers, and by man-made barriers such as roads and railways. On 8–9 of these ranges live more or less discreet populations of wild reindeer, with a few further ranges /

Fig. 2.1 The principal wild reindeer ranges of Norway.



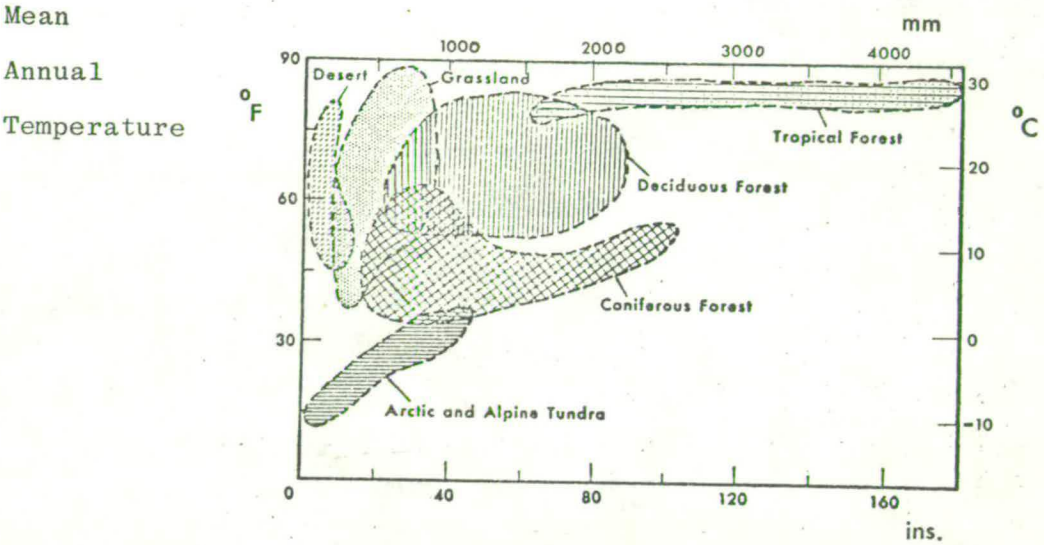
1. Hardangervidda
2. Snøhetta
3. Knutshø
4. Setesdalen
5. Rondane
6. North Ottadalen
7. South Ottadalen
8. Hemsedal - Hallingskarvet
9. Forelhogna
10. Fjellheimen
11. Trollheimen

ranges holding semi-domestic herds. A continuing programme of investigation by Viltforskningen (The Norwegian State Game Research Institute) for several years has been to analyse differences between ranges in regard to the inter-relationships between primary productivity and dietary quality of the vegetation, the density of reindeer population, and reindeers' body condition (Gaare, 1968; Reimers, 1972a).

The main wild reindeer ranges are Hardangervidda, Dovre (Snøhetta-Knutshø), Setesdalen, North and South Ottadalen, Rondane, Hemsedal-Hallingdal, Forelhogna, and Fjellheimen (Table 3.1). These, with a few minor areas, comprise some 40,000km^2 with a total population varying between 15,000 and 50,000 reindeer, presently 30-36,000 (from Holthe, 1976).

Considering the Alpine region of South Norway as a whole there is a climatic and vegetation gradient from west to east. Ranges in the more continental drier East generally display a rich growth of Cladonia spp. and Cetraria spp. lichens. In the Western regions the maritime influence results in more snow, and coupled with the wetter summers this develops grasses or mosses at the expense of these "reindeer lichens". Thus, while the Easterly ranges of Rondane and Forelhogna are rich in lichen-heath communities, Hardangervidda and Fjellheimen have extensive meadow communities of grasses and sedges. On any one range, reindeer tend to concentrate on the continental sector in winter where lichen-heaths predominate and utilise the oceanic areas at calving time and in summer. On most ranges this results in /

Fig. 2.2 Relationship of the major biomes to annual precipitation and temperature.



(From U.S. Tundra Biome, 1971)

in an east-west movement of reindeer in spring (e.g. Snøhetta - Gaare, 1968; Hardangervidda - Gaare, Skogland & Thomson, 1970).

Other differences in the type and condition of vegetation between ranges can be attributed to differences in latitude, topography, geology, and herbivore grazing pressure, particularly as a result of fluctuations in reindeer numbers. Snøhetta suffered a reindeer population explosion in the early 1960's which severly reduced the lichen cover (Gaare, 1968), while essentially similar ranges to the immediate south (North Ottadalen) and east (Rondane) received only moderate grazing utilisation, and maintained their lichen biomass. The main study area of Hardangervidda is described below, while particular characteristics of other ranges visited, notably Snøhetta, North Ottadalen and Forelhogna, are outlined in relation to their appropriate reindeer populations (See Chapter 3).

2.2. HARDANGERVIDDA

2.2.1. Situation and Topography

The Hardangervidda is said to be the largest mountain plateau in Europe, with an approximate area of 10,000km^2 (Østbye, et.al., 1975). It is situated in the south west sector of the alpine region of South Norway at 60^o 10'N, 7^o 30'E (Map, Fig. 2.4.). The area is bordered naturally on the west by sheer cliffs dropping down to the sea level of Hardangerfjord and its tributaries, in the north by the Hallingskarvet Escarpment, while to the east the alpine terrain /

Fig. 2.3 The Arctic and sub-Arctic distribution of tundra-type vegetation.

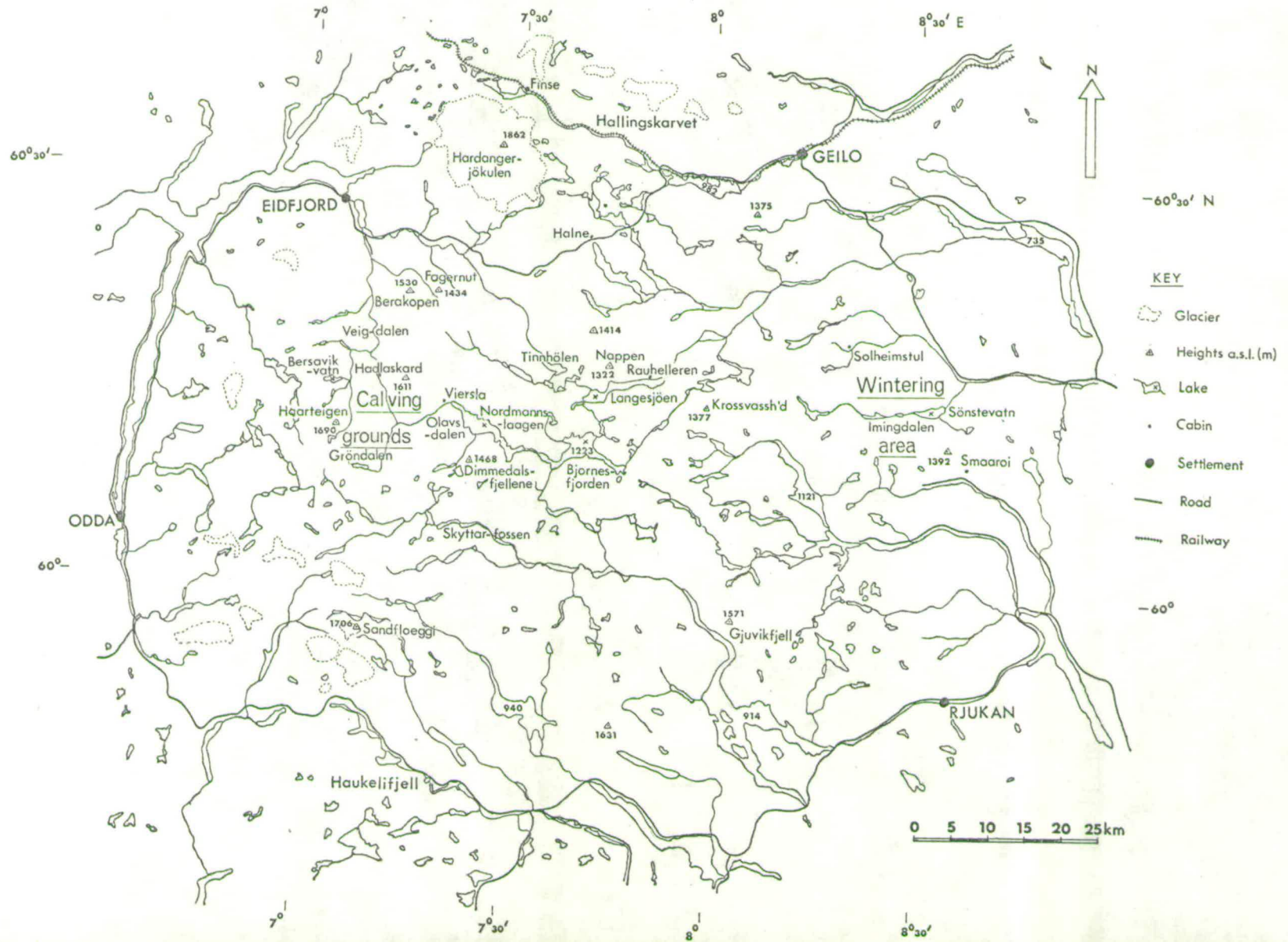
(From Lesnický a Myslivecký Atlas; Praha, 1955)

terrain gradually slopes below 1,000m into sub-alpine birch-woods, coniferous forests, farms and villages. The natural borders to the south are less distinct; the contiguous mountain terrain of Haukelifjell leading on to the Setesdalen Range is separated in places only by the Odda-Rjukan road. While the reindeer population on Hardangervidda is known to be a fairly discreet unit, occasional movement between neighbouring ranges does occur since roads and railways over alpine terrain do not form impassable barriers to reindeer movement (Krafft, Gaare and Reimers, 1970).

Hardangervidda is topographically variable. In the central part the terrain is most plateau-like, with many lakes and mires at 1,200-1,250m, and undulating slopes and hills up to 1,400m (Plate 2). Moving west the terrain becomes progressively more rugged with mountains rising to over 1,600m with steep-sided valleys. Small permanent snowfields are situated on these high mountains in the south west, while north of the Eidfjord-Geilo summer road, the Hardangerjøkulen Glacier rises to 1,862m. East of central Hardangervidda the hills are less rugged and are progressively dissected by east-west oriented valleys which revert to sub-alpine birchwoods below approximately 1,000m. The many rivers and lakes typical of tundra-type habitats appear to comprise some 8-9% of the Hardangervidda land surface, glaciers 3%, while the remaining terrain is a matrix of heath, mire and meadow communities with abundant boulders, rocks, and scree formations on steep slopes and summits.

2.2.2. Climate /

Fig. 2.4 Hardangervidda mountain plateau; indicating place names mentioned in the text.



2.2.2. Climate

Because of its south-westerly position the climate is more oceanic than neighbouring ranges to the north and east. This results in proportionately more cloud, wind, and precipitation, producing relatively mild winters with a heavy snowfall and cool, wet summers with a high relative humidity. The climate parameters in 1970 for Finse, a north-central meteorological station at 1,200m on Hardangervidda (Fig. 2.4.), are shown in Table 2.1.

Most of Hardangervidda is free of snow for only 4 months of the year. This short snow-free season is characteristically wet with 100 days of rainfall accounting for most of the average 1,000mm of precipitation. While the western border of the plateau lies directly above the sea fjord and some 80km from the open North Sea, the eastern border is fully 200km from the North Sea. Annual precipitation thus ranges from 1,500mm in the west to 500mm in the east of Hardangervidda (Østbye et. al., 1975). Average monthly temperatures range from -15°C to +8°C, although air temperatures can fall to below -20°C in winter and rise to over +20°C in summer.

2.2.3. Geology and Soils

Over most of Hardangervidda the bedrock is part of the ancient Pre-Cambrium Shield, the rock mass which forms the sub-structure of the European Continent. Centuries of erosion by ice, water and wind on this hard rock has formed a characteristic undulating and rocky terrain (as in Sutherland, Scotland). The rocks consist for the most part of /

Table 2.I Climatic Features in 1970 at Finse, Hardangervidda (60°36'N, 7°30'E; 1200m).

	J	F	M	A	M	J	J	A	S	O	N	D	Yearly total/ Monthly mean
Average Air Temp.(°C)	-11.3	-14.7	-8.8	-6.8	+1.1	+7.9	+5.5	+7.8	+2.9	-1.1	-6.5	-7.2	-2.6°C
Max. Daily Air Temp.(°C)	-7.5	-10.4	-5.3	-1.4	+5.3	+13.4	+8.8	+11.2	+5.6	+1.4	-3.5	-4.0	+1.1°C
Min. Daily Air Temp.(°C)	-15.8	-19.6	-12.3	-12.0	-2.1	+2.3	+3.4	+4.6	+0.9	-3.5	-9.9	-11.0	-6.2°C
Prevailing Wind Direction	SE	SSE	NNW	NNW	NNW	NNW/ SSE	WSW	SSE	NW	NW	ESE	NW	NNW
Relative Humidity (%)	85	88	87	84	83	81	90	86	86	90	90	87	86%
Precipitation (mm)	42	18	30	22	49	84	180	51	138	83	110	75	882mm
No. of days with rain	1	0	1	3	7	9	29	16	18	9	2	5	100 days
" " " snow	20	17	23	12	5	2	1	0	4	20	22	20	146 days
" " " wind > Beaufort 6	3	0	6	0	2	0	0	0	4	14	14	18	61 days
" " " snow cover	31	28	31	30	31	0	0	0	0	14	30	31	226 days

Data extracted from Norsk Meteorologisk Årbok, 1970.

of granites and gneisses which have given rise to an acid nutrient-poor soil.

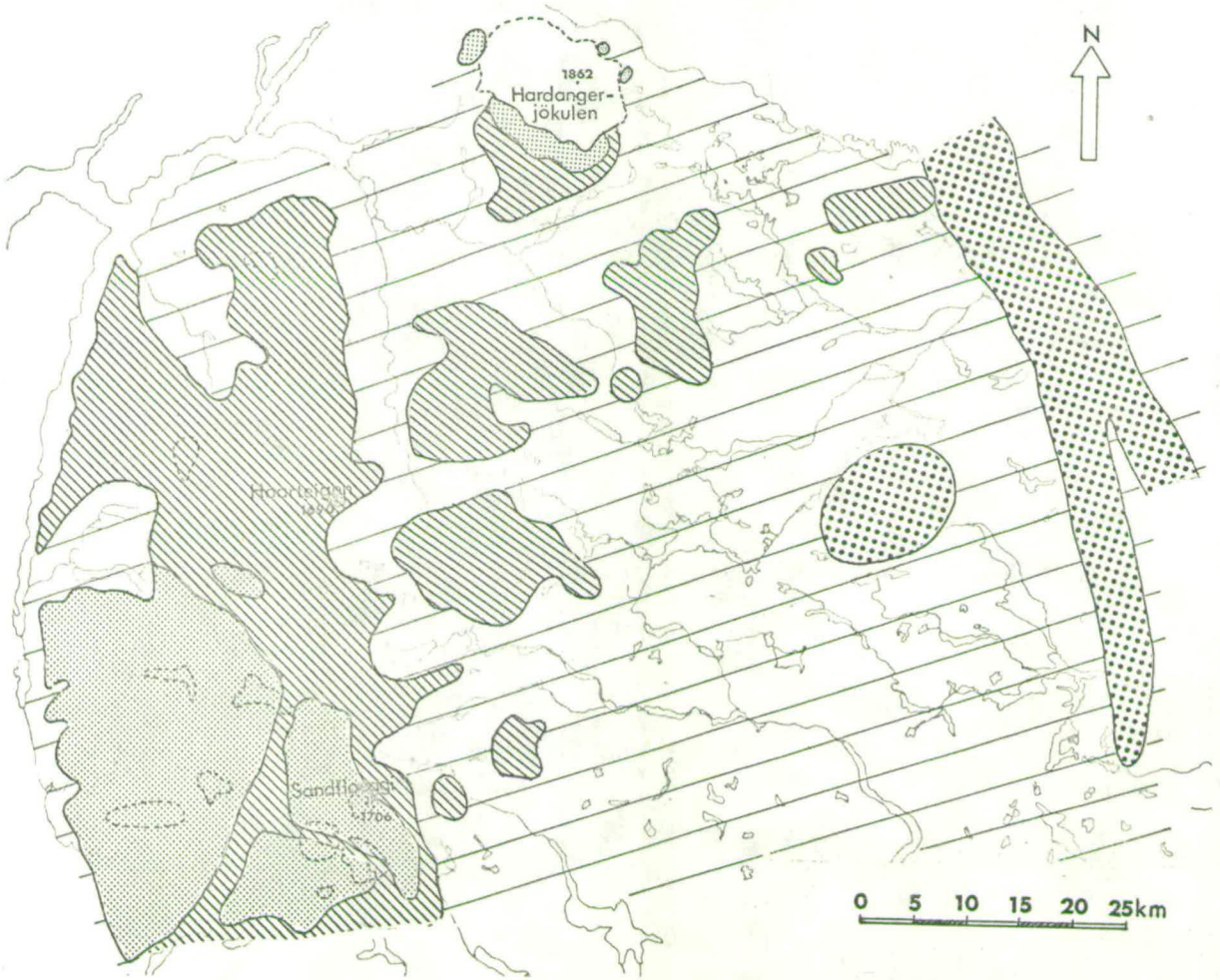
On western Hardangervidda folding movements in the Caledonian era created mountains of Cambro-Silurian sediments (Map, Fig.2.5). These rocks are predominantly slates and phyllites, which often contain limestone and consequently produce a relatively base-rich soil in these areas and a calciphile vegetation. Also in the Caledonian era various igneous intrusions occurred to form the highest mountains on Hardangervidda, namely Hardangerjøkulen (1,862m), Sandfloeggi (1,706m), and Hårteigen (1,690m) (Fig.2.5).

The ice cap retreated some 9,000 years ago, further scarring and eroding the landscape and depositing glacial moraines. Johansen (1973) points out that the phyllite content of the moraine is of particular interest because of its influence on plant species and growing conditions, but generally the ice-moved material has not been shifted far from its parent bedrock (Fig.2.5).

The sandy and gravelly soils are typically shallow and well-drained. In the areas where drainage is impeded, organic soils of up to 30cm or more of peat have developed, whereas normally a shallow podsolic profile is evident. Unlike the true Arctic tundra, there is no permafrost, one reason being that the snow cover is relatively deep and stable (Østbye, et. al., 1975).

2.2.4. Plants /

Fig. 2.5 The solid geology of Hardangervidda.



(Mainly from map in N.O.U. 1974, 30A; Miljøvern-departement, Oslo.)

ROCK TYPES

- Cambro - Silurian sediments
- Igneous intrusions
- Gneisses and Granites
- Quartzite / Conglomerate
- Glacier

2.2.4. Plants

The plant distribution in the alpine areas of South Norway is typically a varied mosaic, quite unlike the Calluna-dominated heaths and moors of the Scottish Highlands. Exposure and moisture relations are critical factors in determining species distribution and both factors are dependent on the prevailing snow cover. Snow falling in early winter is soon blown off summits and ridges and deposited in more sheltered slopes and hollows where it accumulates. This pattern repeated annually in the same area has resulted in a marked zonation of species and plant communities. Only those plants which can survive conditions of exposure, drought, and severe frost, are found on the wind-blown ridges and summits. From these exposed lichen heaths there are progressive floristic changes down to grassy meadows, mires and snow bed areas. On these latter areas the accumulated snow is so late in thawing that only plants such as Salix herbacea, which can tolerate the shortest of growing seasons, and often badly drained soli-fluction conditions,can survive. The relative abundance of each of these main types of plant communities on Hardangervidda, their characteristic species, and their relationship to the depth of snow cover and duration of growing season, is summarised in Table 2.2. (from infor-mation in Gaare and Skogland, 1971; and Østbye et.al., 1975).

Altitude is a further main factor in varying the plant distribution. On ascending from the birch zone which is classed as sub-alpine, there is a characteristic reduction in the number of plant species from low alpine, mid-alpine, through /

Table 2.2 Simplified scheme of the characteristics of plant communities on Hardangervidda.

Plant community	% Cover	Depth of winter snow	Average duration of growing season	Common species	Species characteristic of base-rich sites
Lichen heath	53%	50cm-1m	c.120 days	Cladonia spp Cetraria spp Betula nana Carex bigelowii Vaccinium vitis-idaea Festuca ovina	Dryas octopetala
Meadow	19%	1m	c.100 days	Deschampsia flexuosa D. caespitosa	Anthoxanthum alpinum
Mire	22%	2m+	<100 days	Eriophorum angustifolium Sphagnum spp Rubus chamaemorus	Salix lapponum Carex spp
Snow-bed	6%	several metres	0-60 days	Salix herbacea	Salix herbacea

(Mainly derived from information in Østbye et. al., 1975; & Gaare and Skogland, 1971).

through to high alpine zones (Gjaerevoll and Jørgensen, 1967). On Hardangervidda low alpine communities often extend from the tree line to around 1,200m, mid-alpine to around 1,400m, and high alpine beyond this elevation.

In the low and mid-alpine zones in the east of Hardangervidda, with an acid soil (pH. 4.5-5.0) and a relatively continental climate, plant communities are predominantly of the lichen-heath type. On the most exposed windblown tops and ridges abundant lichen, particularly Cetraria nivalis and the ericaceous dwarf shrubs, Arctostaphylos alpinus, Empetrum hermaphroditum and Vaccinium vitis-idaea are typical. Moving down from the ridges the lichen-heath slopes holding more snow are commonly carpeted with Cladonia mitis and C. alpestris with abundant dwarf birch Betula nana. In areas with snow depth of over 1m grassy meadow communities are typical, characteristically holding Deschampsia flexuosa and D. caespitosa. The flattest areas of deep snow are usually wet mires in summer containing Eriophorum angustifolium, Rubus chamaemorus, or shrub willow Salix spp., and in the most nutrient-deficient mires Sphagnum spp. moss. Where the snow fall lies longest in summer, notably in the western mountains, small snowbed communities are widespread, characteristically dominated by the small herbaceous willow, Salix herbacea.

Over much of the western sector the base-rich soil derived from phyllite rock develops eutrophic communities. On the exposed ridges Dryas octopetala dominates the heath. Lower down the slopes and flats rich grassy meadows (pH. 5.5-6.0) hold /

hold Anthoxanthum alpinum, Poa alpina and a variety of calciphile herbs, while the wet meadows and mires contain shrub willows, notably Salix lanata and particular calciphile sedges, Carex spp..

Detailed study on the primary production of the plant communities has been completed by the I.B.P. "Tundra Biome" Research on Hardangervidda (I.B.P. 1971; Østbye et.al., 1975). Complementary description of plant communities, their phenology, and their seasonal use by reindeer has been an essential aim of the Viltforskningen Reindeer Research (Gaare et.al., 1970; Gaare & Skogland, 1971; Skogland, 1974; Gaare & Skogland, 1975). This brief and necessarily simplified description above is mostly derived from these sources.

2.2.5. Animals

While the reindeer is by far the most conspicuous, characteristic and economically important member of the fauna on Hardangervidda, many other species are equally adapted to life in the mountain environment, and may have a greater impact on the total ecosystem energy flow. For example, whereas a population of reindeer stabilised at 10,000 before calving will consume an estimated 42kJ per m^2 from the primary annual production, the root vole (Microtus oeconomus)population in a cyclic "high" may eat 121kJ per m^2; and as an example of the impact of an invertebrate herbivore the chrysomelid beetle (Melasoma collaris) may consume 63kJ per m^2, entirely from Salix herbacea (Østbye et.al., 1975).

The /

The wolf (Canis lupus) was a major predator on Hardangervidda up to about 50 years ago, but is now rare throughout Norway. The wolverine (Gulo gulo) is now uncommon, and may have suffered not only persecution, like the brown bear (Ursus arctos) and lynx (Lynx lynx) which survive locally in birch and coniferous forests, but may have relied on scavenging from wolf kills.(E.Reimers, pers. comm.). The red fox (Vulpes vulpes) can be seen throughout the mountains, while the Arctic fox (Alopex lagopus) is said to breed in areas of Hardangervidda more or less regularly in the peak rodent years (Østbye et.al., op.cit.). The stoat (Mustela erminea) and the weasel (Mustela nivalis) are also rodent predators and are not infrequently seen.

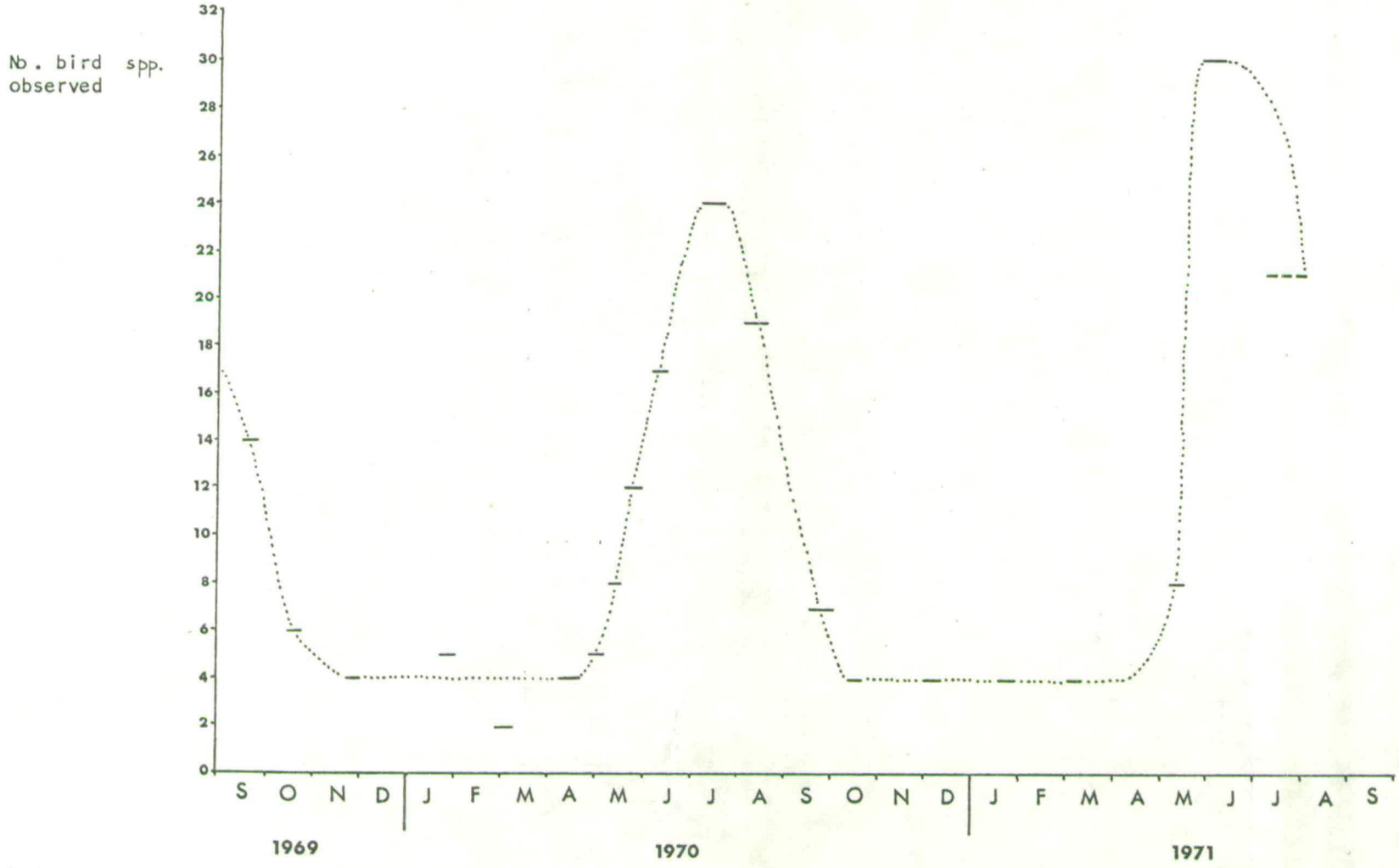
In common with other northern areas the rodent populations are distinctly cyclic. In 1969/70 the root vole (Microtus oeconomus) population was at a peak on Hardangervidda, while in 1966/67 and 1973/74 the lemming (Lemmus lemmus) was the most abundant species. Other rodents which breed are the grey-sided vole (Clethrionymus rufocanus), the bank vole C. glareolus), and the short-tailed vole (M. agrestis). In summer the Microtus species typically inhabit grass and herb communities; the Clethrionymus species live in the drier stonier habitat; while lemmings live in both wet and dry habitats (Østbye et.al., op. cit.). Both voles and their mustelid predators were often seen under hyttes. The Arctic hare (Lepus timidus) was not as often seen as is usual in many parts of the Scottish Highlands, and was most frequent in the low-alpine zone.

The /

The bird life on Hardangervidda and other mountain ranges is sparse in winter with only four to five resident species, then virtually explodes in summer with a recorded total on Hardangervidda of 61 breeders, 31 migrants, and 22 visitors (Østbye et.al., op.cit.). This extreme seasonality was very obvious in the course of the monthly field trips in this study (see Fig. 2.6.).

In winter the only species regularly seen were ravens (Corvus corax), ptarmigan (Lagopus mutus), at least one golden eagle (Aquila chrysaëtos) seen per trip, and flocks of snow buntings (Plectrophenax nivalis), especially in late winter. Willow grouse (Lagopus lagopus) and flocks of redpolls (Acanthis flammea) are found in low-alpine heaths above the birch. The bird population builds up rapidly in May as the spring thaw moves up the mountains (Fig. 2.6.). In late May common gulls (Larus canus) fly in to the central calving area to scavenge, along with ravens, on the placental remains left by reindeer mothers. By early June as many as 30 species may be readily recorded, out of an overall total of 52 species I identified on alpine habitat in the course of the reindeer study. Characteristic breeding birds observed in summer included the dotterel (Eudromias morinellus), golden plover (Pluvialis apricaria), wheatear (Oenanthe oenanthe), Lapland bunting (Icarius lapponicus), shore lark (Eremophila alpestris), and in semi-aquatic habitats various waders such as purple sandpipers (Calidris maritima), Temminck's stint (C. temminckii), dunlin (C. alpina), as well as various species of duck, crane (Megalornis grus), and the long-tailed skua (Stercorarius longicaudus). Of the predatory species the rough-legged buzzard /

Fig. 2.6 Seasonal variation in the number of bird species observed in alpine habitat in south Norway.



buzzard (Buteo lagopus) had particularly regular breeding sites in the two years of observations (notably at Halne, Fagernut, and Rauhelleren; Fig. 2.4.). The commonest falcon was the kestrel (Falco tinnunculus), while the short-eared owl (Asio flammeus) was occasionally seen, and the snowy owl (Nyctea scandiaca) rarely, dependent as it is on cyclic "highs" in the rodent populations.

The flying insects which were most often seen on Hardangervidda included the mosquitoes (Cul icidae), which attack both man and reindeer in the summer (see Chapter 7.7.), crane flies (Tipulidae), butterflies (Lepidoptera), bees (Bombula), and hunting wasps (Ichneumonoidea). On the ground various spiders (Araneida) and beetles (Coleoptera) were common. The biomass and productivity of these and other invertebrates such as the soil-living spring-tails (Collembola), mites (Acarina), nematodes and enchytraeids have been studied under the I.B.P. programme, and the results summarised in Østbye et.al. (1975).

As well as the wild life, there are domestic herbivores which are brought in summer to the saeters (sheilings) on the Vidda. In addition to the several thousand sheep, there are often smaller herds of goats and cattle attached to the saeters (Livingstone, 1973). The impact of these domestic grazing ruminants has not yet been analysed but if competition for summer pasture exists with reindeer it must be largely limited to the areas around these valley saeters and roads. However, I have observed sheep on Berakopen in July at 1,450m, some 100m above large grazing herds of reindeer. /

reindeer.

2.2.6. Human Influence

Man's use of the Hardangervidda for hunting and fishing dates back to at least Stone Age settlements older than 8,000 B.C., which is less than 1,000 years after the Ice Cap had thawed (Johansen, 1973). The later Iron Age settlements in the Hardangervidda mountain valleys produced iron agricultural implements as well as the spears and arrowheads for hunting (Johansen, op.cit.). In historic times the plateau has been used for grazing of domestic animals including tame reindeer husbandry (see Ch. 3.).

Paradoxically, although there is no year-round settlement on Hardangervidda today, man's use of the area has never been more potentially disruptive to the natural ecosystem. In particular the impact of tourism and plans for further hydro-electric power are seen as major threats to the continued existence of Hardangervidda as a wilderness area. Both of these factors intimately concern the wild reindeer population.

Since our observations on the calving grounds in 1970 and 1971 (see Chs.5.4 & 7.5.), and in subsequent years, Skogland has cogently argued that the proposed flooding of the Veigdalen Valley would seriously reduce suitable calving habitat and influence post-calving movement and grazing possibilities (Skogland, 1973). Consequent upon the comprehensive I.B.P. ecological research on Hardangervidda, Østbye et.al. (1975) state that "the conservation of Hardangervidda /

Hardangervidda is not just a dispute about petty local interests" and with particular reference to the hydro-electric proposals they emphatically disassociate themselves from "the criteria and poor ethical principles behind the present lopsided policy of economic growth, which in its destructive course is now wrecking Hardangervidda".

In the long term, however, recreation and tourism may have as great an impact as the proposed hydro-electric schemes. At the present time there are 36 National Tourist Hyttes on Hardangervidda (all the size of Youth Hostels or small hotels) with marked paths between them used by thousands of visiting hill walkers in summer. In addition there are several hundred smaller private hyttes owned by local people or organisations. These are used for hunting in autumn and are hired out for summer pursuits, and for skiing in March and April. An initial impact study of the disturbance to reindeer from this human traffic and hunting was conducted in the course of this study, and was found to have a considerable influence on the populations' energy expenditure (see Chapter 7.9. and Chapter 8). There are plans to control tourist and recreational development by forming a National Park on Hardangervidda, but so far these plans appear to be too limited in scope and area to make an essential contribution to the problem.

CHAPTER THREE STUDY POPULATIONS

Reindeer have a long history in Scotland, from remote pre-glacial times up to at least the 12th century. The Orkneyinga Saga of 1159 relates that the Jarls of Orkney, Røgnvald and Harald, were hunting red deer and reindeer in Caithness.

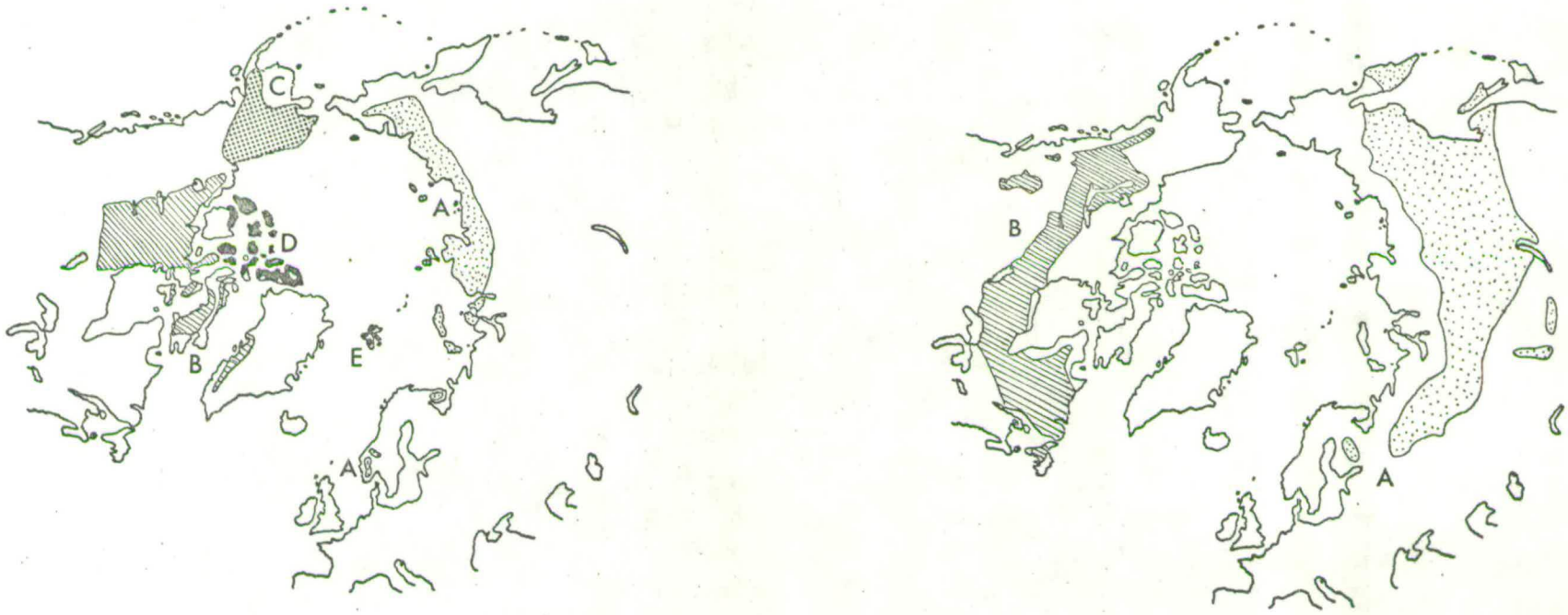
Antler found in a peat bog on the island of Rousay, Orkney. (from Smith, 1869).

CHAPTER THREE STUDY POPULATIONS

Throughout most of Scandinavia reindeer have been domesticated from the mountain type, Rangifer tarandus tarandus L. (Siivonen, 1975). This type is thought to have originally moved in from the South some 35,000 - 45,000 years ago, probably surviving on the Norwegian coastal belt during the coldest phase of the glacial period, before recolonising the rest of Scandinavia. Not until after the last glaciation some 9,000 years ago did the woodland reindeer type, Rangifer tarandus fennicus Lonnb. move in from the east to suitable forest habitat in Northern Sweden and Finland (Siivonen, op. cit.). The present day distribution of mountain and woodland races of wild reindeer and caribou is shown on the circumpolar maps of Banfield (1961) (Fig. 3.1.).

Up to 200-300 years ago, wild reindeer were generally distributed over all suitable mountain and tundra terrain in Norway. Since the 18th century the growth of the tame reindeer herds through partial or complete domestication has meant the ousting of wild reindeer from their habitats. This process has been particularly complete in North Norway so that the only surviving wild populations are dispersed over several mountain ranges in South Norway. With the exception of the Snøhetta range, reindeer areas in the south have a history of some combined use by wild and domestic herds. In contrast to the Lapp family concerns in the North, attempts at commercial reindeer herding in the South have had little lasting success and have successively ceased operations. For example, Hardangervidda held domesticated herds as well as /

Fig. 3.1 The natural distribution of wild Rangifer tarandus in the world.



Mountain/tundra-type

A. tarandus
B. groenlandicus
C. granti
D. pearyi
E. spitsbergensis

Woodland-type

A. fennicus
B. caribou

(Mainly from Banfield, 1961).

as wild up to the early 1950's, Ottadalen up until 1964, while the distinction between wild and domestic on Trollheimen is presently indistinct. On Forelhogna, the present 'wild' population is thought to be wholly derived from domestic ancestors.

The current status of wild reindeer populations in Norway and the area of their mountain ranges is shown in Table 3.1. The location of these ranges are shown on the map of South Norway (Fig. 2.1.). Although reindeer populations in these areas are fairly discreet, individual deer or small groups do occasionally emigrate into adjacent areas. This is particularly frequent when adjacent mountain terrain is separated only by simple artificial barriers such as a road or railway, or by a short belt of sub-Alpine birchwood, but is uncommon when mountain areas are separated by low elevation valleys holding forest, farmland and habitations.

Neither as a whole nor in separate ranges have wild reindeer numbers been a stable entity. The total number tends to fluctuate within the range of 20,000 - 45,000 animals, at an average density of approximately one deer per one km^2 of range. National hunting returns for wild reindeer recorded since 1890 reflect the fluctuations in the total population (Myrberget, 1971). Numbers were at a low ebb around 1900 so that hunting was stopped until 1907 to allow the various populations to recover, which they did, reaching a peak around 1916, and declining again to 1930. During this early part of the 20th century the reindeer's natural predator, the wolf, had been persistently persecuted until it could

no /

Table 3.1 The wild reindeer populations of Norway.

Range	Area (km^2)	Population size*	Winter deer density (animals per sq.km.)
Hardangervidda	8000	12000	1.5
Snøhetta	3400	2200	0.6
Knutshø	1500	1000	0.7
Setesdalen	5200	3000	0.6
Rondane	2700	2500	0.9
North Ottadalen	3200	2900	0.9
South Ottadalen	1500	500	0.3
Hallingskarvet	1900	2000	1.1
Forelhogna	1600	1400	0.9
Fjellheimen	2200	300	0.1
Trollheimen	2500	200	0.1
Other areas	<500 each	c. 3000	
All	40,000	31,000	0.8

* All from counts and estimates made before calving, 1976 (from Holthe, 1976)

no longer be considered a significant factor in reindeer population dynamics. The control of the reindeer populations' natural rate of increase thus became entirely dependent on the hunting pressure. From 1935 the total national population began to increase, at first slowly, then with increasing rapidity in the 1950's, to an all time high in the early 1960's (probably over 50,000). As a result of high densities of reindeer at least two major ranges, Snøhetta and Hardangervidda, suffered considerable overgrazing at overall densities of 3-5 deer per km^2. The history of these populations is presented below. The total number of wild reindeer at present in Norway is around 30,000 (Table 3.1.).

It is important to attempt to piece together the history of a particular population, as what is observed in the field is to some degree determined by past influences or interference. The historical trends in hunting pressure, population density, state of the pasture, and physical condition of the reindeer are different in all of the alpine ranges. Hardangervidda, the largest range with the biggest wild reindeer population, was chosen by Viltforskningen for concentrated research, which conveniently knit with the chosen study area of the Norwegian I.B.P. Tundra Biome Project. I also made observations on two other major ranges, Snøhetta and North Ottadalen, and a minor area, Forelhogna. Since knowledge of population composition was sparse, counts were made in the course of the behaviour study to assist in comparing the population characteristics between the different areas.

UNIV. EDINBURGH

3.1. THE SNØHETTA POPULATION

The Snøhetta high mountain plateau of around 3,400 km^2 has peaks rising to over 2,000m and is dissected by deep valleys down to the sub-alpine birchwoods below 900m. The climate is relatively oceanic in the west towards the fjords, and continental in the east which results in a natural prepond-erance of lichen-heath communities in the eastern sector (Gaare, 1968). The Knutshø area lying to the east over the Dovre road and railway has been regularly utilised in recent winters by reindeer from the Snøhetta population. The total Snøhetta-Knutshø area is ca. 5,000 km^2. The recent history of the population and the range has been turbulent.

Up to the 1950's the Snøhetta reindeer maintained good body condition as culled reindeer samples show (Reimers, 1972b). Through an insufficient hunting cull the population was allowed to increase from a relatively high density of 2.3 animals per km^2 (8,000) to 4.4 animals per km^2 (15,000) by 1960. At this concentration of animals the vegetation was heavily grazed in excess of its productivity (Gaare, 1968), and this corresponded with a marked reduction in reindeer carcase weights and jawbone lengths (Reimers, in prep.). Range investigation by Gaare (1968) at this time found that total plant biomass was considerably reduced as a result of over-grazing, with mosses and gramoids showing a relative increase at the expense of lichens and woody plants. Lichens on the heaths of the eastern winter grazings now made up only 5-25% of the dry weight of the biomass compared with 65-80% 10 years previously (Gaare, op. cit.). In 1962 the hunting quota /

quota permissible was belatedly increased so that the population was reduced from 12,000 in 1962 to 6,000 in 1967, then lower still to an estimated 1,000 - 1,400 in 1969/70 (Krafft, 1972a).

The unexpected and sudden drop in numbers in these latter years may have been the result of factors other than hunting. In November 1969 I observed that two herds of 90 and 100 animals crossed the snow-drifted Dovre road and railway which constitutes the eastern boundary of Snøhetta. In so doing they were utilising the Knutshø area which did not suffer from heavy utilisation in the 1950's and 1960's. In November of that year over 500 deer were known to have moved east into these new pastures (P. Holaker, pers. comm.). This early winter movement out of the Snøhetta range proper has become a regular event in early winter, but may not have been balanced by return movements in the spring and autumn. Over the three years from 1969 to 1971, 26 groups were known to have crossed over from November to January but only 18 groups were observed making the return journeys in April/May and August/September (Krafft, 1972b). It is not known whether the reduction in the Snøhetta population may also have been the result of the poor physical condition of the animals after the over-grazing period, leading to substantial winter mortality.

In any event, only 1,400 reindeer remained on the Snøhetta range by July 1969 (Krafft, 1972a). Three months later I observed at least one third of these animals (475) in Mjogsødalen /

Mjogsødalen in the south part of Snøhetta range from 15th - 22nd October, 1969, during the latter part of the rut. There was a heavily imbalanced sex ratio in favour of females and a relatively low calf production (Table 3.2). Of the few males present most appeared to be young males of 1½ or 2½ years old, with only one or two individual males who could have been older than 3½ years. One of these was a fully mature, well-antlered male who dominated the rutting proceedings, and was possibly an immigrant from another range, such as North Ottadalen. The 1 male : 7 female sex ratio for animals over one year was identical to that found five years previously by Reimers (1972b), and is the result of heavy selection pressure on the obviously larger-antlered males over consecutive hunts. Already by 1965, 91% of males that were being shot were 3 years or younger, since older males had been successively removed in previous hunts (Reimers, op. cit.).

In two groups of around 100 each observed in November, 1969, not more than 3-4 young males were present in each group, which at less than half the male proportion at rutting time suggested that some degree of sexual segregation had occurred. This was confirmed by the presence of 57 males in a group of 72 reindeer on Knutshø on 17th May, 1970, before calving. From a population census of 1,000 in 1970 (Krafft, 1972a), and a male proportion of 9% (Table 3.2), the 57 males in this group therefore represented over 60% of the total males in the known population. On a return visit to the area in December, 1975, I observed a batchelor group of 19 adult males /

Table 3.2 Sex and Age Composition of Rutting Groups at Mjogsødalen, Snøhetta, October, 1969.

Sex/age class	Number of reindeer	Proportion	Ratios
♂♂ over 1 year	25	9%	1 ♂ : 7.2 ♀♀
♀♀ over 1 year	179	63%	
Calves	80	28%	45 calves per 100 ♀♀
Total counted	284	(represents 20.3% sample of Snøhetta population of 1400)	
Total present	475	(represents 33.9% sample " " " " ")	

males, as well as a mixed herd of 136 females, calves and males. Such variability in the extent of sexual segregation in winter is also a feature of the population on Hardangervidda (see Ch.7.1.3.).

There are now clear indications that the Snøhetta range, in particular the depleted lichen resources, are beginning to recover from their severe over-utilisation (Gaare, pers. comm.). Present management policy aims to hold the population at a density around 0.5 deer/km^2 to maintain recovery of the range and the reindeers' physical condition. Since 1968 hunting licences are differentiated according to the sex and age of the animal to be shot, to restore and maintain a more balanced sex ratio in the population.

Research is in progress by paint-and collar-marking of individuals to establish the population's present range use patterns, in particular the eastern and western parts of Snøhetta, and the Knutshø area, and to determine the calving area or areas (Skogland, pers. comm.).

3.2. THE NORTH OTTADALEN POPULATION

To the south of the Snøhetta range lies the Ottadalen area which is divided by a low lying (612m) valley and road into two discrete ranges, 3,200 km^2 as North Ottadalen, and 1,600 km^2 as South Ottadalen (Map, Fig. 2.1.). The rugged alpine terrain of North and South rises from 1,000 m above the sub-alpine birch zone to small permanent snowfields above 2,000 m. As on Snøhetta, winter pastures are mostly located /

located in the eastern and middle parts of the ranges where the more Continental climate has developed plant associations rich with lichens. However, the complex topography creates numerous south-facing slopes which provide several exceptions to the typical seasonal distribution of reindeer (Reimers, 1972a).

From 1954 to 1964 a commercial reindeer company owned 3,000 reindeer and grazed them on 2,400 km^2 of range in both South and North Ottadalen. 2,000 of these were usually kept in the South, which resulted in some heavy utilisation of the pasture in this period (Reimers, op. cit.). In 1964/65 the company disbanded, releasing 400 calves and yearlings in North Ottadalen where they joined an existing 100 wild animals, leaving 700 in South Ottadalen. Since 1965 no movement of reindeer between North and South has been observed.

Reimers (op. cit.) has demonstrated that in only 4-5 years after release of the reindeer from herding practices, the animals in North Ottadalen have increased their weight by 26-64%, and in South Ottadalen by 23-43%. Also, nearly 50% of the 5-month female calves in North Ottadalen now breed successfully, whereas only 10% of them did as domestic animals. Field studies at calving time show that the peak of the calving season on North Ottadalen, May 6th, is six days earlier than on South Ottadalen, and 22 days earlier than on Snøhetta (Holthe, 1975). Since 1967 it is clear that the heavy body weights, good physical condition, early age of first /

first breeding, and the early calving season, make the North Ottadalen population the superior wild reindeer population of Norway. The Forelhogna population has similar characteristics but its mixed ancestry makes direct comparison of doubtful validity (see Ch.3.3.).

Since hunting was initiated in 1967 the low annual cull had allowed the population of North Ottadalen to expand to 700 before calving in 1970. At 0.2 animals per km^2 of range this was considered to be below what the range could readily sustain, as evidenced by extensive un-grazed tracts of lichen heath (Graffer & Lyftingsmo, in Reimers, 1972a). A recent census showed that the population had grown to 3,250 before calving in 1975, or 1 deer per km^2 (Holthe, pers. comm.).

In the latter part of September in 1969 and 1970 I observed the rut in the central region of North Ottadalen, particularly on the mountain terrain above and within the Lordalen Valley. Rutting groups observed in 1969 totalled some 320 animals, 45% of the population. In contrast to Snøhetta, the rut was notable for the presence of all age classes of males, the dominance and courtship patterns of the older large-antlered males, and the participation of 5-month animals in rutting behaviour (Thomson, 1971; and Ch.5.3.). Rutting groups contained all sex and age groups, their overall composition in 1969 being shown in Table 3.3. The nearly balanced ratio of 5 males : 6 females over the age of one year - Reimers (1972b) found 4 males : 6 females from hunt cull samples - and /

Table 3.3 Sex and Age Composition of Rutting Groups at Lordalen, North Ottadalen, September, 1969.

Sex/age class	Number of Reindeer	Proportion	Ratios
♂♂ over 1 year	102	35%	1 ♂ : 1.2 ♀♀
♀♀ over 1 year	118	41%	
Calves	68	24%	58 calves per 100 ♀♀
Total counted	288	(represents 41.1% sample of North Ottadalen population of 700 (1970).	
Total present	ca. 320	(represents ca. 46% sample " " " " " " " " " " " ").	

and the relatively high production of calves is in sharp contrast to reindeer on Snøhetta in the rut in the same year (compare with Table 3.2.).

I observed calving in early May, 1970 and 1971, in the north-west region of North Ottadalen, particularly on the mountains around the Asbjørndal Valley. Group composition was dynamically variable at this time, although a general pattern prevailed. Before calving the observed groups tended to consist of pregnant females, yeld females, and yearling animals, with adult males virtually absent. Pregnant females would normally become isolated in the course of parturition, then within a few days they would seek the company of other mothers and calves to form nursery groups. As calving progressed these nursery groups would grow in size and by the end of calving time take on an increasingly integrated nature as they were joined by groups of calfless adults, including the winter-segregated adult males. The steady increase in the number of new mothers and calves joining a nursery group over four days in May 1970, until finally "swamped" by a large influx of calfless adults on the fifth day, is shown in Table 3.4. In 1971, four groups seen from Skarvhø Mountain on 8th May consisted of two stationary nursery groups of 140 and 22, a moving group of 320 animals containing few mothers and calves, and a distant group of around 50, comprising at least 530 adults or about half of the known North Ottadalen population.

The observed high productivity of females (70 calves/100 females one year and over observed on 13th May, 1970) and their /

Table 3.4 The Enlargement of a Nursery Group from 10th to 14th May, 1970, Asbjørndalen, North Ottadalen.

Date	Number of reindeer (excluding calves)	♀♀ with calves	♀♀ over 2 years without calves	Yearling ♀♀ without calves	♂♂ over 2 years	Yearling ♂♂
10th May	47	29	0	3	4	11
11th May	45	34	0	3	2	6
12th May	52	36	0	3	2	11
13th May	88	42	8	11	4	28
14th May	216	61	N/C	N/C	N/C	N/C

N/C - no count.

their good body condition at the start of calving (Reimers, in prep.) is undoubtedly related to the superior quality of the pasture. The lichen and heath vegetation looks visibly lush, and this is confirmed by lichen biomass studies, which show that North Ottadalen seldom supports less than 800gm/m^2 compared with 200-400gm/m^2 on the Hardangervidda winter range (Gaare et.al., 1975).

3.3. THE FORELHOGNA POPULATION

To the north and east of the Snøhetta range lies the relatively small 1,600km^2 mountain plateau of Forelhogna (Map, Fig.2.1.). The Continental climate of this easterly range has developed good tracts of lichen heaths from 800m at birch level to the highest points around 1,250m. On this range the reindeer population can be considered 'feral', as it almost certainly derives from earlier domestic herds. In addition, these mountain-type reindeer still have small influxes of woodland-type reindeer from the adjacent Røros tame reindeer district (Gaare, pers. comm.). The mixed ancestry of this population therefore makes it an unsuitable one for direct comparison with other wild reindeer populations, although behaviour observations in winter showed no obvious differences, except for a lesser flight distance.

Air flights in mid-February 1970 estimated a population of 850, in particular one large herd of circa 700, and four other dispersed groups, totalling circa 100, were seen. Two weeks later I located about 120 reindeer in 5-6 predominantly male groups in the Sandfjell area. Although the size and composition of the groups varied from day to day under the prevailing /

ing blizzard conditions, there were in general three all-male groups of 20, 16, and 8 males, and two predominantly male groups of 68 and 9. The herd of 700 which had been spotted from the air, and presumably comprised the female/calf concentration, had left the Sandfjell area by the time of observation in early March.

The following year ground counts in May after calving found a relatively high calf proportion (71 calves/100 females over one year) and a sex ratio only slightly imbalanced by hunting (52 males/100 females) (Aune, 1971). As well as calf production, the growth rates of Forelhogna animals are comparable with those of North Ottadalen, as gauged by carcase weight analysis and jawbone length measurements (Reimers, in prep.). However, when considering this latter criteria of physical condition, the possible influence of genes from woodland-type reindeer cannot be dismissed.

A suitable optimal population size for this area is particularly difficult to determine. By 1975 the population had grown to a minimum of 1,700 before calving, and an overall density of one deer/km^2 (Meli, 1975). However, the population's winter use of Forelhogna is usually heavily concentrated on the Sandfjell area, comprising approximately 300km^2 (Gaare & Hansson, 1975), representing an effective winter density of 5.6 deer/km^2. Further increases in population may not therefore be advisable unless it can be established that this locally high density is still within the carrying capacity of the range in winter.

3.4. THE HARDANGERVIDDA POPULATION /

3.4. THE HARDANGERVIDDA POPULATION

3.4.1. History

The Hardangervidda mountain plateau has a long history of occupation by reindeer. Archeological excavations at Stone Age sites show that as early as 8,000 B.C. man lived in small settlements on the plateau living off the reindeer in a similar way to that of caribou-dependent Eskimo and Indian peoples in North America (Johansen, 1973). Long stone walls and cairns were erected to guide reindeer herds towards lakes where animals would be speared from boats, or towards camouflaged trapping pits into which they would fall and be killed. For thousands of years man, as well as wolf, has been a predator on the reindeer population.

Over the last few centuries the wild reindeer population on Hardangervidda has been most affected by three inter-related factors: viz. the introduction of firearms for hunting, the introduction of domesticated reindeer, and the demise of the wolf. In 1782 a Kristoffer Hjeltnes brought 100 domestic reindeer to Hardangervidda, and over the next 100 years further introductions of reindeer were made by local farmers bringing deer from Finnmark and the Røros districts (Harangviddens Fjeldbeitekomiteen, 1911). By 1911 there were thought to be 21,000 reindeer on Hardangervidda, comprising 11,000 in domestic herds and approximately 10,000 of the indigenous wild population. As elsewhere in Norway the desire for total protection of the domestic stock led to increased killing of the natural predators. However, the domestic reindeer companies on Hardangervidda constantly suffered from losing their stock to the wild herds and progressively ceased operations. /

ations. By the early 1950's the entire range was being administered by the local and national authorities as a wild reindeer area for licensed hunting only.

Use of the gun for hunting over the last 300 years has resulted in selective culling of wild reindeer, as well as resulting in an efficient elimination of the reindeer's main predator, the wolf. Since the 1930's no wolves are known to have bred on Hardangervidda. In contrast to the wolf, which concentrates on young, old, weak or unsynchronised animals (Miller, 1975), or the primitive hunter whose drives would kill sections of the population without discrimination, the hunter with a rifle and a quota limited to one or two animals elects to shoot the largest and best-antlered reindeer he can find. As a result the population structure becomes imbalanced in favour of females, resulting in a population with a particularly high growth rate. However, if the shortage of older age classes of males becomes particularly acute then calf production can be jeopardised on a large scale, either by many females not being covered in the rut, or mating being left to the young males. As young males are later to rut this can result in late-born calves which have less of the plant growing season available for their growth and may, therefore, have difficulty surviving their first winter. In the last few years the hunting administration have attempted to rectify the sexual imbalance and possible precarious situation on Hardangervidda by specifying on the hunting licences issued the sex of the animals to be shot (see Ch.3.4.6.).

3.4.2. Population Size

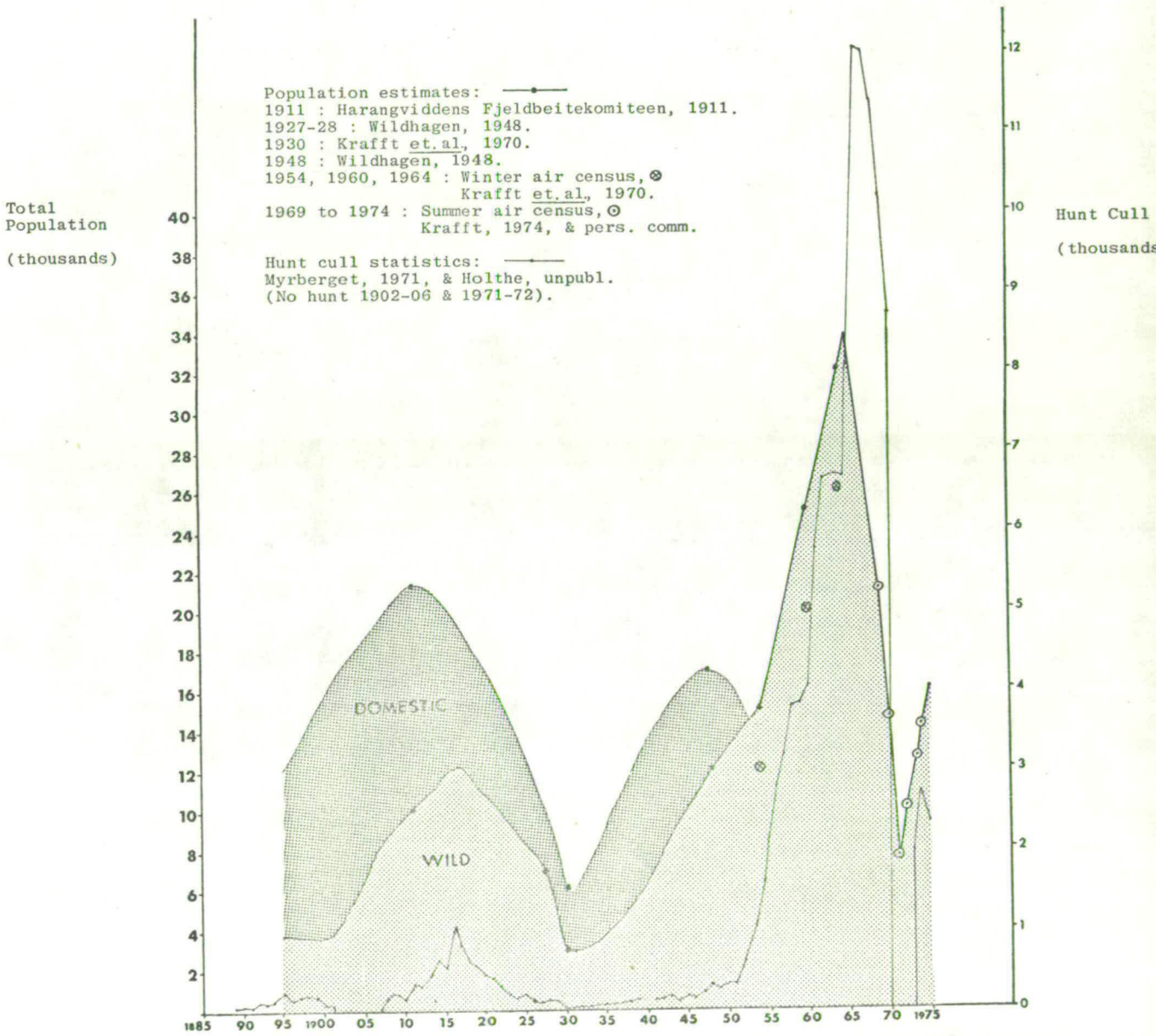
The /

The first air census of the Hardangervidda population was made in winter 1954, then repeated in 1960 and 1964. Since 1969 the Direktoratet for Vilt og Ferskvannsfiske (the national hunting administration) have made annual flights in early summer to photograph the large post-calving aggregations. From hunt cull statistics which are available for the Hardangervidda area since 1889 (Holthe, unpubl.), and from information in diverse reports I have estimated the extent of population fluctuation prior to 1954 (Fig.3.2.).

At the turn of the century the wild population is said to have been severly reduced by excessive hunting, so that hunting was banned between 1902 and 1906 to allow the population to recover (Krafft, Gaare & Reimers, 1970). This it did, so that by 1911 there was an estimated 21,000 reindeer on Hardangervidda, some 10,000 wild and 11,000 domestic (Harangviddens Fjeldbeitekomiteen, 1911). The wild population is thought to have reached a peak in 1916, which is also reflected in the hunt cull statistics at that time (Fig.3.2), before being reduced to around 2-3,000 by 1930 (Krafft et. al., op. cit.). The population then grew again to an estimated 12,000 by 1948 (Wildhagen, 1948) which was the same number observed in the first winter air census of 1954. By this time the last of the domestic reindeer companies had given up herding. From then on the wild reindeer population grew rapidly, with an increase in hunt quota failing to compensate for the population annual increase (Fig.3.2.).

By 1964 the winter population had reached an all-time high of 26,000 (3.3 deer/km^2), or an estimated 32,000 on the summer range /

Fig. 3.2 The Hardangervidda reindeer population, 1895 to 1975.



range (4.0 deer/km^2). By this time it was becoming recognised that the continuing expansion of such a large population could result in overgrazing of the range, particularly by diminishing the lichen resources of the eastern winter range (Krafft et. al., op. cit.). The hunting quota was stepped up, and sex-specific licences issued so that more females could be removed from the population. The 25% hunt cull in 1965 finally reversed the population trend, and between 1965 and 1968 the 27% cull effectively reduced numbers. Following a 45% cull in 1969 the population was further reduced to a winter level of below 12,000 animals (1.5 deer/km^2) (Fig. 3.2.).

By 1970 the I.B.P. and Viltforskningen research, begun on Hardangervidda in 1969 was beginning to evaluate the impact on the winter grazing pastures of the high population in the previous ten years. Low carcase weights and reduced jawbone lengths of reindeer sampled in 1969 reinforced the view that the animals were by this time in poor physical condition. These arguments were set out in locally distributed reports by Krafft et. al. (op. cit.), and Reimers and Gaare (1970), which concluded that the winter population must be reduced to less than 10,000 to allow recovery of both the range and the physical condition of the animals.

The Direktorat somewhat rashly decided to achieve this further reduction within one year, and although the air census showed a summer population of 14,600 in 1970, licences for 8,700 animals were issued unspecified in regard to sex or age. In the three-week hunt in September 1970, with legal and illegal shooting, some 9,000 reindeer were removed from the population, equivalent /

equivalent to a 60% cull. Males older than 3 years were almost eliminated so that the rut in October 1970 was seen to depend on the few remaining 2½-and 1½-year males (see Chapter 7.8.). Fortunately breeding did occur, albeit the calf production in May 1971 from ground counts was found to be significantly lower at 49 calves per 100 females over 2 years,than in the previous year, 65 calves per 100 females over 2 years (see Table 3.5.).

In 1971 and 1972 no hunting licenses were issued in order to allow the population to recover in size and stability, in particular to permit the young male segment to mature.

3.4.3. Population Composition

Because of hunting selection, it was known that the statistics of the annual cull could not give a representative picture of the sex and age distribution of the population. When the I.B.P. studies commenced on Hardangervidda in January 1970, I attempted to obtain reliable sex and age counts in the field as an aid to future management. Three main difficulties were encountered, viz. the problem in recognising all of the main sex and age classes at any one time of the year, the varying degree of geographical segregation of sexes, and the necessity of obtaining a sufficiently large count to be representative of the total population. No one time of year was found to satisfy all three conditions. The large mixed summer herds could not be relied on to have a full complement of males, in the rut the observed mixed groups constituted only a small sample of the population, while in winter the degree of male segregation and calf proportions was found to be extremely variable in different groups. /

Table 3.5 Principal population composition counts on Hardangervidda reindeer, 1970 and 1971.

Type of Count	Period	Classified Counts		Ratios	95% confid-* ence interval	Estimated sample of population
CALF PRODUCTION		calves	females over 2 yrs.	calves per 100♀♀		
	Calving 1970	163	252	64.7	± 11	c. 5%
	Calving 1971	518	1062	48.8	± 13	c. 35%
CALF PROPORTION		calves	whole herd (incl. calves)	calf %		
	Summer 1970	1089	4238	25.7	± 4.9	c. 29%
	Summer 1971	705	3609	19.5	± 5.0	c. 47%
	Rut 1971 (S)	61	441	13.8		c. 6%
YEARLING PROPORTION		yearlings	whole herd	yearling %		
	Summer 1970	247	1173	21.1	± 6.2	c. 8%
MALE PROPORTION		males over 2 yrs.	females over 2 yrs.	males per 100♀♀		
	Summer 1970	20	87	30.1		c. 1%
	Rut 1970			c. 10		
	Rut 1971 (S)	55	325	16.9		c. 8%

* 95% confidence intervals relate to differences between individual groups or days and cannot be assumed to apply to the whole population.

(S) Count by T. Skogland.

groups.

The most consistently difficult classes to recognise apart at all times of the year were young males and adult females, so that few accurate total male counts could be achieved. With red deer in Scotland there is a similar difficulty in distinguishing in the field between the adult hinds and the young male "knobbers" (J.D. Lockie, pers. comm.).

From caribou counts on Alaskan tundra in summer, Hemming and Pegau (1972) considered that a 10% sample of each sex or age class was a minimum for reliable population estimates. For Hardangervidda, counts of the overall calf proportion in the herd (number of calves/total animals x 100%) well exceeded a 10% sample at most times of the year, whereas yearling and male counts achieved were usually substantially less. All factors considered, the best composition counts obtained on Hardangervidda in 1970 and 1971 are those shown in Table 3.5. From these it has been possible to estimate the proportions of main sex and age classes in the population (Table 3.6.). The main differences between the estimated sex and age structure of the population in the two years is due to the severe 1970 hunt severely reducing the population size and eliminating older males, and the significantly low calf production in 1971 (Fig. 3.3.).

3.4.4. Calf Production

Although the possession of antlers by female reindeer tend to make composition counts more difficult because of their similarity to young males, a peculiarity in their time of casting antlers /

Table 3.6 Estimated population structure of Hardangervidda reindeer in 1970 and 1971.

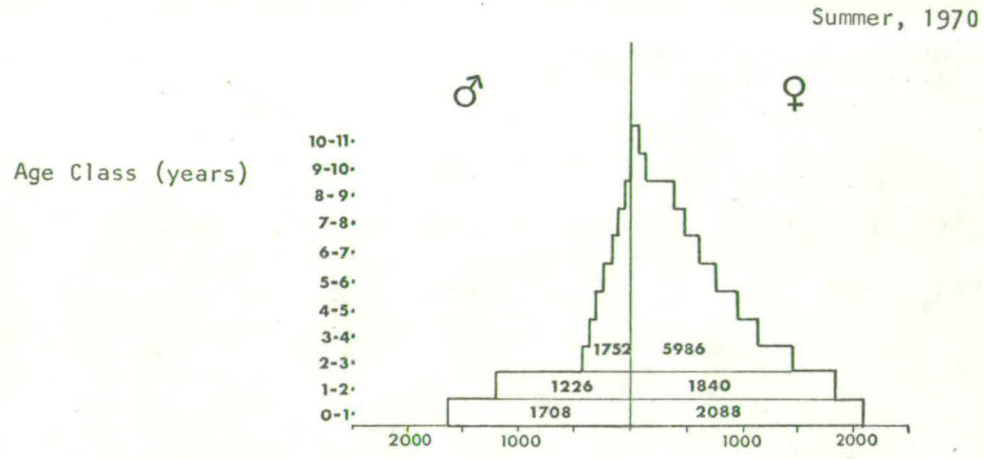
	Calves	Yearlings	♀♀ over 2 years	♂♂ over 2 years
Summer 1970	26%	21%	41%	12%
Summer 1971	20%	21%	50%	9%

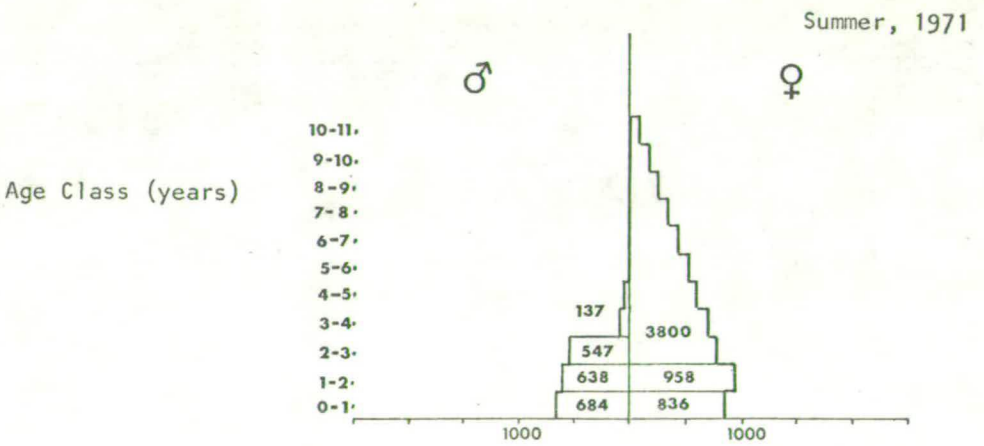
antlers permits an unique opportunity to determine the proportion of females which are pregnant. Pregnant females retain their antlers until after they have calved, while yeld females of that year drop their antlers in late winter, about one month before the calving season. Skoog (1959), Lent (1965b) and Espmark (1971b) have provided quantitative evidence of this close relationship. They demonstrate that the number of females with antlers at the start of calving can be marginally less than the actual number of females pregnant, but this tends to be equalised by rare instances of stillbirths.

On the calving grounds on Hardangervidda, one apparently unantlered female was observed to give birth, but otherwise antler status appeared as a clear indicator of reproductive status (this study; Skogland (1974); Kjos-Hanssen (1973b)). This phenomenon was known to the Harangviddens Fjeldbeitekomiteen in 1911, and is also the norm for domestic reindeer populations in North Norway (Skjenneberg & Slagsvold, 1968). Females were observed to cast their antlers a few days after giving birth. Espmark (1971b) found that a range between one to eleven days was possible, but that normally antlers were cast three to eight days after calving.

Daily counts were made on the calving grounds in 1970 and 1971 of antlered females plus females with calves, and compared with the number of yeld unantlered females present to estimate calf production and to guage the daily progress of calving. In the Olavsdalen area of Hardangervidda in 1970 I found that 64.7% of females over 2 years were productive (163/252) with no significant variation between the four days of counting (Table 3.5). In 1971 a ten-day tour of the calving area found an overall /

Fig. 3.3 Estimated sex and age pyramids for the Hardangervidda population, 1970 and 1971.





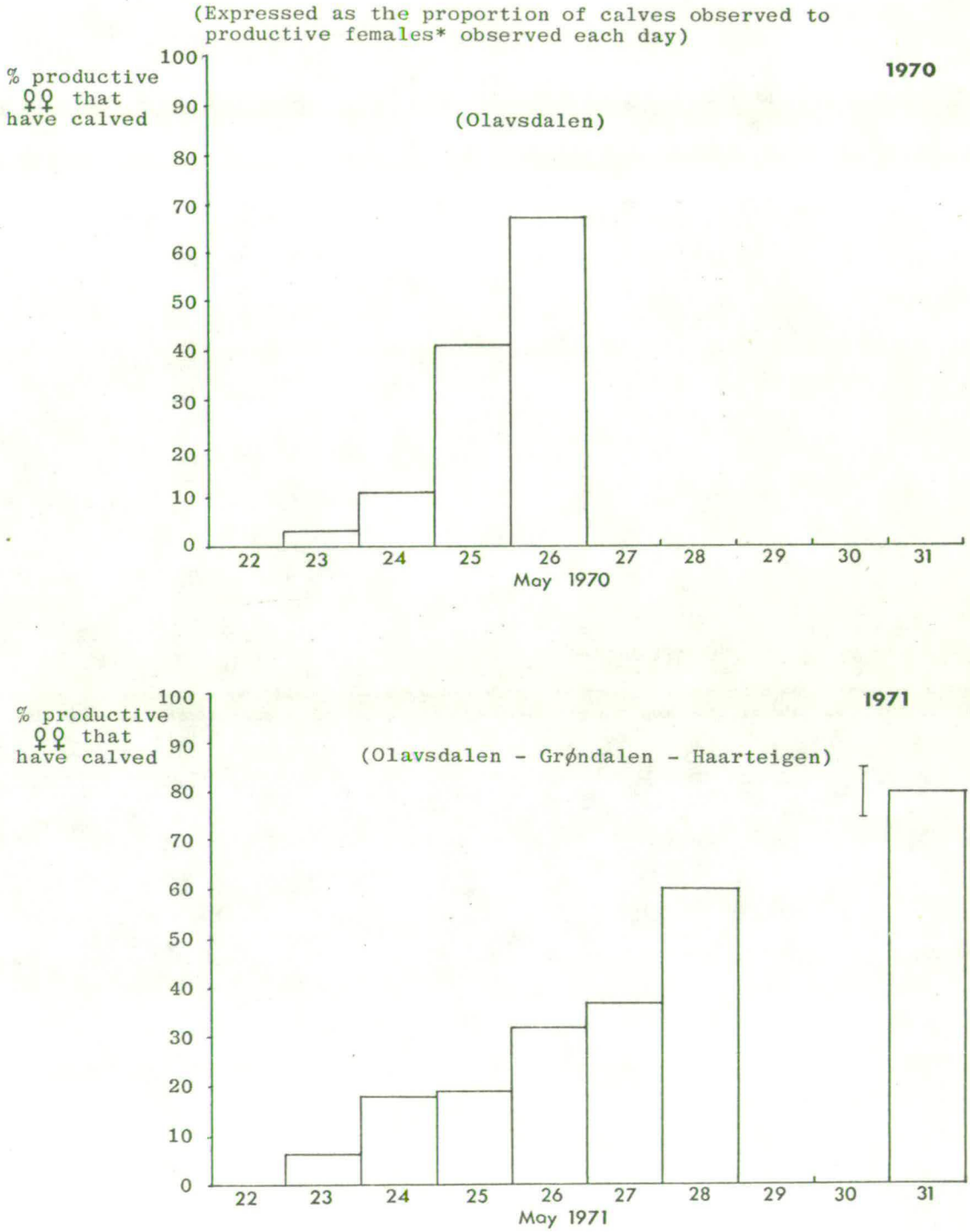
overall 48.8% of females were productive (518/1 062) with a significantly higher population of productive females present in the Haarteigen area than in the Olavsdalen area. The proportion of calves observed to productive females increased rapidly over the days of observation in both years (Fig.3.4).

The difference in calf production between the two years was reflected in counts of the large post-calving herds in summer, where it was found that the 19.5% calf proportion in the herds in summer 1971 (705/3,609) was significantly lower than the 25.7% of the previous year (1,089/4,238; $P<0.1$, Table 3.5). Counts in subsequent years found a ratio of 59 calves per 100 females in 1972, and 78 calves per 100 females in 1973 (Skogland, 1974), which indicates a steady recovery in female productivity.

The proportion of females with milk in their udders, as sampled in the autumn hunts of 1969, 1970 and 1973/74 (from data in Fagerhaug, 1976) is 7, 6 and 7 females per 100 females less than the field counts made in the respective years at calving time. This indicates a calf mortality of 8-11% by the end of summer each year, so that the mothers of deceased calves would have stopped lactating by the time of sampling in autumn. At calving time in 1970 and 1971 there was no evidence of substantial mortality of calves. Dead calves discovered on the calving grounds, usually "signposted" at a considerable distance by gatherings of scavenging ravens and occasionally foxes or an eagle, accounted for 3% of the calves actually observed.

The apparent improvement in female productivity from 1970 to 1973 /

Fig. 3.4 The progress of calving on Hardangervidda, May 1970 & 1971.



* Productive females are females which are pregnant (antlered) and females with newborn calves.

1973 may be related to the physical condition of the females. As an indicator of physical condition the carcase weights and jawbone lengths of females sampled from the hunt are significantly greater in 1973/74 than in 1969/70 (Fagerhaug, 1976). The unusually low birth ratio in 1971 (49 calves per 100 females over 2 years) may conceivably have partly or wholly resulted from fewer females coming into oestrus because of their poor physical condition at that time. Alternatively, the severely imbalanced sex ratio at this time, as outlined below, may have been the important factor.

3.4.5. Sex Ratio

As an example of the preference of hunters for male deer it is known from hunt cull statistics from Snøhetta that between 1946 and 1950,5 to 18 times more males were shot than females, on average 9 times more (Wildhagen, 1952). Over the country as a whole at this time 3 times as many wild reindeer males were being shot as females (Wildhagen, op. cit.). Continued hunting of a population with an imbalanced structure means that there are ultimately fewer males for hunters to select from and this is similarly reflected in the cull statistics. On Hardangervidda between 1946 and 1964 twice as many males were being removed as females, varying from 1.2 to 2.8 times as many in any one particular year (from Holthe, unpubl.). Between 1965 and 1969 sex-specific licences were introduced on Hardangervidda to promote the survival of older males and to eliminate more females (Krafft et.al.,1970). By summer 1970, several mature males were evident in the large summer herds, with a sex ratio of approximately 1 male to every 3 females for animals over two years (Table 3.5). After the reduction hunt, mature /

mature males were not present in the observed rutting groups; the only surviving males being yearling males, 2½-year males, and a few 3½-year males, with a sex ratio in the groups of approximately 1 male to every 10 females for animals over two years. One year later, without further hunting, Skogland (1974) found that recruitment from the previous year's male yearling segment had increased the adult sex ratio to around 1 male to every 7 females over two years.

Where the male segment of a hunted population is kept constantly small, this develops a population with a high potential for expansion, as long as the surviving males can serve all the females in the rut. The point at which the imbalance in sexes becomes critical is not known for the wild population and is difficult to evaluate as it relates to rutting behaviour patterns as well as to the purely physical capabilities of the males. Experience from domestic herds shows that selected males can service up to 20/30 females in the course of one rut (Baskin, 1970), and that younger males are often chosen for breeding purposes. However, the absence of mature males and their ritualised courtship behaviour patterns in the 1970 Hardangervidda rut appeared to result in a greater expenditure of energy in running and chasing by both males and females, and possibly also the necessity for oestrus females to "encourage" the inexperienced males towards copulation (see Ch. 7.8.). From these behavioural indicators, the possibility remains that the absence of mature males and/or the lack of males generally in the 1970 rut was a principal cause of the poor female productivity in the following spring.

3.4.6. Future Management Policy /

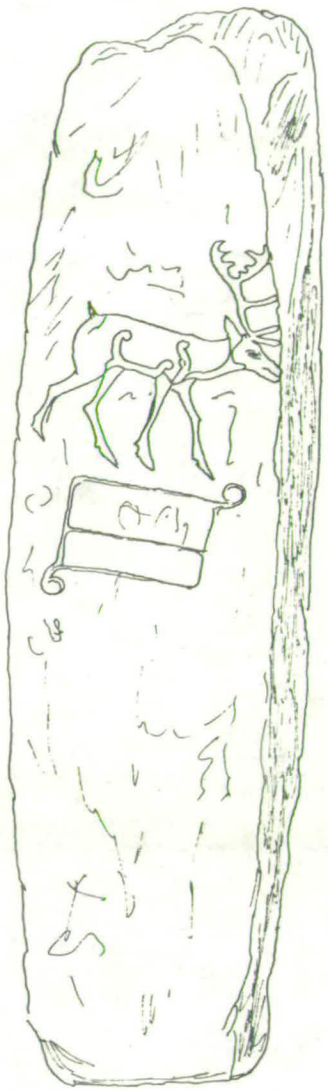
3.4.6. Future Management Policy

When it was known that the 1970 hunt had removed around 9,000 animals to leave a population of around 6,000, the national hunting administration (Direktoratet for vilt og ferskvannsfiske), with support from local hunter representatives, issued no licences in 1971 or 1972 for the Hardangervidda and Hallingskarvet areas. This was done to avoid further decreases in population size and to allow the surviving males to grow in maturity. By 1972 these short-term objectives had been realised, in that a summer air census found 10,100 animals (Krafft, unpubl.), while ground counts in October 1972 indicated a sex ratio of around 43 males per 100 females older than two years (Skogland, 1974).

Since then the Direktorat and the Hardangervidda Villreinutvalget (the local wild reindeer council) have agreed in principle to a winter population of between 8,000 and 10,000 animals (one deer/km^2) in the meantime (Krafft, 1974). From experience on Hardangervidda and other wild reindeer ranges it appears that a density on the total range of 3-5 deer/km^2 leads to overgrazing, while 1-2 deer/km^2 is usually within the carrying capacity of the range unless it has been overgrazed in previous years, in which case 0.5 deer/km^2 or less is necessary to allow the recovery of the vegetation. Since 1973 the hunt quota on Hardangervidda continues to be specified with regard to sex and age, but so far a total cull equivalent to the annual calf production has not been achieved so that the population is currently expanding again (see Fig.3.2). Part of the difficulty in achieving a balance is that the relationship between the hunt quota agreed and the actual number shot varies annually from /

from 50-55% in a poor year, to 75-80% in a good year (Holthe, pers. comm.). Also it can happen that the hunt quota is agreed on before the annual air census has been undertaken, so that the quota underestimates the cull which is necessary to achieve a stable population (Krafft, 1974).

If these difficulties in practical management can be overcome, and the main difficulties are political in the sense of differences in individual attitudes in the light of reasonably well established facts and relationships, then there is hope that a recently developed model of population growth can become an effective management tool. This model has been developed and designed by Viltforskningen in co-operation with Runit, the computer section at the Technical University of Trondheim, since an international Rangifer modelling workshop was held in October 1973 at Trondheim. The model simulates population trends on the basis of the input data available and offers predictions on the effect of different hunting strategies and quotas. It also offers the opportunity to test and store information on different reindeer populations, and with modification is suitable for simulating population trends for other Cervid species. The model is in its final stages of testing before being introduced to the national and local wildlife management authorities.



Engraving on a quartzose sandstone boulder, circa 1.1m high, found buried on a heathery knoll near Grantown, Inverness-shire. Probably about 10th century A.D. (from Smith, 1869).

CHAPTER FOUR LIFE CYCLE

"Distant peaks bring memories of other days, other herds;
Newborn calves struggling to rise,
The swooping eagle kill,
Summer herds massed on glaciers remote from midges and tourists,
Blood, meat and skins of hunt,
Ritual display of bulls in rut,
And then the winter shroud."

(On Snøhetta, December 1975)

Before detailing and discussing the various acts of individual behaviour, social behaviour, and social organisation, this chapter briefly describes the main morphological characteristics of Rangifer tarandus, and presents an introductory picture of their life cycle, with particular reference to the seasonal ecology of wild reindeer on Hardangervidda.

4.1. MORPHOLOGICAL CHARACTERISTICS

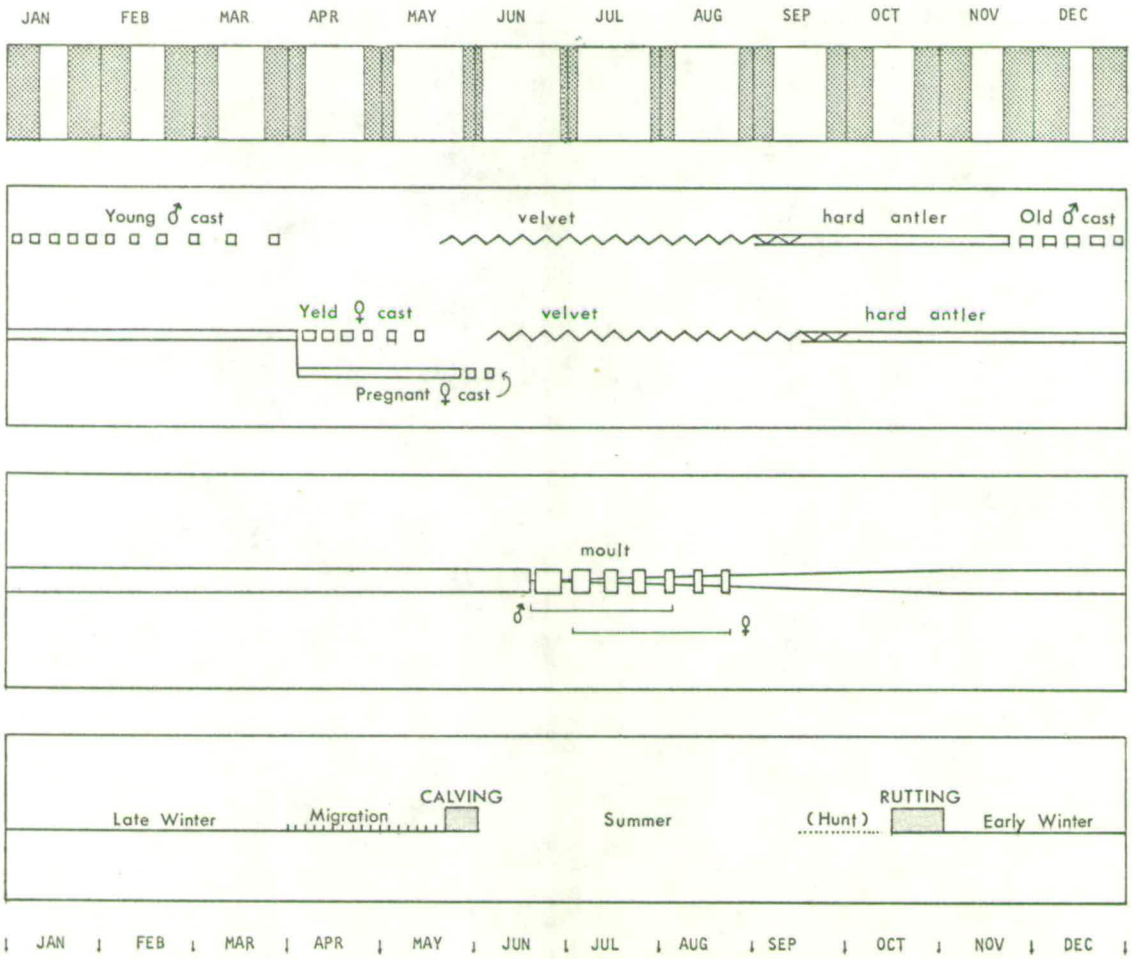
In shape and bearing, Rangifer tarandus is similar to other Cervid species. It differs particularly in its immensely thick coat, comprised of hollow, air-filled hairs which act as an efficient insulator against cold, its broad hooves, and the possession of antlers by both sexes.

The antlers of mature reindeer males are large and heavy with long curving main beams with distinctive tines and often a characteristic palmate brow-tine in front of the eyes (Plates 22-24). /

22-24). Males younger than four to five years have progressively less developed antlers. On Hardangervidda, the antler configuration of males in their second year is very similar to that of adult female antlers; i.e. relatively small, light, and with few branches (Plates 3 & 4). Adult males cast their antlers after the rut in early winter (November and December), younger males later, while the 1½- and 2½-year males may retain their antlers until March. Females carry their antlers throughout winter, until in April/May the yeld females cast. By calving time yeld females are unantlered, while pregnant females retain theirs until a few days after they calve. The pedicles of the new growing antlers start to become conspicuous on males in late May, and on females in June (Plate 11). The velvet covering the growing antlers in summer eventually falls off or is scraped off the fully-grown antler of males in late August, and a few weeks later in females (Fig.4.1).

The broad hoof and dew claw of the reindeer shows in their tracks, and must assist in spreading the body weight of the animal, which is particularly important when moving over marshy ground, soft snow, or 'rotten' snow with a light, easily broken crust. Support on slippery icy surfaces is said to be enhanced by the sharp edges of the hooves, and by the hair between the hooves which is elongated in winter to cover the pad (Kelsall, 1968). The front hooves are used constantly in winter for shovelling away snow or cracking ice covering their food plants. Reindeer are strong swimmers, the combination of the broad treading surface of the hoof in propelling the animal through the water, and the buoyancy offered /

Fig. 4.1 The annual cycles of antler development, coat moult and reproductive phases of reindeer on Hardangervidda.



* Light and dark hours on Hardangervidda calculated from the Almanakk for Norge, 1971

offered by the air trapped in the hollow hairs of the thick coat is an effective combination.

Coat colour and hair length alter seasonally. In winter the pelage is thick, long-haired and greyish-brown, becoming progressively greyish-white as winter proceeds. This winter coat starts to moult in June revealing the dark chocolate-brown hair of the new short summer coat below (Fig.4.1). The moult in deer is thought to be initiated by increasing day-length with the rapidity of moult determined by prevailing air temperatures (Ryder, 1977). In early summer, reindeer have a patchy 'black and white' appearance before all the winter hair has been shed (Plates 5 & 6). By the autumn rut, the summer coat has grown and lightened to a greyer brown which, in males particularly, contrasts markedly with the dark short hair on the face, legs and belly, and the long lighter hair of the mane and neck (Plates 22 & 25).

Reindeer are stockier than red deer (Cervus elaphus) by about 20cm at the shoulder (van den Brink, 1967). They are, however, of similar weight; an adult male mountain reindeer in Scandinavia averages 100 kg and an adult female 80 kg (Steen, 1968), which is similar to the average weights for mountain red deer in Scotland. The Hardangervidda reindeer are presently lighter than this average at approximately 90 kg average live body weight for adult males, and 60 kg for females (Reimers, unpubl.). The precise weight of an adult animal varies seasonally, the weight drops over the winter as fat reserves are used up and is put on again as the nutrition improves from spring onwards /

onwards (Reimers, unpubl.). The rate of growth is dependent on the quality of the food, in particular its metabolic energy and crude protein content (Steen, 1968; Fig.4.2). In turn, plant growth and quality is strongly influenced by the duration and depth of snow cover, the length of daylight, and air temperatures (Fig.4.2). In such Northern latitudes, seasonal cyclic changes in the environment not only influence antler cycle, moult, and body growth, but as will be considered in subsequent chapters, many other aspects of the reindeer's biology, including their breeding cycle, range distribution and movements, food selection, and social organisation.

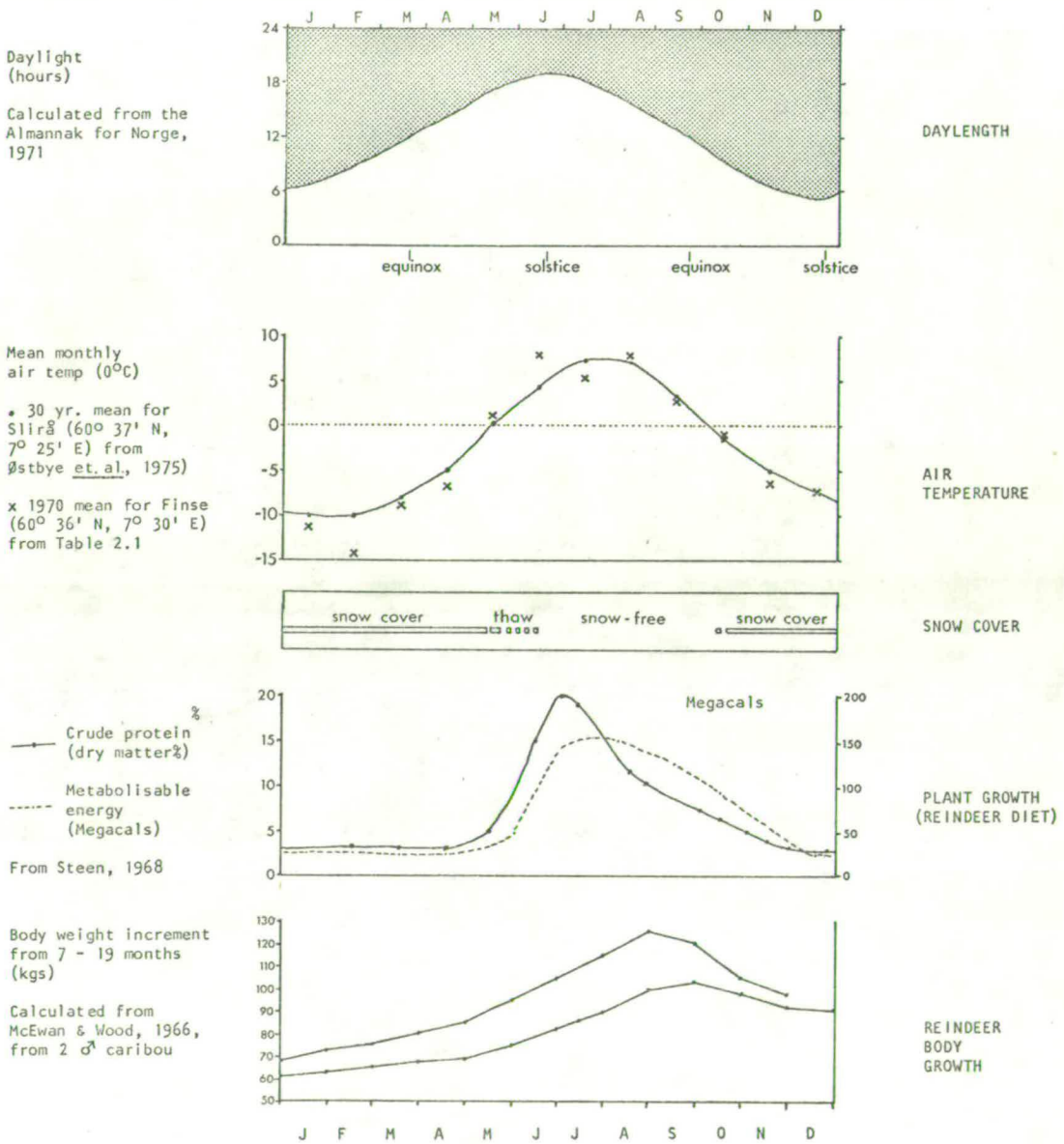
4.2. SEASONAL ECOLOGY

Barren-ground caribou have been described as chionophile, i.e. animals highly adapted to living in an environment dominated by snow (Pruitt, 1959). Similarly reindeer on the mountain ranges of south Norway live and thrive in a habitat typically enveloped in snow for seven to eight months in the year, on average from mid-October to late May.

4.2.1. Winter

With the first few heavy snowfalls of early winter the reindeer have no difficulty in digging craters or troughs in the snow to feed on the underlying plants. Craters of 60-80cm are not uncommon in soft snow and up to 1m depths may be found. Sooner or later, wind carries the loose snow from off the tops and ridges and deposits the snow in the more sheltered valleys and /

Fig. 4.2. The interrelation between reindeer body weight increment, plant growth, and seasonal changes in daylength, air temperature, and snow cover on Hardangervidda.



and lower slopes (Fig.14, p.51, App.3). The reindeer do not attempt to dig in these areas of deep snow, but graze on the areas of relatively shallow snow on upper slopes, ridges and summits. Such areas tend to carry the dry lichen heath communities, so that the preponderance of lichen in the diet of reindeer in winter is partly determined by plant availability alone, and partly by actual preference (Gaare & Skogland, 1971). The more snow is shifted by the wind and resettled elsewhere, the denser it becomes (Skogland, 1974). The reindeer respond to this by not digging through the same depth of snow that they could in soft snow, but will dig through snow depths of 40cm, 30cm, and 20cm, as the snow becomes progressively denser or develops a hard surface crust.

On Hardangervidda the main lichen heath communities are in the rolling hills of the east-central part of the range, and it is this part which comprises the main wintering area for the reindeer (Map, Fig.2.4). In early winter the deer are found in this area in various sizes of groups and herds of up to 1,000 or more. The activity of groups at this time is very regular - individuals in the herd synchronise their activity into a grazing period in the morning, lying for 2 to 2½ hours around mid-day, and grazing again in the afternoon (Plate 3). The next day the pattern is repeated. Groups do not usually move much on the winter range, only 1 to 2km in 24 hours on average, just enough for occasional movement on to the next available grazing site. During a grazing period there is frequent interchange of snow craters and feeding spots between /

between animals. A well-antlered female or a young male who has not yet cast his antlers will move towards a lower ranking animal such as a poorer-antlered female, a male who has cast his antlers, or a yearling, and as it withdraws, feed from the crater vacated. If the subordinate shows a reluctance to withdraw, the dominant animal lowers its antlers in threat, and if this is still insufficient it will strike or push its antlers against the other until it retires. (Antagonistic behaviour, Ch. 5.2.). The social hierarchy of winter is as clear an expression of dominance as is seen in the rut, but without the excitement and intensity of the rut. The implications of these hierarchial relationships on body condition and ultimately survival are discussed in Chapter 7.2.

As daylength increases in February and March the reindeer now show two or three lying periods interspersed with grazing periods. In winter only two external factors tend to disturb the regularity of active periods of grazing alternating with lying periods of rumination and rest. One of these factors is disturbance. In winter the reindeers' senses and response to danger is acute, so that the herd bunches together and if sufficiently alarmed they run off at the scent or sight of people, or when a golden eagle or raven flies over, or to a lesser degree if they experience a loud noise such as a snow scooter or low-flying aircraft (Plate 14). Once the 'danger' has passed, they usually quickly settle to their previous activity, whether grazing or lying (Disturbance, Ch.7.9.).

The other factor which disturbs the regular winter activity pattern /

pattern is a storm with high winds. A week or fortnight of clear sunny weather with cold air temperatures of -10°C to -25°C is often followed by a temperature rise and several days of snow-fall and winds. Occasionally, this cyclonic weather produces strong winds which create storm or blizzard conditions. With winds of over 30km/h, reindeer clump together, often for many hours, with animals lying with their backs against the wind, and a few standing with their heads held low into the wind (Plate 37). Occasionally the whole group will start trekking slowly up-wind, then may turn and gallop down-wind. Their activity is interpreted as behaviour to maintain body heat under these wind-chill conditions (Ch.7.3.). When the wind abates slightly the group may move quickly out of the area in which they have spent many weeks. A further consequence of such days of high winds and fluctuating temperatures is that the snow becomes even denser and develops a solid icy crust, which further limits the grazing possibilities for the deer. As a result, reindeer in March and April are often confined in their grazing to bare summits, where they may require to crack a thin ice layer formed over the lichens. Large boulders protruding from above the prevailing snow cover are often visited by reindeer at this time, where they can be seen grazing and gnawing at the foliaceous lichens growing on them (Plate 9).

By the middle of March the reindeer are showing more tendency for movement in the active periods. Adult females particularly are the first to move out to adjacent grazing areas, and a string of animals trekking across the snow invariably has an adult /

adult female at its head as leader (Plate 38). Males by contrast show least tendency to move at this time, and as groups split and join with others the effect is a concentration of males in groups at the rear, resulting in a partial segregation of the sexes. Throughout the winter herds are usually mixed in sex and age structure, although some of the males over-winter in the north area around Hardangerjøkulen (Fig.2.4), and then move south in summer to join the mixed herds.

By April most deer are west of the winter range, spread out in small groups over the available grazing on the bare summits or plateaux, with periods of movement when they typically trek across the snow in long lines towards the next bare ground or beyond. Individuals and groups tend to use the same route as animals that had travelled before them, apparently conserving their energy by not having to create new tracks in the snow. The slow but persistent westerly migration takes the adult females and juveniles some 60-100km west of the winter range to a traditional calving area; in the rolling hills and valleys in west-central Hardangervidda (Map, Fig.2.4). Aerial reconnaissance in mid-May showed a high concentration of animals in this calving area, while males predominated in scattered groups along the migration routes and elsewhere.

4.2.2. Calving

On the calving grounds, immediately before and during the calving period, reindeer activity is notable for its variability /

ility. The synchrony in activity, characteristic of winter groups no longer applies, as groups fragment frequently or coalesce temporarily in different formations. At no other time of the year is the population so split into small groups and individuals (see Fig.7.1). Pregnant females in particular (recognised by the possession of antlers) show least signs of affiliation with others, and often actively move out from a group or stay behind as a group moves on. Yeld females tend to associate together in small groups with their calves of the previous year (now yearlings).

As day-time temperatures rise above $0^{o}C$ resulting in steadily enlarging areas free of snow, the animals concentrate grazing round their edges, often digging through the shallow slushy snow there (Plate 4). Travel between adjacent grazing patches tends to be in single file as in April. Animals often wade through the thawing snow with difficulty, but where night temperatures fall below $0^{o}C$ an icy crust is formed which can be sufficiently strong to hold their weight.

As her time for parturition approaches, the pregnant female shows restlessness but may not actively seek isolation for calving. Signs of labour are inconspicuous, except that the female gets up and lies down alternately many times in the hour before and after the calf is born. The calf is delivered on the ground rather than on snow, but the female may be either lying or standing at the precise moment of birth (Plate 31). The new-born calf is licked almost constantly in its first hour, while it moves around making increasingly successful attempts /

attempts to stand and walk (Plate 33). The first sucklings may be made while both mother and calf are in a lying position, then subsequently from the common standing position with the calf suckling the udder while the mother licks the calf's rear and belly (Plates 34 & 35). Calves of a few hours old spend much time on lying, rest, and in their short active bursts, as well as suckling and rubbing against the mother, they increasingly test their legs by walking, running and exploring their immediate physical environment. Even before they are a day old, calves may nibble tentatively at ground vegetation, usually lichen. The fur of the young calf is reddish-brown which tends to merge inconspicuously into the dried vegetation of the previous year, in contrast to the greyish-white winter coat of the adults.

Unless disturbed, the mother and calf tend to remain in the vicinity of the birth-place for one or two days before the mother moves off, with frequent checks on the progress of its calf which bounds along behind (Plate 32). Mothers then readily associate with other females and their calves to form nursery groups. Despite this voluntary association, mother females in the first few days will not allow a close approach of other females or calves. Unlike the wanderings of calfless groups in the calving season, nursery groups tend to be very static and seldom move more than 1 to 2km over the day. Calves of a few days old increasingly confront and respond to each other in a variety of playful ways, including head bobbing, running chases, and tentative threats (Play, Ch.6.4.).

The /

The calving season is very concentrated. In 1970 and 1971 the first calf on Hardangervidda was observed on 23rd May, and over the next six to eight days 80% of the calves were born. By the first week in June most calves are grazing steadily for short periods. By this time snow has cleared from over half the terrain (Plate 39). The timing of calving on Hardangervidda matches the first emerging vegetation, in particular Carex bigelowii, Betula nana, then later Salix herbacea (Skogland, 1974). On the North Ottadalen range where calving is three weeks earlier, only winter vegetation is available for grazing, and there is a considerable amount of digging at the ground by females to reach the roots of dwarf shrubs (see Ch.5.1.1.).

4.2.3. Summer

From early June the nursery groups grow rapidly in size as mothers and calves are joined by yeld females, yearlings, and males. One month later, aggregation has occurred to such an extent on Hardangervidda that virtually the whole population may be seen in 2 or 3 massed herds of thousands, which make long-ranging movements over the snow-free terrain. On average these herds move 15km and up to 25-30km during the day, becoming relatively stationary in the few hours of darkness.

In one day a herd may range over valley bottoms, up and across slopes and onto mountain tops and ridges, grazing as they go in the bogs, on grassy meadows, and on lichen heaths. The individual reindeer in the herd may be trotting along, then walking /

walking, occasionally taking a few grazing mouthfuls as it walks, stopping to feed at one favoured spot for a few seconds, breaking into a trot again, and so on. An individual's rate and alignment of movement is influenced by that of its immediate close neighbours. Looked at as a herd the strict alignment and proximity of animals to each other results in constant changes in pace and direction, as one part of the herd may surge forward at a trot drawing those behind with them. This surge may 'die out' and more stationary grazing develop, until another part of the herd breaks into a trot. Viewed from a vantage point, a massed herd of thousands at this time often has the appearance of an amoeba, ebbing and flowing as the pace and direction changes. When there is a wind, movement is usually directed into it, until the deer reach the limits of their range in which case they drift to the side.

Although the calves by this time are integrated into the trotting/walking/grazing pattern of the herd, they still show a greater requirement for lying at rest, and are typically the first animals to lie and the last to get up in the short summer lying periods. Not surprisingly, mothers and calves often become separated in these massed moving herds, so that individual females and calves can be seen trotting back against the direction of the herd grunting constantly to locate each other. Successful reunions are usually confirmed by the calf suckling the mother. When a mother does permit its calf to suckle in summer, nearby calves often join in successfully before the mother decides to step over them and break the engagement. The calves' propensity to lie, occasional nursing events /

events, and separations from their mothers, results in a greater concentration of calves and mothers in the rear of moving herds, while males at this time are often found at the head of herds determining the pace of travel.

In the latter part of July, and in August, herds are in hundreds rather than thousands and movement becomes less extensive. However, this general trend towards reduced movement and smaller herd sizes as summer progresses, is often masked or temporarily reversed by harassment from parasitic and blood-sucking flies, the outstanding influence on the reindeers' summer activity and behaviour. Every warm day between mid-June and late August is notable for the emergence and activity of vast numbers of mosquitoes, blackflies, horseflies and warble flies, which distract and irritate the reindeer; and profoundly affect their behaviour as individuals and as a herd.

The first signs of insect harassment can be seen on still days as air temperatures rise above $7^{o}C$, when individual reindeer grazing or walking along start wagging and flicking their tails, shaking their heads and bodies frequently, and occasionally twitching in discomfort and throwing back their heads to bite at some affected area. As the temperature increases and insects become correspondingly more numerous, they react by moving closer together and speeding up their movement by trotting and running as well as grazing into the wind. A fast aligned movement develops similar to the voluntary massed movement of the large herds in early June (Plates 5, 6 & 41). This insect- /

insect-induced movement slows down or stops when the animals arrive in a habitat where insects are scarce or non-existent. In early July, harassed herds on the western side of Hardangervidda run on to the remaining snowfields on the north-facing slopes, and lie or stand on the snow for many hours, during days of little wind and temperatures up to and beyond 20°C. In the central plateau area of Hardangervidda there are no such snowfields, and animals under severe harassment there mass together and move up to hill tops to receive the maximum available wind, which can reduce the harassment to some degree. If this proves ineffective, a herd will move down to the shallow water along the shores of lakes, or in mires, where the combined effect of massing tightly together and trampling the water creates an insect-relief situation by reducing the degree of insect attack on the individual and herd alike (Insect Harassment, Ch.7.7.).

On non-insect days in August it is clear that herds are breaking up into smaller units and dispersing widely over the range. Reindeer are attracted to edible mushrooms at this time, and their scattered distribution may assist this late summer dispersal (Skogland, 1974). All sex and age classes continue to associate together so that the groups, although smaller, remain integrated in readiness for the rutting season.

4.2.4. The Rut

Observations of undisturbed behaviour in the period leading up to the rut are limited, because traditionally the reindeer hunt /

hunt by local people takes place for three weeks in September in the immediate pre-rut period. The concentration of hunters in the field is often such that a reindeer group is disturbed frequently. Even at night when shooting is illegal the presence and movements of hunters in the field may not allow reindeer to concentrate much time on the essential grazing and lying, or the social patterns conducive to rutting. On Hardangervidda in September 1970, a particularly severe "reduction-hunt" (re.Ch.3.4.2.) meant that the deer were on the move either running, trotting, or walking for over half their time, with the remainder of their time spent on grazing and lying, with few signs of pre-rut behaviour (Thomson, 1971). Observations in two subsequent years when hunting was not allowed, showed that in 1971 the rut took place several weeks earlier than before, which suggests that in some years hunting may have a real effect on delaying the time of rutting (Skogland, pers.comm.).

Unlike calving time, reindeer do not move to a fixed area for the rut, but are often found at this time of year in the east-central part of Hardangervidda (Fig.11, p.37, App.3), distributed in small herds over the mires, flats, and lower slopes. On Snøhetta in October 1969, and even more so on Hardangervidda in October 1970 (after the severe hunt), mature males were conspicuously infrequent, so that rutting behaviour was left to the younger males, who do not display the full repertoire of behaviour typical of the mature males, fully observed in North Ottadalen in September 1969 and 1970. Apart from this, the social structure and behaviour patterns at this time were found /

found to be similar in all three areas (Ch.7.8.).

There is no constancy in the size, location, or spacing of groups at rutting time. Groups of up to and over 100 in size move about steadily grazing with lying periods. Despite the males' preoccupation with courtship and displays, there is no attempt by the male to either maintain a geographical territory, or to herd a group of females together in a harem. Instead he will consort with a female who is soon to be in oestrous, and will charge any younger or subordinate males who approach him or the female too closely, and dispute with rival males for dominance. The mature rutting male may be considered to carry his own mobile territory around with him.

As rutting time approaches the males spend less and less time on grazing, until finally the mature males stop grazing completely and spend all their active time on sex-motivated behaviour, including threat displays, self-marking posture, bush thrashing, and antler clashes and fights. These rutting patterns are described in Chapter 5.3. (also Plates 20-25). The female on the other hand continues normal grazing and lying periods at the peak of rut, and in avoiding an adult male's attention merely takes a few trotting or walking steps on to continue her grazing. When a female being persistently courted or "tended" by a single dominant male shows minimal response to his approaches, then a mounting attempt usually follows. Only a small proportion of mountings observed were deemed to be successful copulation (Ch.5.3.1h). Occasionally,wild chasing of a female occurs; this is particularly likely when a /

a large proportion of younger males are present, and at such times of excitement, mounting attempts and fights between males are common. Groups may split up as animals race about over the terrain.

By the middle of October the rut on Hardangervidda is drawing to a close, and as snow falls about this time the deer revert to the steady winter activity of grazing and lying periods on the easterly winter range.

PHOTOGRAPHS

Locations:

Hardangervidda: 1-6,9,12-15,26-31,36-39,41-43.

North Ottadalen: 19-25.

Cairngorm, Scotland: 7,8,10,11,16-18,32-35,40.

All photographs by B.R. Thomson, except Plate 1 by G. Hansson, and Plate 42 by E. Gaare.

1. Winter observation with spottingscope.

2. Hardangervidda - Central plateau from Nappen, 1300 m.

3. Lying period developing in a herd of 130 at Smaaroi, 1200 m, January 1970.

4. On the calving grounds, Smaagrananutane, 1400 m, May 1970: Two pregnant females and a yearling.

5. Summer herd under insect harassment, Langesjøen, 1200 m, July 1971.

6. Female and calf harassed by insects, Langesjøen, July 1971.

7. Nibbling at lichen (unantlered male).

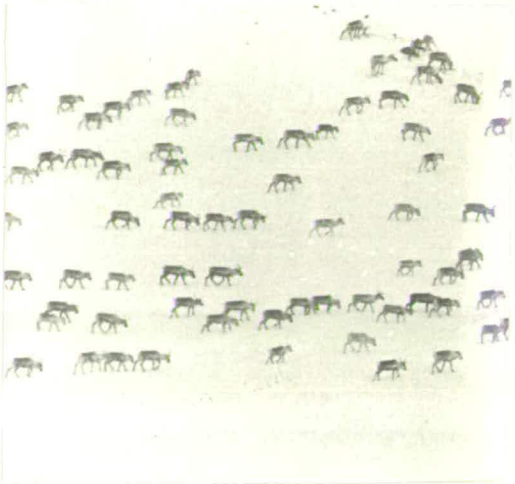
8. Pawing at a thin snow crust.

9. Feeding on lichens off boulders amongst a grazing herd in late winter, Imingdalen, March 1971.

10. Antler-chewing.

11. Drinking.

12. Standing in alarm-urination pose.



13. Walking between adjacent grazing sites in winter.

14. Running in fright by a group disturbed by snow scooter.

15. Stretching after lying.

16. Shaking water out of coat.

Individual Behaviour - Comfort

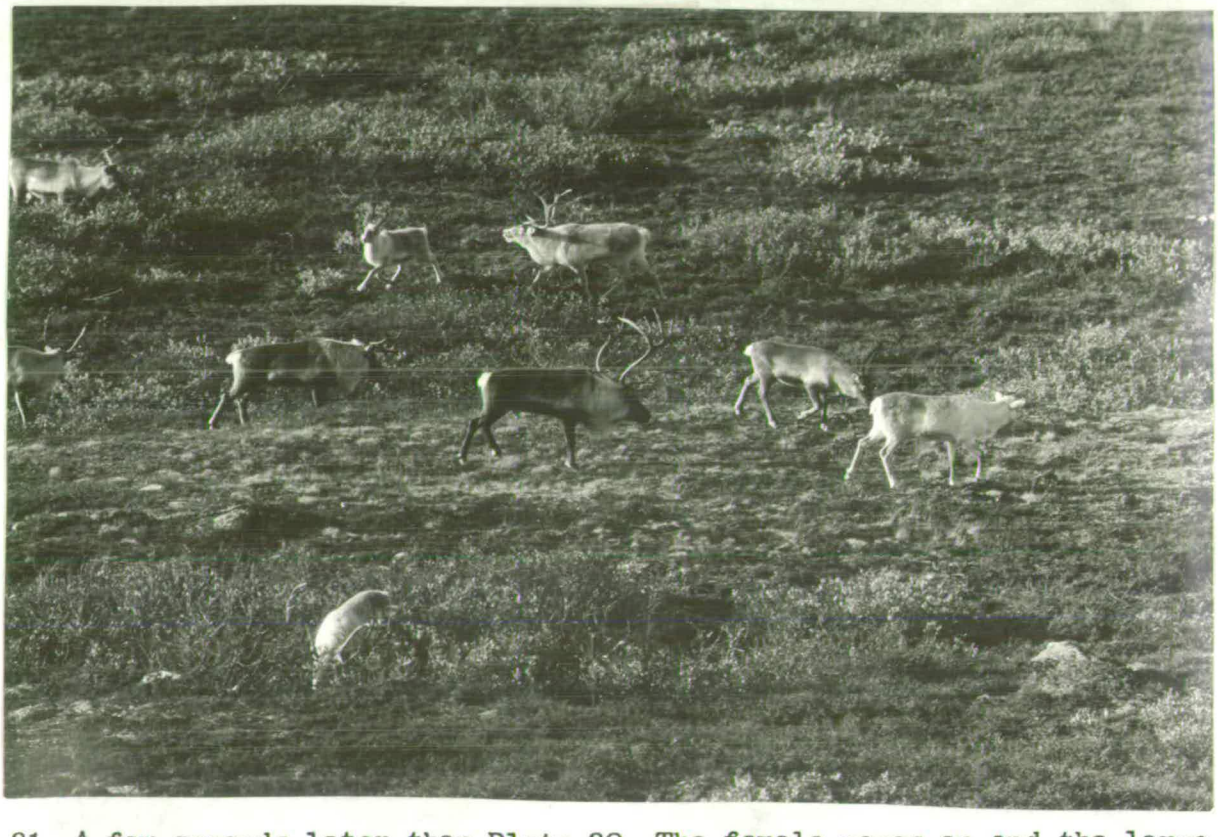
17. Rubbing head with a hind leg.

18. Licking/biting at an irritation.

19. Dead velvet strips hanging from the antlers of a yearling male, North Ottadalen, September 1970.

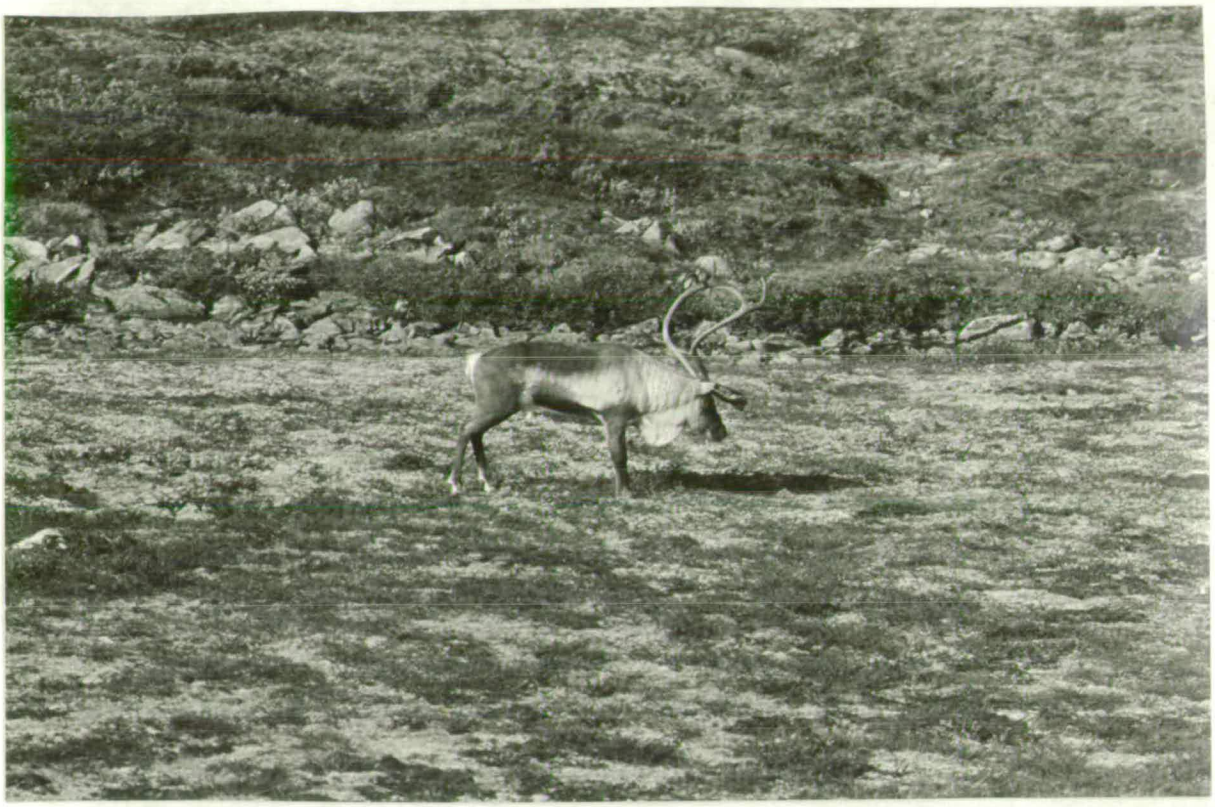
The Rut (North Ottadalen)

20. Large mature male approaching female. Two males are bush-thrashing (foreground), and a young male follows a female calf (background).

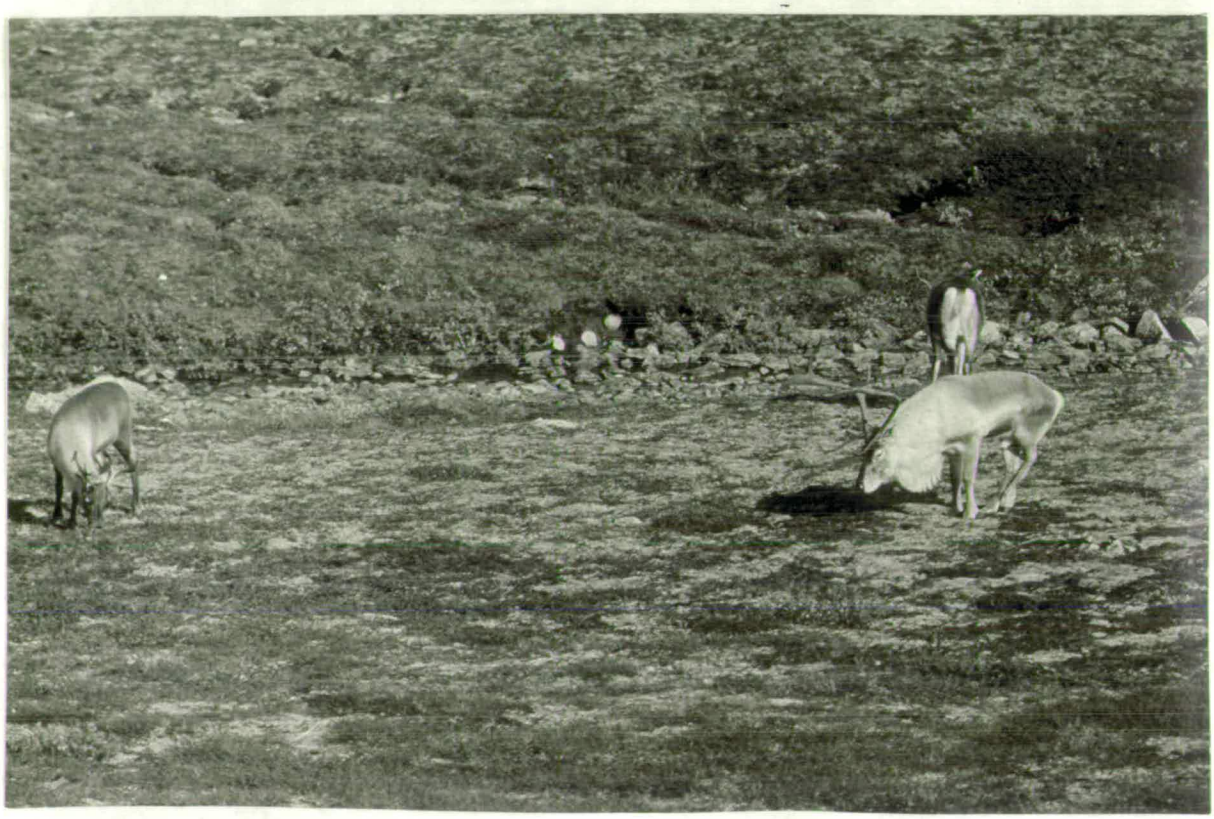


21. A few seconds later than Plate 20. The female moves on and the large male stops. In the background, the same female calf is now being driven by an immature male, with the original young male looking on.

Male Rutting Behaviour



22. Standing pose.



23. Hunching and urinating; consort female on the left.

24. Muzzling and pawing at urine patch; rubbing inner hind legs; contacting hind hoof with antler.

25. Fighting with pushing by mature rivals.

26. Sparring by young males in winter.

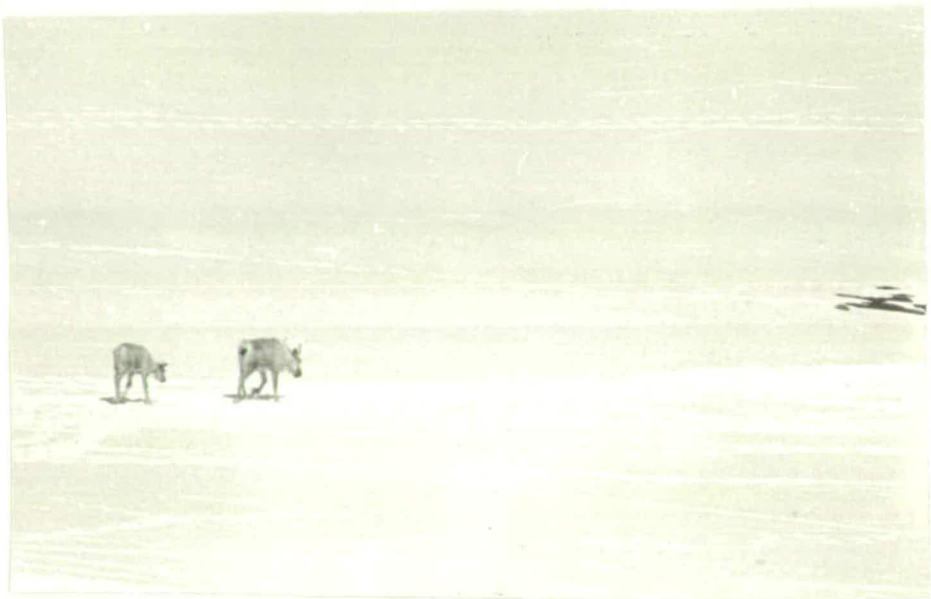
Calving sequence (Hardangervidda)

27. A group of 45 females and yearlings on Smaagrananutane, 23rd May 1970.

28. A foetus is showing from the vulva of an antlered female in the group.

29. The female stops occasionally and turns its head round towards its rear.

Calving sequence (continued)



30. The female moves away from the group followed by a yearling.

31. The female gives birth to a calf, on snow-free ground, watched by the yearling.

32. Calf following mother.

33. Mother licking calf.

34. Lying mother is suckled, and licks calf's rear.

35. Calf comes in to side-suckle mother; she turns to lick the calf's rear; then terminates by stepping over calf.

36. Leadership : Adult female leading a disturbed herd across a frozen lake, Sønstevatn, March 1971.

37. Winter Winds : Herd standing facing into strong wind, Imingdalen, March 1971.

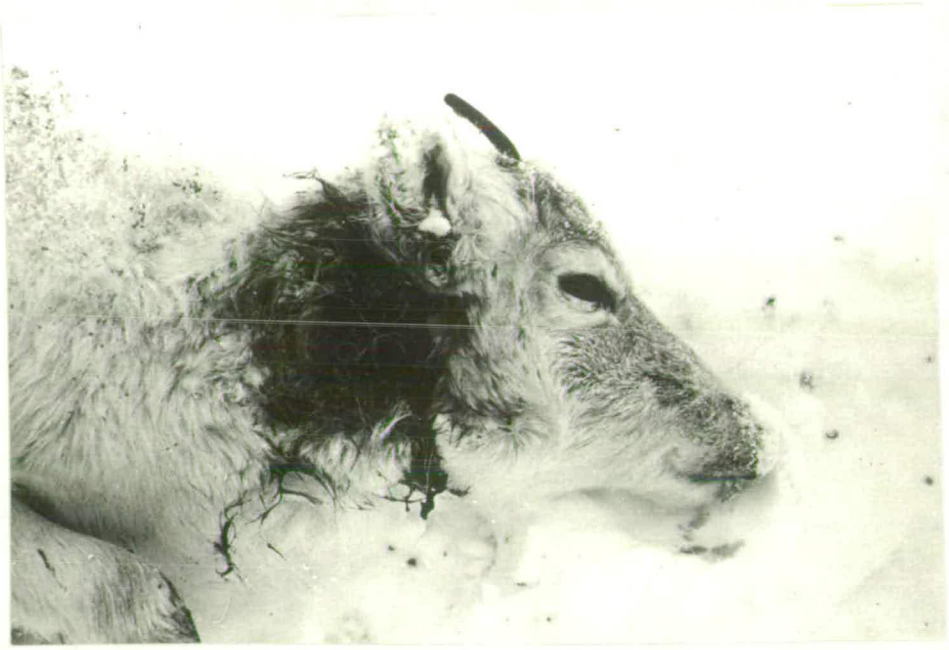
38. Migration : Herd in late winter showing migratory tendencies, Imingdalen, March 1971.

39. Calving Grounds : Snow receding rapidly in the course of the calving season, Smaagrananutane, 1400 m, late May 1970.

40. Mother nurses calf, with yearling looking on, Cairngorms Herd, June 1972.

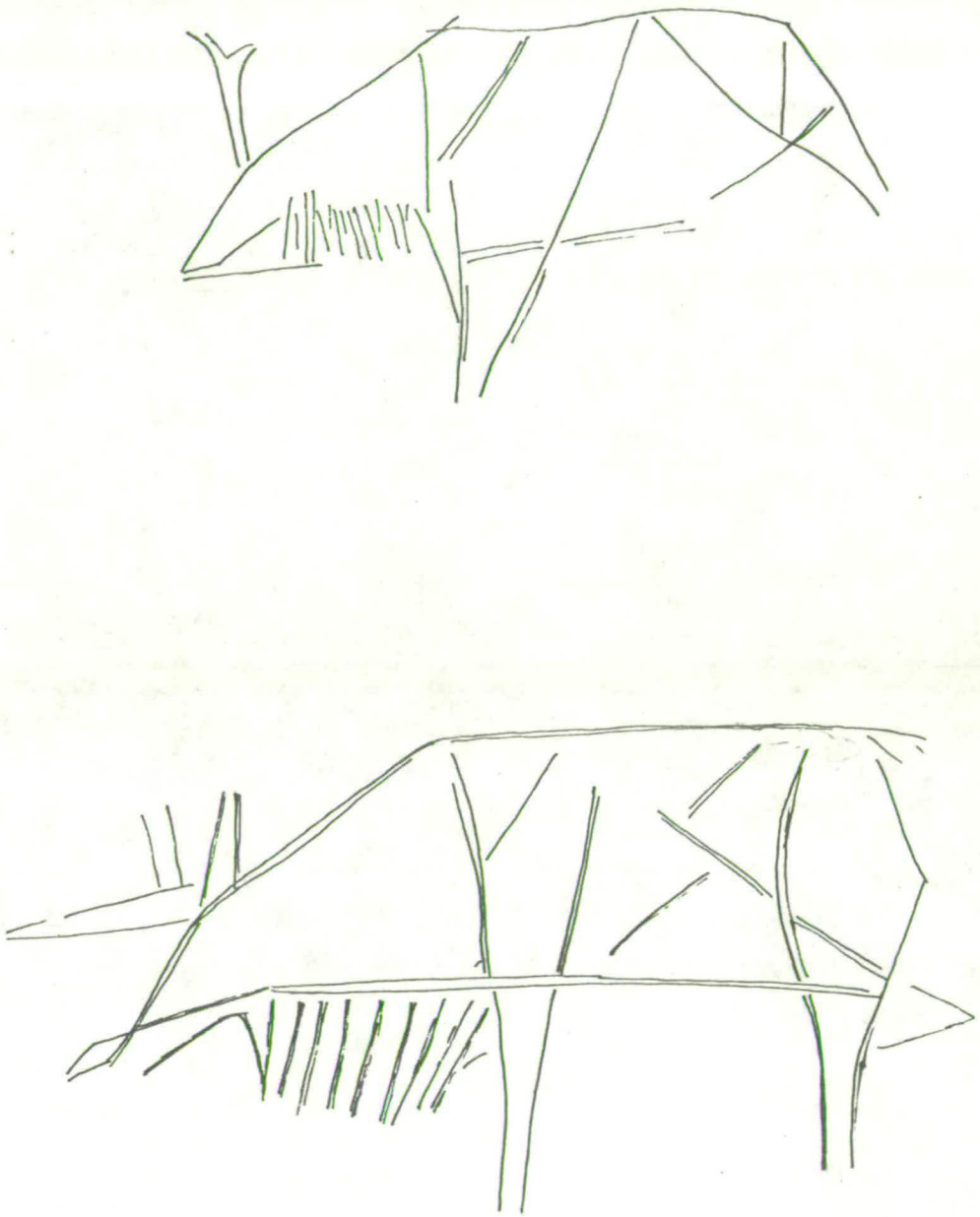
41. Massed herd moving fast under insect harassment, Langesjøen, July 1971.

Natural Mortality



42. Nine-month calf dying from attack by Golden Eagle, Smaaroi, January 1970.

43. 1½ - 2½ year male with broken leg found dead, hole in the back pecked by ravens. Near Sønstevatn, March 1971.



Symbolic representations of reindeer carved on rock by Stone-Age Man (between 6000-2000 B.C.) at Hell, North Trøndelag, Norway. (from Maringer & Bandi, 1953; Hagen, 1965).

CHAPTER FIVE INDIVIDUAL BEHAVIOUR PATTERNS

"There are no such processes as eating, drinking, breathing, and reproducing taken apart from the organisms involved."

Edward Goldsmith, The Ecologist, June 1971.

Following the introductory picture of the seasonal life cycle and responses of wild reindeer in the previous chapter, their types of behaviour are now considered in more detail. This chapter describes the behavioural repertoire of an individual in maintaining itself by ingestion processes, locomotion and comfort behaviour, and interactions between paired individuals in relation to antagonism, sexual behaviour, and the mother-infant bond. The next chapter considers the social behaviour which influences or involves the group as a whole.

5.1. MAINTENANCE BEHAVIOUR

5.1.1. Ingestion

In their natural environment reindeer were found to spend 60-90% of their time on grazing and subsequent rumination of ingested plants, more time in winter than in summer (Thomson, 1971; 1973). Their feeding selection is extremely varied and alters seasonally with plant phenology and snow cover (Gaare & Skogland, 1971; 1975). The vegetative diet was seen to be supplemented by antler chewing, nibbling of small roots, earth licking, eating snow and drinking.

(a) Feeding /

(a) Feeding

On snow-free ground the characteristics of feeding behaviour vary with the type of vegetation being selected. When grazing on plants close to the ground, the reindeer moves its muzzle steadily through the vegetation, its lips nibbling continuously at the lichen or other easily-removed material such as soft herbaceous plants (Plate 7). When grazing on sedges, grasses, and stiffer herbs, the muzzle perceptibly pulls back slightly but sufficiently to sever the selected stems, leaves or flowers between the lower incisors and the upper pad of the mouth. On the woodier vegetation of dwarf shrubs the deer takes a twig into its mouth and pulls upwards, which strips off the leaves or severs a stem. When feeding on larger woody shrubs such as the mountain willows (Salix spp.), this upward raising of the head is a vigorous tugging action as the deer strip off the leaves from selected branches. While reindeer can break off twigs with this half-tugging, half-biting action, their feeding behaviour appears more adapted for material which they can graze. Direct observation of caribou feeding on Alaskan tundra showed that their considerable use of dwarf Salix shrubs was concentrated on stripping off the leaves and flowers. This was verified by analysis of rumen and oesophageal fistula samples at this time, which showed that woody twigs comprised not more than 1-2% of the particles in the diet (Skogland, unpubl. data). Strong chewing of shrub branches as recorded for caribou (Kelsall, 1968) was not observed.

Not all plant particles taken into the mouth in the course of grazing /

grazing are passed down the oesophagus as food. In the continuous grazing process of selection-chewing-swallowing, plant particles may be seen to be expelled from the diastema at both sides of the mouth towards the rear of the jaw. Material such as dead grass stems may be seen to leave the mouth in this way. It has been suggested that the deer are thus able to reject undesirable dead material which they cannot avoid taking in at the first selection. However, dead plant particles in the rumens of four Alaskan caribou averaged as high as 14% of all particles, and similarly, experimental reindeer in the same area had a mean of 22% dead plant particles in samples from their oesophageal fistulas (White, Thomson, Skogland et.al., 1975). This does not support the hypothesis that they are capable of discriminating against and ejecting non-green material from the mouth.

In winter the feeding process is essentially similar, except that craters or trenches are dug through the snow to reach the food plants. These craters are not dug at random. I examined feeding areas by digging down through the snow and reached bare ground, rock and unpalatable plants many times, whereas the craters dug by reindeer did not fail to reach food plants, and were not in excessively deep or hard snow. Prior to digging in snow, reindeer lower their muzzles and will stick them into soft snow and may paw a few times. They will then walk on, or begin cratering at this spot. In an experiment in Newfoundland it was found that three hand-reared caribou successfully scented and dug artificially-buried Cladonia lichens down to 18-25cm under the snow, but much less than 18cm when the snow was /

was compacted (Bergerud & Nolan, 1970). The importance of the physical characteristics of snow in determining which parts of a range caribou or reindeer will or will not be found in winter is well established (Pruitt, 1959; Kelsall, 1968; Skogland, 1974). I consider that these thresholds of snow depths, density and hardness do not reflect the deers' ability to dig through the snow so much as their capacity for scenting food under the snow. For reindeer in south Norway this capacity is much greater than that suggested by the Newfoundland experiment. Reindeer on Hardangervidda regularly dug 60-80cm craters, and up to 90cm in soft snow, with decreasing depths for dense or hard snow. Egorov (1967) notes that the wild reindeer of Yakutia, U.S.S.R., in winter depend mainly on food covered by 60-80cm of snow and have to rely on their sense of smell to discover it.

At one time it was a popular myth that reindeer used their antlers to scrape in the snow for food. Even as notable an ethologist as Konrad Lorenz wrote:
"The antlers of stags, for example, were developed in the service of rival fights, and a stag without them has little hope of producing progeny.....Only the reindeer has based an invention on this necessity and 'learned' to shovel snow with a widened point of its antlers." (Lorenz, 1966.)
In fact, on one occasion on Snøhetta in November 1969 an antlered female was seen to do just that, shoveling away the soft snow in a crater with its antlers before eating. However, out of the thousands of digging events observed, this was clearly exceptional. Even an antlered animal severely wounded in /

in a front leg was seen to use this leg to attempt scraping in the snow, while balancing its weight on its other three sound legs.

Grazing in winter is not all achieved by digging through snow or selecting from exposed 'bare' areas. In late winter, particularly when animals are moving between adjacent grazing areas, individuals or part of a group may visit large boulders sticking above the snow to graze on the rock lichens growing there (Plate 9). This they do by nibbling as for ground lichens, or occasionally by scraping the lichen growth off with their incisors. The frequency of this behaviour is also evident from rumen samples of wild reindeer in April 1970, which showed that on average 25% of lichen fragments were comprised of rock lichen species, whereas in samples from early winter and summer, rock lichens comprised less than 1% of the lichen intake (Gaare & Skogland, 1971).

A more unusual aspect of reindeer feeding behaviour was seen in early spring before the first new growth of buds and leaves had become available. It was recorded on Hardangervidda in late May 1970, but more particularly from North Ottadalen in the first half of May in both 1970 and 1971. For example on 12th May, 1970, 17 out of the 34 adults grazing in an Ottadalen nursery group, were at one stage occupied in digging on a snow-free area. The surface vegetation was thoroughly torn up, the soil exposed, and with subsequent scrapes at the soil the deer appeared to nibble with a slight pulling motion, (as described above for grass and sedge stems). Subsequent examination /

examination of these areas, which ranged in size from 0.3-1.0m in diameter, revealed severed ends of small rootlets of a dwarf shrub, apparently Empetrum hermaphroditum, with no evidence that the soil itself was an attraction. The aerial stems and leaves of this species were regularly found in rumen samples throughout winter 1970/71 on Hardangervidda (Gaare & Skogland, 1971). Since root sap flow starts earlier in spring than shoot growth, it is possible that by digging for rootlets the animals can obtain a diet richer in protein than they can from the senescent aerial parts of the plant at this time. There is a record of caribou eating the roots of Pedicularis lanata at Bathurst Inlet, Canada, also in spring (Kelsall, 1968).

Reindeer do not deliberately lick or ingest earth in early spring when they 'root' for food, although they do at other times. Distance usually prevented my being certain of this in wild reindeer, whereas I did observe calves of the tame reindeer herd in Scotland nibble at peat and soil in the course of grazing (Table 5.1). Soil eating was also observed by all domestic reindeer calves observed by Espmark (1971a), and was thought to be related to intestinal development. Isolated instances have also been recorded for adult Rangifer (Skoog, 1968; Pruitt, 1960; Calef & Lortie, 1975), and probably indicate a mineral deficiency. On 26th November, 1969, investigation of a grazing area on Knutshø, Dovre, which had just been vacated by a mixed herd of 90 wild reindeer, revealed at least six small patches of earth, about 7-10cm in diameter, which had at first been apparently pawed, then licked, until the /

Table 5.1 Comparison of the food selection of 4 female and 3 calf reindeer, by direct observation on 29 - 30 May, 1972, at Cairngorm, Scotland.

Food selected	Females		Calves	
	No. of bites	%	No. of bites	%
Trichophorum caespitosum	96	54	21	34
Cladonia spp	53	30	22	35
Vaccinium myrtillus	19	11	2	3
Carex spp	4	2	5	8
Molinia caerulea	2	1	-	-
Calluna vulgaris	3	2	-	-
Arctostaphylos uva-ursi	-	-	2	3
Rock lichens	1	<1	3	5
Earth	-	-	2	3
Peat	-	-	3	5
Snow	-	-	2	3
Other (clothing)	-	-	1	1

the brownish soil was bare and smooth.

Edwards and Ritcey (1960) observed mountain caribou in British Columbia eating yellowish slush from a frozen lake in an area where they suspected an outflow of mineral rich water. Wild reindeer in Norway have been observed licking at human urine patches in the snow (E. Gaare, pers.comm.), and also from each others' urine patches in the snow (T. Skogland, pers. comm.). Eskimo trappers have utilised the caribou's taste for minerals by baiting traps with urine or salt water (Kelsall, 1968). In Scotland, as in many Scandinavian and Soviet herds, domestic reindeer are supplied with mineral salt blocks to lick. It has been claimed that salt in winter is a vital necessity and that each reindeer requires 5 grams per day to keep it in health (Merlen, 1953).

(b) Antler Chewing

Cast antlers found on the ground or snow are a favourite, although obviously restricted item of the reindeer diet. A reindeer coming across an antler may chew on it for up to 20 minutes, and have to catch up with the herd afterwards which was not observed to happen with any other food source. The points of the antler are thoroughly chewed with a sideways motion of the jaws, as the back molar teeth grind on it. The antler is held from the side of the mouth and may be momentarily lifted in the air. Blood marks found on at least one recently chewed antler, suggest that reindeer mouth parts are not efficient at coping with this hard bone material, although over a long period the antler may be worn down to a stub /

stub, particularly when successive animals chew on it. Most reindeer antlers found in the mountains have been chewed, and this is invariably by the reindeer, as antlers chewed by carnivores or rodents are seldom found (Kjos-Hanssen, 1973a).

Chewing of cast antlers was observed 13 times in this study, 6 times by females (both lactating and yeld) at calving time, 4 times by females in autumn and winter, and twice by males (Table 5.2). Calves were not recorded as chewing antlers.

The range of observations in Table 5.2 fit with Kelsall's (1968) belief for barren-ground caribou that females do most of the chewing, particularly in the spring. However, since one would expect to find cast antlers on the calving grounds, this is perhaps not so surprising. The observations also show that the behaviour is not restricted to any one range in Norway.

There were some amusing incidents connected with antler chewing. For example, a Hardangervidda female grazing at calving time caught sight of a white antler-like structure some 30m down slope and trotted purposefully towards it, only to give it a perfunctory sniff - it was a dead juniper branch. In the January 1970 event (Table 5.2), the young antlered male chewing the antler paused to threaten a nearby calf, then proceeded to 'spar' with the dormant antler for a few seconds, before continuing chewing. A female in March 1971 chewing on a large male antler partly embedded in the snow, was repulsed by a passing male who scratched his face on the points of the antler /

Table 5.2 Observations of chewing of cast antlers.

Date	Range	Reindeer chewing antler
15/10/69	Snøhetta	Female (calf accompanying)
17/10/69	Snøhetta	Female
20/10/69	Snøhetta	Unclassified adult
26/1/70	Hardangervidda	Young male
4/3/70	Forelhogna	Mature unantlered male
20/5/70	North Ottadalen	Mother female
23/9/70	Hardangervidda	Female
5/3/71	Hardangervidda	Female
9/5/71	North Ottadalen	Female
23/5/71	Hardangervidda	Female
25/5/71	Hardangervidda	Five consecutive females
30/5/71	Hardangervidda	Mother female
30/5/71	Hardangervidda	Female

antler, pawed at it with a hoof, then walked off allowing the same female to return and continue chewing.

In the course of sample culling of reindeer in January 1970 (Gaare et al., 1970) it became apparent that antler chewing behaviour is not restricted to cast antlers. Eight out of nine reindeer shot (7 females, 2 calves) showed evidence of having had their antlers chewed on. The antlers of one female had been reduced on each side to 15cm and 5cm from the skull, while the antler spikes of a calf had been chewed down so far into the head hair that the calf appeared unantlered. The behaviour causing this was looked for but not observed until 7th December, 1971, when in the course of a lying period a female standing was watched chewing steadily on the single spiked antlers of a lying female for over 10 minutes. As the standing female chewed first one side, then the point of the other antler beam, the lying female moved its head occasionally, but otherwise remained unperturbed throughout, quietly ruminating. A similar situation was seen in the tame herd at the Cairngorms, Scotland, in November, 1972, when a female stood chewing the gradually diminishing antlers of another lying female, for over 45 minutes (Plate 10). Apparently this particular old female is responsible for much of the antler chewing in this herd (M. Utsi, pers.comm.).

Related to this behaviour was an observation in September, 1970, on North Ottadalen, when a female stood over a lying calf and ate bits of the dead velvet hanging in strips from the calf's spikes. Unlike antler chewing, the velvet is of doubtful /

doubtful dietary significance. Similarly, ingestion of the placental afterbirths by mother females at calving time (Ch.5.4.2.) more likely has a value in disposing of material which could attract predators, rather than a nutritional benefit. Remnants of the placenta were evident in the rumens of caribou mothers two or more weeks after ingestion (Miller & Parker, 1968). Indeed, it may seem surprising that rumen microfauna can cope with this kind of material at all, although reindeer have been recorded as ingesting animal material such as fish, birds' eggs, nestlings and lemmings (Jacobi, 1931).

(c) Drinking and Eating Snow

The reindeers' water requirements are served by the moisture content of the diet, by drinking water in summer, and by fortuitous or deliberate ingestion of snow in winter. Animals were seen drinking on 20 separate occasions from May to October at any time when open water was available in lakes, pools or rivers. On a September morning following a night frost, a female was seen to break the thin ice over a small stream by stabbing with her front hoof before drinking there for fully a minute. In the rut, mature males cease grazing and ruminating, but will occasionally take a drink. On some occasions a whole group were seen to wade into a lake and stand there drinking.

To drink the animal lowers the tip of its muzzle into the water and without lapping the tongue, it appears to suck up water before bringing the muzzle out when satisfied (Plate 11). In summer and autumn, drinking by the two experimental deer was often seen, and is probably commoner in wild reindeer than was /

was recorded, owing to its resemblance to grazing at a distance.

In winter the experimental reindeer were offered water, but refused to drink (A. Skaar, pers. comm.). In Alaska, too, it was found that penned reindeer calves in winter refused to drink but showed a craving for eating snow (Reimers, in Luick et.al., 1971). In winter considerable ingestion of snow must occur in the course of normal grazing, through ice and snow adhering to the food plants, particularly lichen. Eating soft snow in winter has also been observed (T. Skogland, pers.comm.).

The reindeer's aversion to water in winter is not reversed in summer - on three occasions in spring and early summer I observed wild reindeer eating snow from snow fields. Edwards and Ritcey (1960) have similarly observed caribou eating snow on hot summer days in the mountains.

(d) Rumination

In all ruminants, ingested feed is sooner or later regurgitated from the rumen back to the mouth, where it is re-chewed and re-swallowed. After an active period of grazing, a herd will lie for rumination and rest. The timing, duration and influences operating on these alternating grazing and lying periods was studied in detail over two years for the Hardangervidda population (Gaare, Skogland & Thomson, 1970; Thomson, 1971; Thomson, 1973; Gaare, Thomson & Kjos-Hanssen, 1975; Appendices 1, 2, 3 & 4). Herd lying periods start as a few animals cease grazing and start to lie, then others progressively /

ively join them. Lying sites in winter are usually off the main grazing area on a flat or sloping area of snow, and before lying down an individual may scrape the snow a few times before settling (Plate 3). To lie a reindeer kneels on one foreleg then the other, then brings both hind legs forward under the body and its rear sinks down. As the body comes to rest with a slight rocking motion this allows a final readjustment of the legs. After an hour or more of lying many animals will have stopped rumination and will often tuck their heads round into their body in a sleeping position. In warm sunny weather in winter animals may lie with their legs stretched out to the side and head resting laterally on the ground. This does not occur on warm days in summer when insects are active. Occasionally animals will ruminate while standing and this becomes the rule when they are harassed by insects in summer, or blizzards in winter.

Rumination usually begins within a few minutes of lying down. A bolus of herbage may be seen to intermittently pass up the oesophagus into the mouth, followed by the steady lateral jaw movements of 'chewing the cud'. Rumination time is known to be longer with poor quality herbage of high fibre content and low moisture content (Hafez, 1969). Samples of the reindeer diet were found to have a higher fibre content in winter than in spring or summer (Gaare & Skogland, 1971). This may be reflected in the calculated activity times in that the average length of lying periods in winter (2.3 hours) and the average time spent on lying (35%) is significantly greater than in summer (1.1 hours and 25% time respectively) (Thomson, 1973; App.3). /

App.3). Ruminating time was not measured separately but it seems likely that the winter diet requires a longer mastication time.

Calves may be observed to graze tentatively from their first day of life, but not until about the age of 10 days are the first intermittent signs of rumination seen. By the age of 3 weeks calves are ruminating regularly for short periods. Throughout their first summer the rapid chewing movements of the calf while ruminating contrasts with the slow steady jaw movements of the adults. The cyclic alternation of grazing and rumination remains the basic maintenance behaviour of the reindeer throughout its life.

(e) Urination and Defecation

The final stage in the feeding process is the elimination of unused material through defecation and urination. While eliminative behaviour is an involuntary regular process, there are certain features of behavioural interest.

An animal passes faeces with a slight raising of the tail in the course of its normal activity, whether moving, grazing, standing, or even lying; whereas urination only occurs while an animal is stationary, either standing or grazing. Females and young animals nearly always spread their hind legs apart to urinate and may flex them a little in a squatting position, with the tail usually raised to a horizontal position. Males, on the other hand, do not normally spread out their hind legs, and as the penis directs urine just forward of the hind legs, they /

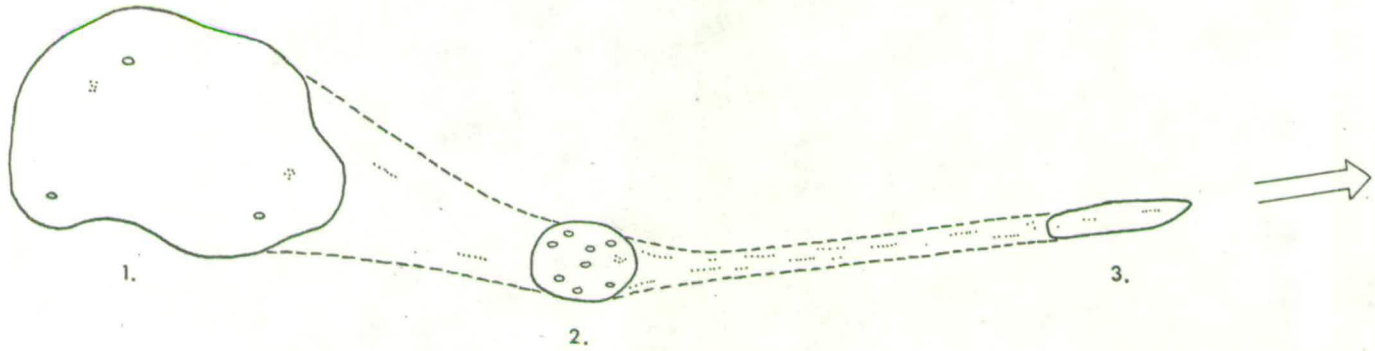
they avoid soiling themselves. This difference in urination position assisted in sex identification during herd composition counts.

Urination and defecation are particularly common after a lying period. In situations of alarm there is an interesting response - when alerted an animal will urinate with hind legs apart and continue holding this position (Plate 12). This acts as a visual alarm signal to other reindeer who also take up the stance and urinate (Communication, Ch.6.1.). If an alarm is confirmed and the deer run off, they invariably defecate while running. Thus, while urination occurs in the tense situation of possible alarm, defecation is the response to the release of tension represented by running. Observations and investigations of the snow tracks of many alarmed herds in winter showed this typical pattern (Fig.5.1). The probability of a link between a state of tension and urination is further suggested from observations of animals displaying searching behaviour (Ch.6.2.1.). For example, in the course of one hour a lone female searching for a herd appeared ultra-nervous and alert and gave the urination position at least seven times.

Continuing to hold the back legs apart after urinating also occurred in situations other than those of tension or alarm, for example by animals who waded into water or moved across snow patches. Cold on the legs or belly may have been a physical stimulus to urinate. Holding of the urination position is also seen amongst sub-groups of males in winter, especially when they are involved in residual sex behaviour, and in so doing they may be seen to sniff each others urine patches (Ch.5.3.3.). In the rut, urine appears to be a powerful olfactory /

Fig. 5.1 The urination and defecation responses amongst an alarmed herd as evidenced by trails in the snow.

(Based on the flight behaviour of a herd of 90 on Snøhetta on 26th November, 1969)



1. Herd grazing peacefully - scattered urine spots and pellet groups.
2. Herd clump together in alarm - many urination spots.
3. Herd run off in flight - many strings of pellets.

o Urination
⁘ Defecation

olfactory stimulus, and mature rutting males display a hunching posture which directly enables them to splash their legs and neck mane (dewlap) with their own urine at this time (Ch.5.3.1(c).).

5.1.2. Locomotion

(a) Walking, Trotting, and Running

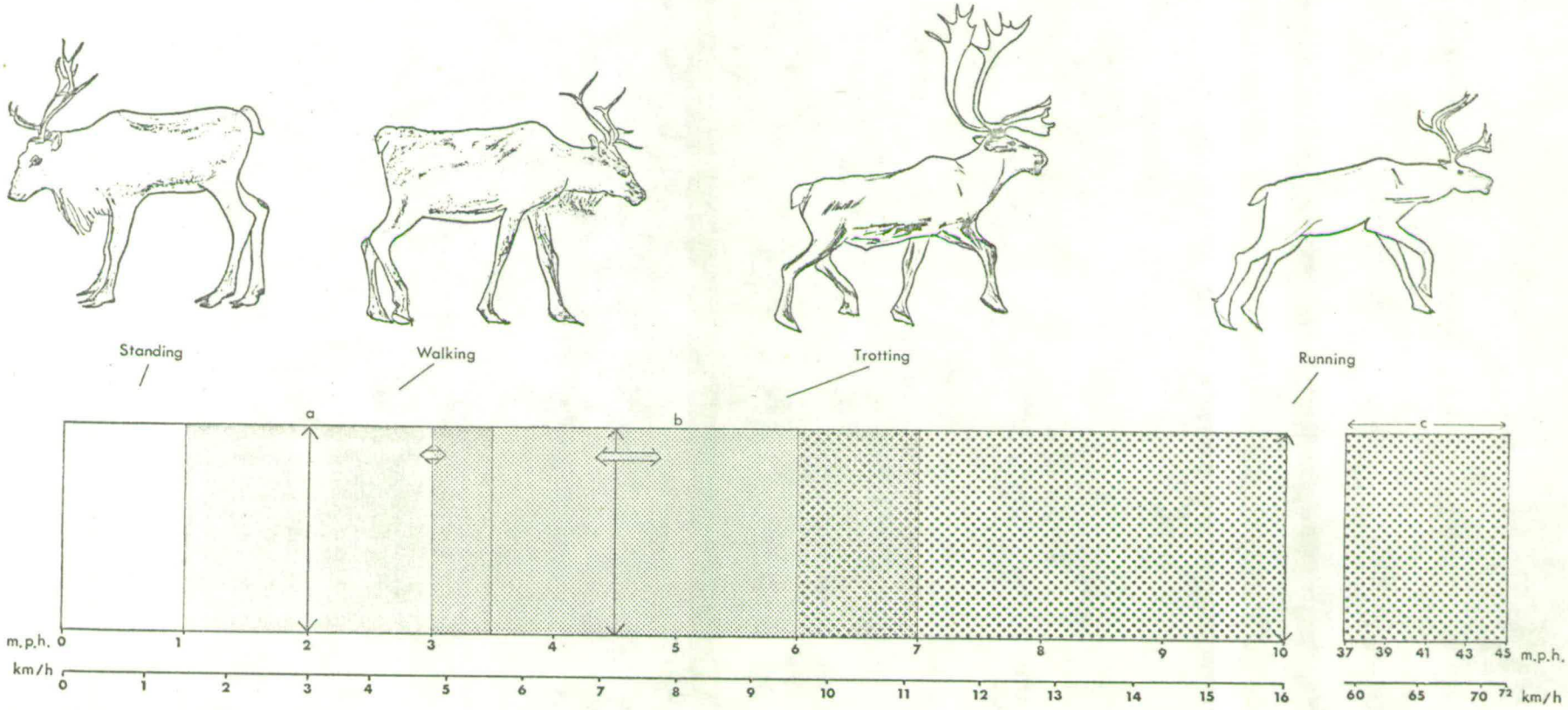
Movement in reindeer can be readily classified into one of three types - walking, trotting, and running. While walking, the hind hooves are placed in the track that the fore-hooves have vacated, while only alternate hind and forelegs leave the ground at the same time. The track pattern is similar with trotting except that the animal springs off its legs so that three, or all four hooves may be off the ground at the same time. With running, the alternate pattern merges into a bounding motion in that the hind legs are brought up together towards the forelegs which reach out for the next bound (Plates 13 & 14).

Walking, trotting and running represent increasing speeds of movement but not fixed speeds. At Prudhoe Bay, Alaska, the speed of movement for experimental reindeer was measured (Fig. 5.2.). While grazing intensely the reindeer's walk is usually a deliberate step at a time. Normal walking without grazing is a steady trek at 1.5 - 3.0 mph (2-5km/h), and beyond 3.0 - 3.5 mph (4.5-5.5km/h), the animal breaks into a slow trot. Reindeer trot at varying speeds of up to about 6 - 7 mph (10-11km/h), beyond which they switch /

switch to running (Fig.5.2). Trotting and running are infrequent activities in winter except when moving down slope, or at times of alarm, whereas they are common activities during the summer grazing periods. Full speed running or galloping is typical of disturbance situations, including severe insect harassment, and calves at play. A two-month old caribou calf at Prudhoe Bay raced at at least 30 m.p.h. (48km/h) over the tundra for 2 minutes of play. Mean speeds of movement in free-ranging animals were estimated as 2 m.p.h. (3.2 km/h for walking, 4.5 m.p.h. (7.2km/h) for trotting, and 10 m.p.h. (16km/h) for running (Fig.5.2). There is no conflict between these means and the few previous estimates of speeds of locomotion. Dugmore (1913) considered the regular walking speed for caribou to be around 2 m.p.h.. Pruitt (1960b) found that a caribou female and calf moved easily over hard snow or a frozen lake for 1½ miles at a speed of 5 m.p.h. - presumably while trotting. When stretched at full pace in front of a train or snow scooter, caribou have been clocked at 37 m.p.h. up to 45 m.p.h. (Banfield, 1954). The importance of movement in reindeer's energy expenditure is assessed in Chapter 8.

Variations on the basic forms of movement are occasionally seen. On being disturbed, reindeer often circle round the alarming stimulus and trot off with a springy stiff-legged gait with tails raised high before breaking into a run. This exaggerated trotting gait is especially characteristic of individuals suddenly surprised at close range. Other reindeer seeing this gait react with alarm, while the circular or winding route taken by the animal is thought to spread more effectively alarm scent from the caudal glands of the upraised tail /

Fig. 5.2 Speeds of movement of reindeer from trials at Prudhoe Bay, Alaska.



Range of speeds from 9 walking trials over a 120m stretch, and 6 trotting trials over a 800m stretch, indicated by horizontal arrows. Estimated means for types of movement are indicated by vertical arrows. Studies on experimental female reindeer by B.R. Thomson and R.G. White, at Prudhoe Bay, Alaska, July 1972.

Other estimates:
(a) Considered as average walking speed of caribou (Dugmore, 1913).
(b) Speed of caribou female and calf moving over level hard snow (Pruitt, 1960b).
(c) Maximum range of speed of caribou chased by trains and snow-scooters (Banfield, 1954).

tail (Lewin & Stelfox, 1967; Ch.6.1.4.). This springy trot is also a main play pattern of calves (Ch.6.4.1.).

In winter, in deep snow incapable of holding the reindeer's weight, animals will bound rather than try to plough through it. Following heavy snow falls in January 1970 at Smaaroi, Hardangervidda, a herd of 200 bounded through deep soft snow in single file. In thawing snow at North Ottadalen, a nursery group were watched bounding and trotting downhill through shoulder-deep snow. The calves leapt, fell, and tumbled through the snow but eventually all succeeded in following their mothers.

Reindeer seldom have occasion to jump and, unlike other Cervids , show little proficiency when the occasion presents itself. Twice in summer a group were watched leaping over the banks of a small stream, animals springing from their back legs, and landing with all four legs together. Although the distance was no more than 2-3m, some deer chose to wade across the stream. When confronted with small pipelines no higher than 0.3m off the ground, caribou at Prudhoe Bay, Alaska, were observed to step over them at a walk or trot. Any higher than this formed a barrier which caribou would not attempt to jump over.

Reindeer, especially single animals suddenly frightened at close range, will occasionally bound off from the back legs as they run off, but never exhibit the exaggerated vertical leap and twist performed by caribou, and termed the spy-hop (Murie, 1935) or /

or excitation jump (Pruitt, 1960). This is one of the few individual behaviour patterns which differ between reindeer and caribou (see Ch.9.4.).

(b) Swimming

Water is not usually a barrier to reindeer movement, and when crossing rivers they will readily swim where the depth of water requires it. Also, on three occasions on Hardangervidda herds of reindeer were watched swimming across lakes. In mid-July 1970, a mixed herd of 700 moved onto a strip of land jutting out into Nordmannslaagen, and massed together on the shore with much vocalisation. When a female waded in and had swum 10m followed by its calf, the rest of the herd moved in without further hesitation to swim the 30m stretch. Their thick air-filled coats make reindeer buoyant swimmers; the head is carried high, the tail held erect, and the legs used as paddles for propulsion. On climbing out of the water a reindeer would typically walk a few steps up the bank, stop and shake vigorously several times so that a cloud of water is released. They would then start leaping, bounding, and running wildly, apparently as a reaction to the cooling stimulus of the water. On another occasion in August, a massed herd of 850 was seen to swim 15m at Tinnhølen led by a female, with much shaking, bounding, and leaping afterwards, but without running. On 8th September 14 animals swam 40m at a frequently used crossing place between Nordmannslaagen and Bjornesfjorden, and after shaking, trotted off in an orderly fashion led by a female. A group of 10 adults without calves were watched in early spring (1st June) skirting open water in the middle of ice-covered /

ice-covered Bersavikvatn lake when one yearling broke through the thin ice, and on clambering out shook 8 times and trotted about agitatedly while the others continued walking.

5.1.3. Comfort Behaviour

The individual reindeer keeps its coat, skin, and muscles in good condition and relieves irritations by a variety of comfort behaviour patterns. Stretching and shaking are the two commonest patterns. Other grooming behaviour includes contact by the muzzle or antler to rub, scratch, bite, or lick some part of the body. With the exception of grooming of the young calf by the mother (Ch.5.4.3.), mutual grooming does not occur, unlike some other Cervid species, notably the Odocoileus genus (Linsdale & Tomich, 1953; Palmer, 1951; Miller, 1971).

Comfort behaviour is most commonly associated with lying periods. When the primary needs of feeding and moving are temporarily satisfied, reindeer are particularly prone to scratch or rub themselves. Comfort behaviour is socially facilitated in that animals are stimulated to groom themselves when they see others doing so. Grooming appears to be low in the 'hierarchy' of behaviour, in that it does not often occur until other more urgent needs are satisfied.

However, there are times when comfort itself is an urgent need, in particular to relieve an immediate irritation on some part of the body, for example due to the discomfort caused by the emergence /

emergence of warble larvae through the skin, the growth of the antlers, insect attack in summer, or because of hooves breaking through hard icy crusts. Summer insect harassment in particular causes constant efforts to alleviate discomfort, coupled with avoidance behaviour, and is distinct enough to be considered separately from normal comfort behaviour (Ch.7.7.).

In addition a number of minor comfort patterns connected with relief of the respiratory and digestive tracts were recorded, in particular sneezing, coughing, belching, and yawning.

(a) Stretching and Shaking

Stretching is performed by animals which have risen from lying. The head is pushed forward and upwards, the tail is erected vertically, the legs stiffen, and the animal leans its weight back so that the front legs are stretched out ahead of it. It then leans its weight forward onto its front legs, so that the hind legs are now stretched out behind it (Plate 15). It may then take a few stiff-legged 'goose-steps' before relaxing its muscles. The complete sequence is particularly common in reindeer getting up after the long lying periods of winter. In the course of lying periods also an individual will often get up, stretch, then lie again; or less commonly will remain lying and stretch out its head and stiffen its tail for a few seconds in a lying stretch.

By stretching, the animal is presumably relieving any stiffening of the joints and the muscles which could occur after a long /

long lying period, and preparing the muscles for action. The pattern appears stereotyped and is even performed as a matter of course where its function is unnecessary; young animals particularly often show an exaggerated stretching complete with goose-steps even when they have only lain for a minute or two. Similarly, adults which have not lain long but are forced up by a threat from a dominant animal may go through the whole stretching sequence. Conversely, even after a long lying period in cold winter weather, not every animal will stretch.

Shaking often occurs after lying but unlike stretching is not restricted to such times. Shaking of the head alone can occur while lying, whereas in a standing animal the shake begins at the head and with a rapid vibratory motion ends at the tail after a few seconds, in similar fashion to a dog shaking itself. Shaking has an obvious function in restoring the coat to its full insulative properties by shaking out the hairs which are flattened by lying. Shaking is also frequent under wind-chill conditions in winter (see Ch.7.3.). Similarly, whenever the coat becomes wet, for example during the rain or after lying in a boggy area, animals invariably shake off the moisture. If the coat becomes very wet, as it does after swimming or in heavy rain, the animal may shake several times in succession, sending off dense sprays of water (Plate 16). Shaking of the head or body is also one of the responses to insect harassment in summer. Frequent head shaking and tail flicking are the first signs that there is some mild insect harassment, generally from mosquitos (Thomson, 1971; and Ch.7.7.). /

(Ch.7.7.). The act of shaking remains the same whether the reindeer are shaking out the coat to its full insulative properties, shaking off moisture, or shaking off insects.

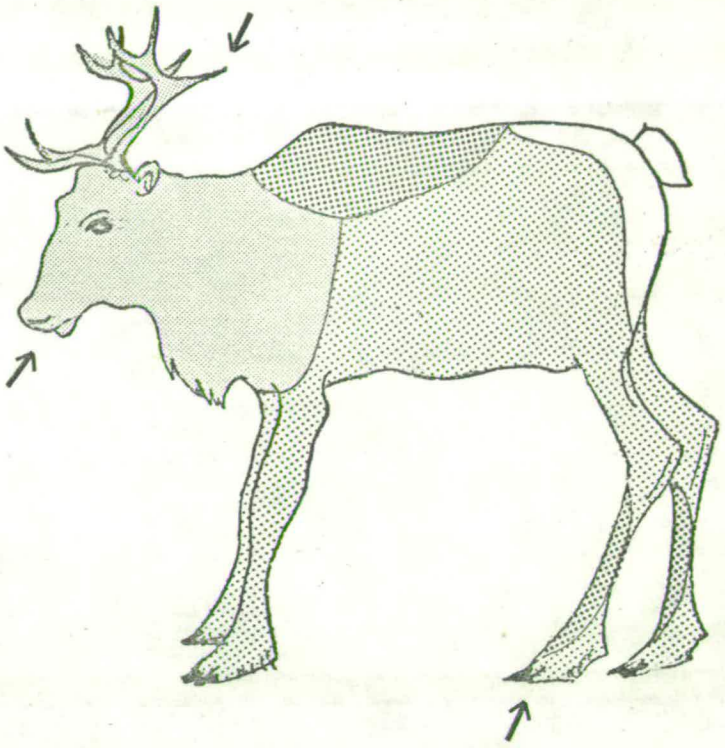
(b) Contact Grooming

Unlike shaking, when an animal grooms itself the act is localised to that part of the skin surface where the animal experiences a particular irritation or itch. From hundreds of observations of animals variously scratching, rubbing, biting, or licking themselves, it would appear that there is no part of its body that a reindeer cannot contact, with the possible exception of the extreme rear, and part of the back if the animal is unantlered. (Fig.5.3). Thus, a hind leg is lifted forward so that the hoof can scratch the antlers, head, and neck regions (Plate 17); the head is turned back so that the muzzle can rub, bite, or lick the rear portion and legs (Plate 18); and the (hard) antler is laid over the back to scratch, or turned to contact the back leg, which is brought up to meet it. The variety of contact grooming patterns are most frequent just before, during, and after the lying periods.

At particular times of the year, skin irritations are more frequent. In summer, the growing velvet antlers seem to be particularly sensitive and are often gently rubbed or tapped with a hind leg. This behaviour is even more pronounced following rain, the animal probably responding to the cooling effect of evaporation from the velvet antler.

From June to August the sudden turning of the head round to rub /

Fig. 5.3 The self-grooming capability of reindeer.



Area scratched by hind leg

Area scratched by antlers

Area bitten or licked by muzzle

rub or bite at the side of the body is more frequently seen than at other times. Warble fly larvae (Oedemagena tarandi) which have over-wintered and grown under the reindeer's skin, are emerging and dropping to the ground to pupate at this time. The emergence of these larvae presumably causes discomfort, and the reindeer respond by turning to contact the area. On warm days in summer turning suddenly to bite at a part of the body is also a common response to attack by the adult warble flies (Ch.7.7.; and Espmark, 1968). In early summer, turning to bite at a skin irritation on the side of the body often results in the animal getting a mouthful of its own loose winter hairs, which are moulting in tufts at this time. Any shaking which occurs also causes the old winter hairs to fall out.

In winter, the whole variety of contact grooming patterns are irregularly apparent. However, on Hardangervidda in January, 1971, the particular frequency of licking of the front and back legs just above the hooves was considered to be the result of discomfort caused by the deer frequently breaking through the icy hard but brittle crust which had formed on the snow surface at this time.

(c) "Velvet-Cleaning"

It is generally assumed that in Cervid species cleaning velvet from the fully grown antlers is a deliberate act of grooming. Caribou are said to strip their velvet and "polish" their antlers by forceful rubbing and scraping on young trees or shrubs (Kelsall, 1968). However, it is not suggested what adaptive value velvet-cleaning or polishing of the antler could have. /

have.

For reindeer males in August and September, bits of the velvet occasionally come off when an animal scratches its back legs with an antler, and is soon entirely removed when the male begins its antler sparring matches with other males, or thrashes its antlers through bushes. However, this behaviour does not stop when velvet is removed, on the contrary, it builds up to a peak in the rut, long after the velvet has gone. The male's use of its antlers at this time is connected with his sexual libido, and the initial stages of his developing rutting behaviour removes velvet as a mere incidental. The antlers of female reindeer take some weeks longer than the male's to cease growing (re.Fig.4.1), so that in the rut many females still have their fully grown hard antlers covered or partly covered by dead velvet. Occasional bush-thrashing by some females in the rut occurs regardless of whether the female still carries velvet or not, and strips of velvet may be seen hanging from the antlers of females or juvenile males without any attempts to remove it (Plate 19). Indeed, some of the females and calves culled in late winter were found to still have bits of dried velvet adhering to their antlers. There is no firm evidence for specific velvet-cleaning behaviour in reindeer of either sex; antler thrashing of shrubs may remove velvet but only has significance in relation to sexual behaviour.

The antlers and head are a region of the body which receives special attention from the animal, particularly by the male. However, /

However, contact in the head area cannot always be unequivocally designated as comfort behaviour because of the relation to both aggressive and sexual behaviour. The hard antler is used in antagonistic threats and disputes by all animals, notably by males in the rut, and by females asserting their dominance in winter and at calving. The prolonged sparring bouts of young antlered males in winter, on the other hand, has both playful and erotic connotations, as evidenced by occasional penis erection of one or both sparring partners (see Ch.5.3.3.). Even after males have cast their antlers in winter the borderline between grooming behaviour and erotic stimulation is very indistinct. Unantlered males in winter may deliberately rub their heads with a back leg, or rub against the heads of other males, and in the process they too may show some erection. It is an open question whether in the process of relieving an itch they become aroused, or whether they spar or scratch to attain erotic stimulation at this time.

Such motivational variation in apparently simple behaviour of head scratching or 'velvet-cleaning' is clearly an example of the dangers of taking too naive or anthropomorphic a view of the function of a behaviour pattern.

(d) Sneezing and Coughing

In summer the nostril fly (Cephenomyia trompe) ejects viviparous larvae into the nostrils of reindeer. These larvae migrate into the nasal channels where they grow over winter and are sneezed or coughed out by the reindeer in late winter /

winter (Skjenneberg & Slagsvold, 1968; Zhigunov, 1968). Hardangervidda reindeer culled in April were found to have heavy infestation of nostril fly larvae in the nose and throat passages (Gaare, Skogland & Thomson, 1970).

Bouts of sneezing and coughing were particularly recorded in late winter and were presumed to be the result of this larval irritation. Caribou have been described as "coughing like consumptives in the last stage" at this time (Munsterhjelm, 1953). Of the 25 sneezing bouts recorded from 4th March to as late as 26th September, 21 occurred in April and May (Table 5.3). An animal about to sneeze could be lying, or alternatively it would stop grazing, bring its head up, and as it sneezed its head would go down then forward explosively emitting air, its nostrils quivering, and then its head brought up again slowly. This would be repeated from 5-12 times at intervals of 2-5 seconds, before the animal would lick its mouth and nostrils and continue its activity. Sneezing gave every impression of being as involuntary and stereotyped a pattern as it is in humans. After a few close observations sneezing could be visually recognised from the characteristic movement of the head.

Coughing was also heard in April and May, less frequently than sneezing (Table 5.3). The head is lowered and with the stomach convulsing the animal emits coughing sounds at 1-2second intervals up to 10 times. On three occasions that a sound of coughing could be traced in the herd, it proved to be by calves of the previous spring. Coughing out the larvae gave the

Table 5.3 Recorded instances of sneezing and coughing.

S - sneezing bout C - coughing bout

Date	Female	Calf	Unclassified reindeer (heard only)
March 4, 1971	S		
April 12, 1970	S,S	S	S,S
April 13, 1970			S
April 14, 1970		S	S
April 16, 1970	S	S,C,C	S,S
April 18, 1970		C	S
May 10, 1970	S		S,S
May 11, 1970			S,C
May 13, 1970			S
May 24, 1970	C ?		S
May 25, 1970	S,S		
July 14, 1970			S
August 2, 1970			C/S ?
August 28, 1970			C
September 26, 1970	S	S	

impression of being more of a voluntary act than sneezing.

Relatively loud sneezing and coughing was quite distinct from the various low wheezes, belches and snorts which could be heard within a lying herd, but only at very close range. These sounds probably mainly derive from expellation of methane and other gases in the rumination and digestive process. It is suggested that they may play a role in communication by boosting the "in-group feeling" of the herd (Ericson, 1975; & Ch.6.1.3.).

Opening and closing of the mouth without sound was described as yawning and was particularly frequent amongst lying or ruminating animals. Yawning and even a convulsive hiccuping movement, was particularly common amongst females with new calves, and probably relates to the female's constant licking of the newborn calf, and digestive difficulty with the un-accustomed material of the amniotic membranes and placenta.

5.2. ANTAGONISTIC BEHAVIOUR

"In sheep, and probably large cervids, horn size parallels dominance order. Hence predictability of social relationships is preserved even if strange individuals meet. In species with a rank system based on horn or body size one can expect open societies in which troupes periodically assemble from strangers." V. Geist, 1966.

Any behaviour associated with conflict of fighting, including defence /

defence, escape or "freeze" patterns can be defined as "agonistic" behaviour (Scott, 1956; Etkin, 1964; et.al.). As such, it includes all responses towards a predator, whether active defence by fighting or flight behaviour. In this study, the range of responses towards potential predators and other disturbances has been considered separately (Ch.7.9.), and any threat, conflict or withdrawal behaviour between two individuals is redefined here as antagonistic behaviour.

No single neuro-hormonal basis has been established for defensive-aggressive behaviour. The hormone adrenalin can play a role, as can the sex hormones, LH (luteinizing hormone) and testosterone, which are thought to increase particularly aggressiveness of females caring for their young and of males in the mating season (Etkin, op.cit.; Hafez, 1969). At other times, antagonism can be frequent, for example in the form of threat and withdrawal, but without obvious aggressive motivation.

Reindeer were observed to compete with each other or defend space in relation to food, a lying site, a mate or young, and in so doing exhibited antagonistic behaviour. This could take the form of a threat associated with the acquisition or defence of individual feeding spots, or occasionally lying sites, in winter; with the actions of a mother female in maintaining a space around herself and her young calf; and with the rutting behaviour of the male in acquiring exclusive proximity to a near-oestrous female, by chasing off subordinate males and clashing with rivals. The types and frequency of threat /

threat and conflict patterns were recorded in this study. Reindeer rarely inflict injury to one another through use of their antlers or fore-legs. Even in the rut when male aggression is high, fights between rival males usually take the form of ritualised antler clashes (see Ch.5.3.1e.). At all times of the year overt conflict or disputes between individuals is relatively uncommon and when it does occur it is limited to individuals of very similar ranking status. When a lower ranking animal receives a threat signal from an individual of higher rank it invariably withdraws, thus making an attack situation or conflict unnecessary. The lower ranking animal has correctly "assessed" that it would come off worse in any dispute.

From thousands of observations throughout the year it was clear that the presence and size of an individual's hard antlers were a vital attribute in determining rank viz-a-viz other individuals. A large body size also confers status, particularly in the unantlered or velvet-antlered period; and for animals of similar size and antler status a male is dominant to a female. At some times of the year, notably rutting and calving seasons, a high level of individual aggression also plays a role. However, even a small difference in the size of the hard antlers normally provides an accurate visual guide to predict which animal will be the dominant one.

Unlike hierarchies as reported for many other social animals, the infrequency of disputes within the reindeer hierarchy cannot be due to recognition of individuals as such, since the sheer /

sheer number of reindeer and their movement between groups must preclude this, but appears based on an instant assessment of another individual's hard antler size, body size, and sex, viz-a-viz its own characteristics in this respect. The structure of the hierarchy in winter and its implications for the population's productivity is discussed further in Chapter 7.2..

5.2.1. Threat Types

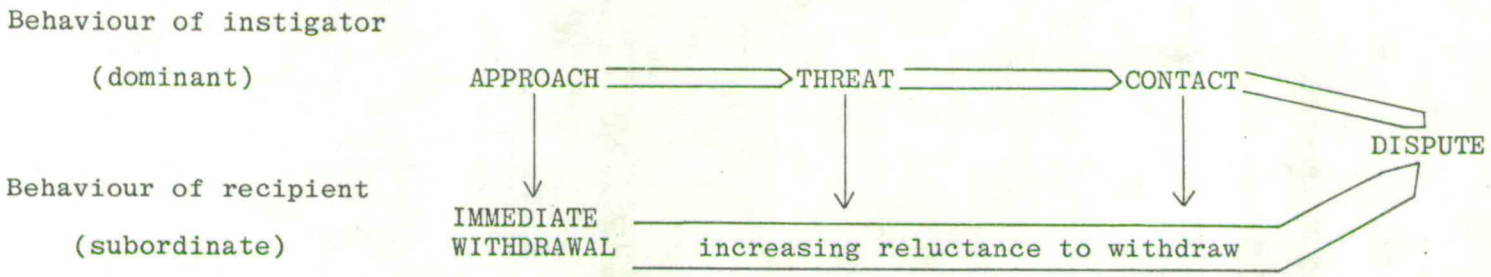
There are various types of threat by posture and movement which a reindeer may use to signal a warning to another of lower rank. According to the readiness or reluctance of the subordinate animal to make way, the dominant will proceed in sequence from a simple approach to a threat signal to physical contact (i.e. the consummation of the threat). On the few occasions when the receiving animal does not consider itself lower ranking than the instigator of the threat, a short dispute occurs to settle the issue (Fig.5.4).

Eight specific threat postures were observed. These are described below, and illustrated in Figure 5.5. One type of antler threat occasionally seemed to merge with another but normally they were distinct enough to be classified separately. As a rule animals in hard antler use threats and contact based on the antler, while animals who have cast or are in velvet use their forelegs and hooves.

(a) Antler-Low Threat

The antler-low threat is the most prominent antagonistic pattern amongst /

Fig. 5.4 The progression of an antagonistic event, its point of termination being dependent on the point of withdrawal of the recipient.



amongst reindeer in hard antler, and is a constant feature of the grazing and lying periods of winter. The head is slightly lowered and the muzzle pulled down and in towards the forelegs, so that the full antler stand is directed forward to the recipient. If there is no withdrawal the threat is followed up by moving forward to butt the animal on the nearest part of its body, usually its flanks, or to tussle with the antlers if dominance is disputed. Occasionally, a lying animal may direct an antler-low threat to another passing by (although the antler hook (c) is the more common threat used while lying).

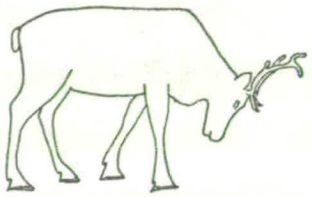
(b) Rush Charge

This is a high intensity version of the antler-low threat, in that the dominant runs at the subordinate and lowers its antlers in attack. To avoid contact, and possible injury, the subordinate retires immediately. The level of aggression exhibited by animals using this threat-attack sequence is always high, and is particularly a feature of mother females driving out yearlings from nursery groups, and mature males chasing off subordinate males in the rut.

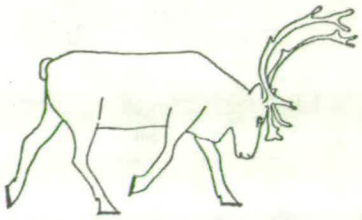
(c) Antler Hook

This variation of the antler-low threat is often seen amongst animals grazing tightly together in winter. The animal swings its head up or round to hook at the side of a lower-ranking neighbour. Even with this quick movement, physical contact is usually prevented by rapid avoidance on the part of the recipient. Lying animals in winter often swing their heads in this /

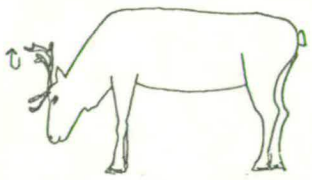
Fig. 5.5 The types of antagonistic threat-attack postures used by reindeer.



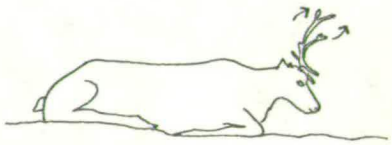
a. ANTLER - LOW THREAT



b. RUSH CHARGE

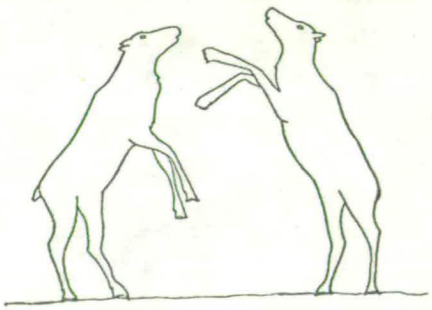


c. ANTLER HOOK

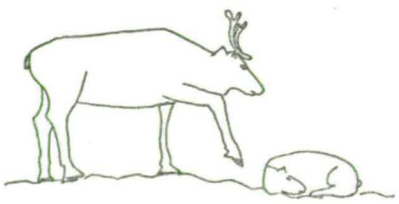


d. ANTLER SHAKE

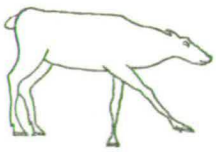
e. HEAD STRETCH



f. REARING - UP

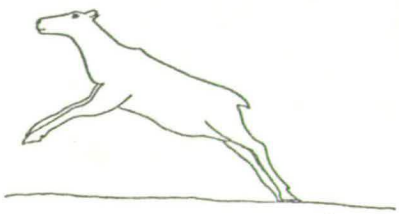


1.



2.

g. FORELEG KICK



h. RUSH CHARGE & KICK

this way at an animal passing through their midst.

(d) Antler Shake

This uncommon version of an antler threat is peculiar to lying animals. The lier waves its antlers from side to side for a few seconds at a passing subordinate to indicate its intention not to allow the animal to settle close by.

(e) Head Stretch

This is another infrequent threat performed by lying animals. The head is stretched out so that the antlers, if present, are laid across the back and the muzzle points forward towards the subordinate animal. Although this is an uncommon pattern in reindeer, it is apparently a common threat in active caribou (Pruitt, 1960; Lent, 1966). It is of special interest, however, because it is this head stretch at a slight tilt which forms the essential part of the active rutting male's driving approach towards females in the rut (see Ch.5.3.1b.).

(f) Rearing-Up

When an animal casts its antlers in winter it loses rank in the social hierarchy to those who maintain them, but establishes a new place in the"ranking order" by rearing-up towards similarly un-antlered animals. The animal throws its head upwards and then rears up onto its hind legs with its forelegs lashing out in a scissors motion towards the recipient. If on perceiving the threat of intention to rear up the subordinate withdraws quickly enough, then the full rearing-up pattern does not occur. Every gradation of rearing-up may be /

be seen according to the willingness or reluctance of the recipient to withdraw. If there is no withdrawal the recipient receives blows on the head or body from the forelegs of the attacking animal. If dominance is disputed, then the two unantlered or velvet-antlered animals both rear up balancing for a few seconds on their hind legs and kicking out at each other. Darling (1937) appropriately describes this as a "boxing match" in red deer hinds, and it is also characteristic of stags, but only when unantlered or in velvet (Lincoln, et. al., 1970).

(g) Foreleg Kick

An alternative antagonistic pattern by reindeer in the unantlered or velvet-antlered stage is a kick with a straight foreleg aimed at the subordinate. In the calving season mother females may direct such kicks towards calves other than their own, or with a bent foreleg jab at the strange calf until it withdraws.

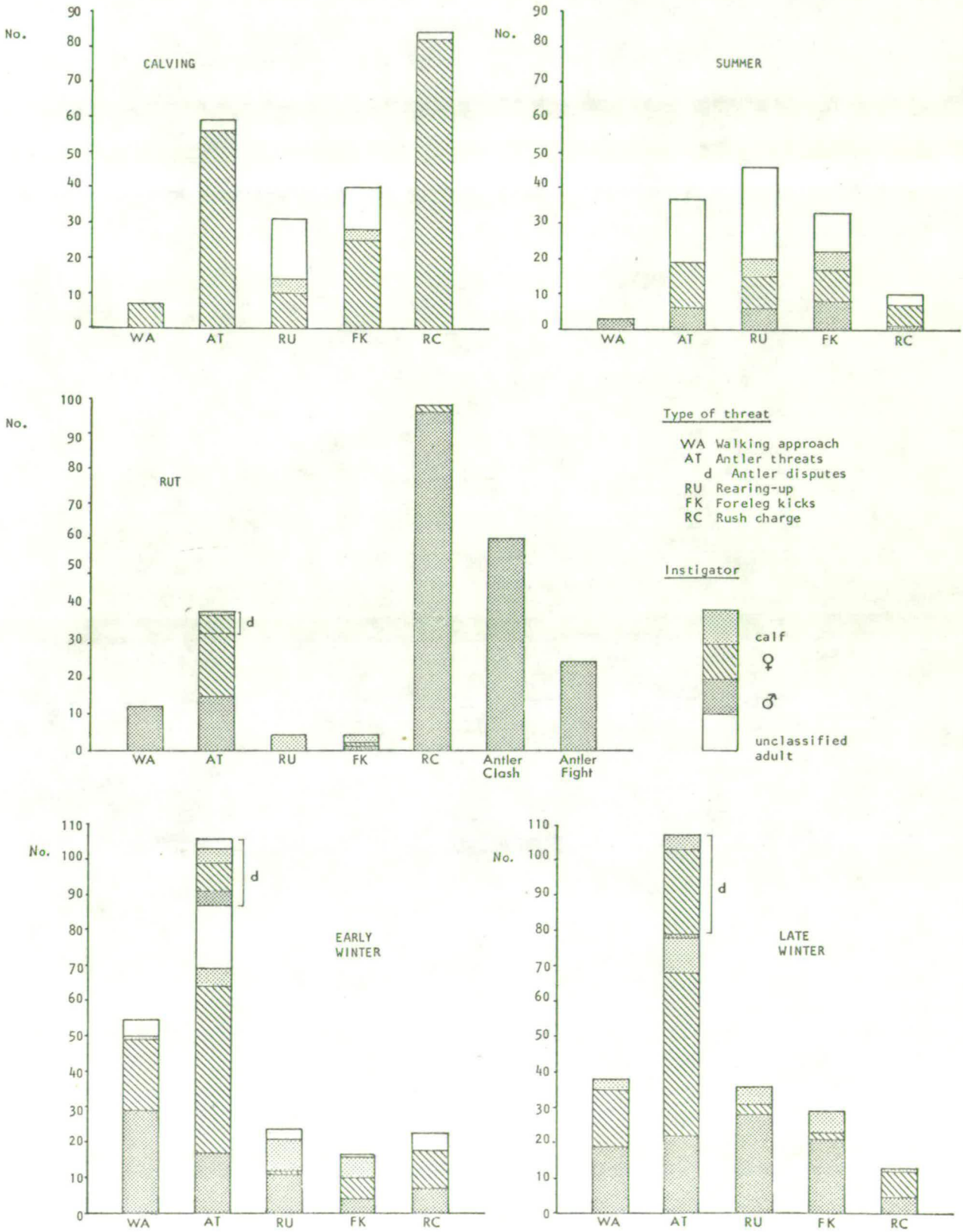
(h) Rush Charge and Kick

This is a high intensity version of the foreleg kick in that the animal runs at its adversary, and lifting itself off the ground jabs with both front legs simultaneously. As with the antler-low rush charge (b), immediate avoidance action must be taken by the recipient.

5.2.2. Frequency of Antagonism

The relative frequency with which these eight threat types were used by different sex and age classes was recorded throughout the year (Fig.5.6). The use of a particular threat type depended /

Fig. 5.6 The relative frequency of use by reindeer of different threat types at different seasons.



depended on an individual's antler status and on its level of aggressive motivation. Animals in hard antler, namely all reindeer during the rut, females and young in winter, and pregnant females in spring, use a threat based on the antler (a-e). Unantlered or velvet-antlered animals, namely males in winter and spring, yeld females in spring, and all reindeer in summer use foreleg threats (f-h). Animals exhibiting a high degree of aggression were particularly likely to rush charge (b and h) as a high-intensity threat attack. Rush charge was the most frequent antagonistic pattern of mothers at calving time, and of dominant males in the rut (Fig.5.7.). The relative frequency of occurrence of the different threat types in broad categories at different seasons is shown in Figure 5.8.

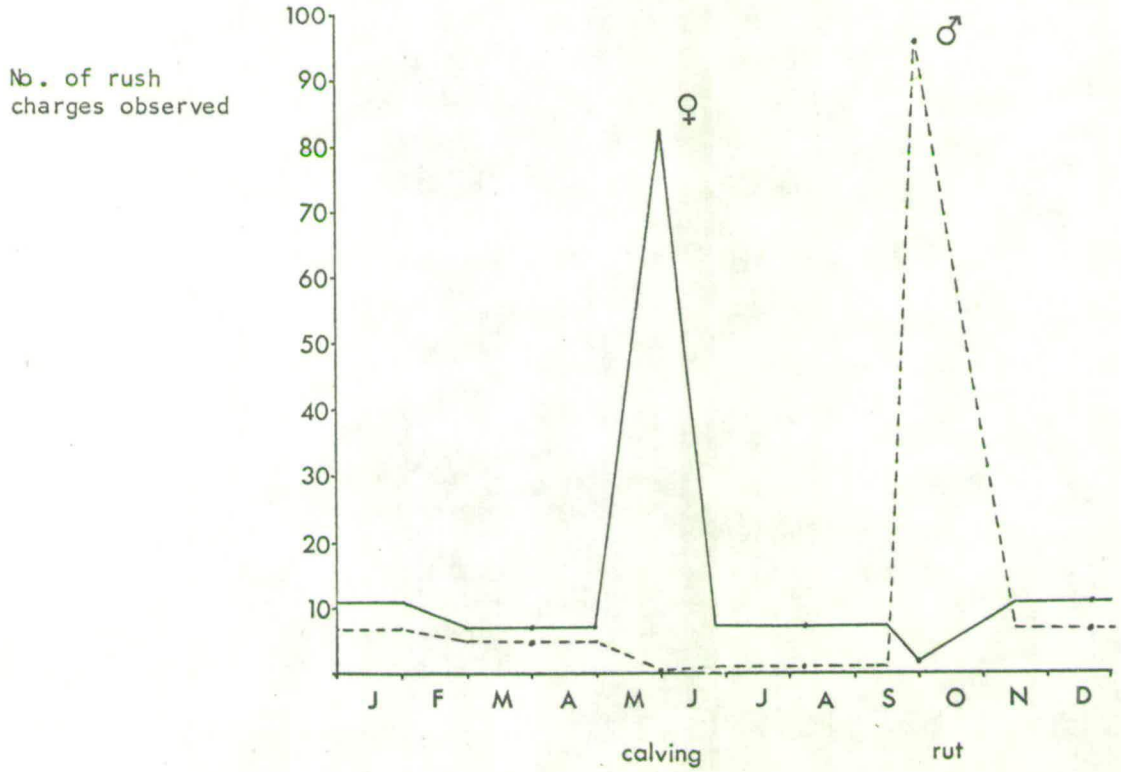
The absolute frequency of antagonistic encounters did not depend wholly on individual levels of aggression. In winter, approaches, threats and withdrawals are part of a constant process as animals compete for feeding spots in the grazing period, and occasionally lying sites, although aggression as such is not marked, as evidenced by the relatively few high-intensity threats which occur in winter (Fig. 5.8). In summer by contrast, there is both a lack of aggression and a virtually unlimited food resource at this time, so that antagonistic encounters are infrequent (Fig.5.9).

Seasonal features of antagonistic behaviour are now considered in more detail.

5.2.3. Antagonism at Calving

Females /

Fig. 5.7 The incidence of rush charges as an indicator of seasonal aggression in adult female and male reindeer.



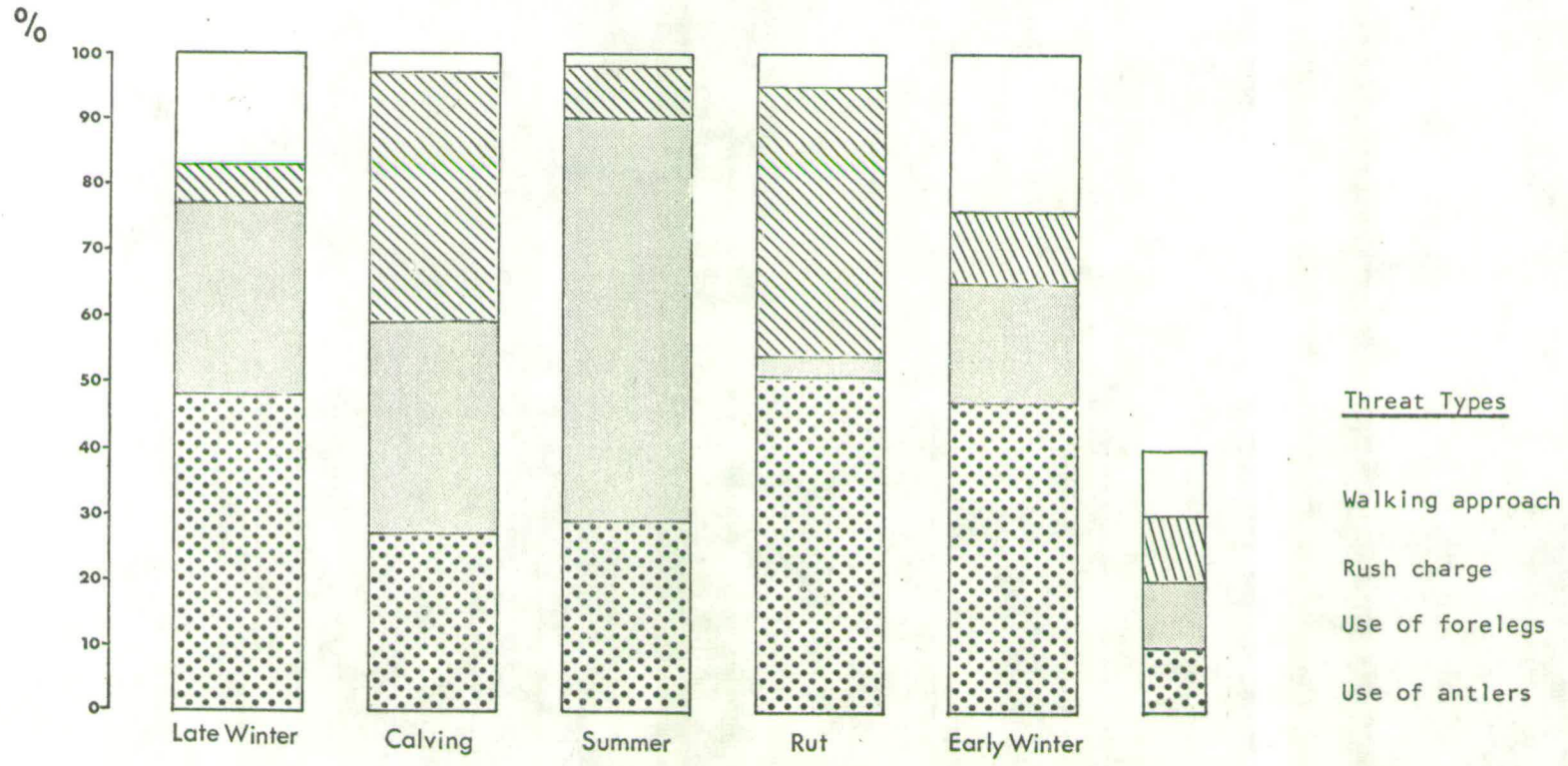
Females immediately after parturition show a high degree of intolerance towards other reindeer nearby, and taking advantage of the dominant status afforded by their retention of antlers, will threaten off yearlings, yeld females, and if present any males. Although the mother associates with other females and calves to form a nursery group, it remains intolerant of them particularly for the first few days.

While the mother was seen to be totally inhibited from threatening or attacking its own calf, it showed no such inhibitions towards other calves, and rush charged (13 events), directed antlers (33 events), or kicked (21 events) at any strange calf which wandered too close. Such antagonism by mother females towards strange calves is also recorded for caribou, and occasionally fatal blows have been dealt (de Vos, 1960). On seven separate occasions reindeer calves of a few days old showed insufficient avoidance and were kicked severely before being able to retreat, apparently unharmed. In each case the calf appeared frightened, even at the approach of its own mother.

The response of the mother to a threat or attack on its own calf by another mother female depended to some extent on her proximity to her calf, but also on her own social rank viz-a-viz the attacking female. Often a mother could be seen standing watching her helpless calf being kicked but making no attempt to intervene. The relative ranking of mother females in a nursery group is complex and alters frequently as mother females drop their antlers a few days after calving. Unlike /

Fig. 5.8 Seasonal change in the use of antlers, forelegs, rush charge and walking approach as antagonistic threats in reindeer.

(Expressed as a % of the total events recorded at each season)



Unlike the winter hierarchy the size of antlers at this time did not definitively indicate rank as the level of aggression evident was highest in the days immediately following birth of the calf, while some mothers were more persistently aggressive than others.

Interactions between mother females included rush charges (24), antler threats (16), and rearing up (9). Females in nursery groups tend to maintain individual distance from each other (Ch.7.1.2.), and over a few days become gradually more tolerant of each other and other calves. By contrast, any calfless adult which attempts to move into or through the nursery group is rush-charged by successive mother females, until it is chased to the edge of the group. Of 57 antagonistic acts recorded from mother females towards yearlings, 45 (79%) were rush charges. The increasing tolerance of mothers towards each other was evident when an attacking mother would be seen to rush past other mothers to charge a yearling and so force it to retire quickly, before trotting back to its own calf and ignoring other females and calves on the way.

Sub-groups of yearlings and yeld females driven to the fringes of nursery groups usually remained associated, but occasionally voluntarily left the area of the nursery group altogether. Antagonism seen between these calfless, usually un-antlered animals in the course of grazing was rearing-up (17), or fore-leg kicks (11), and seldom antler threat (3) or rush charge (1).

5.2.4. Antagonism in Summer /

5.2.4. Antagonism in Summer

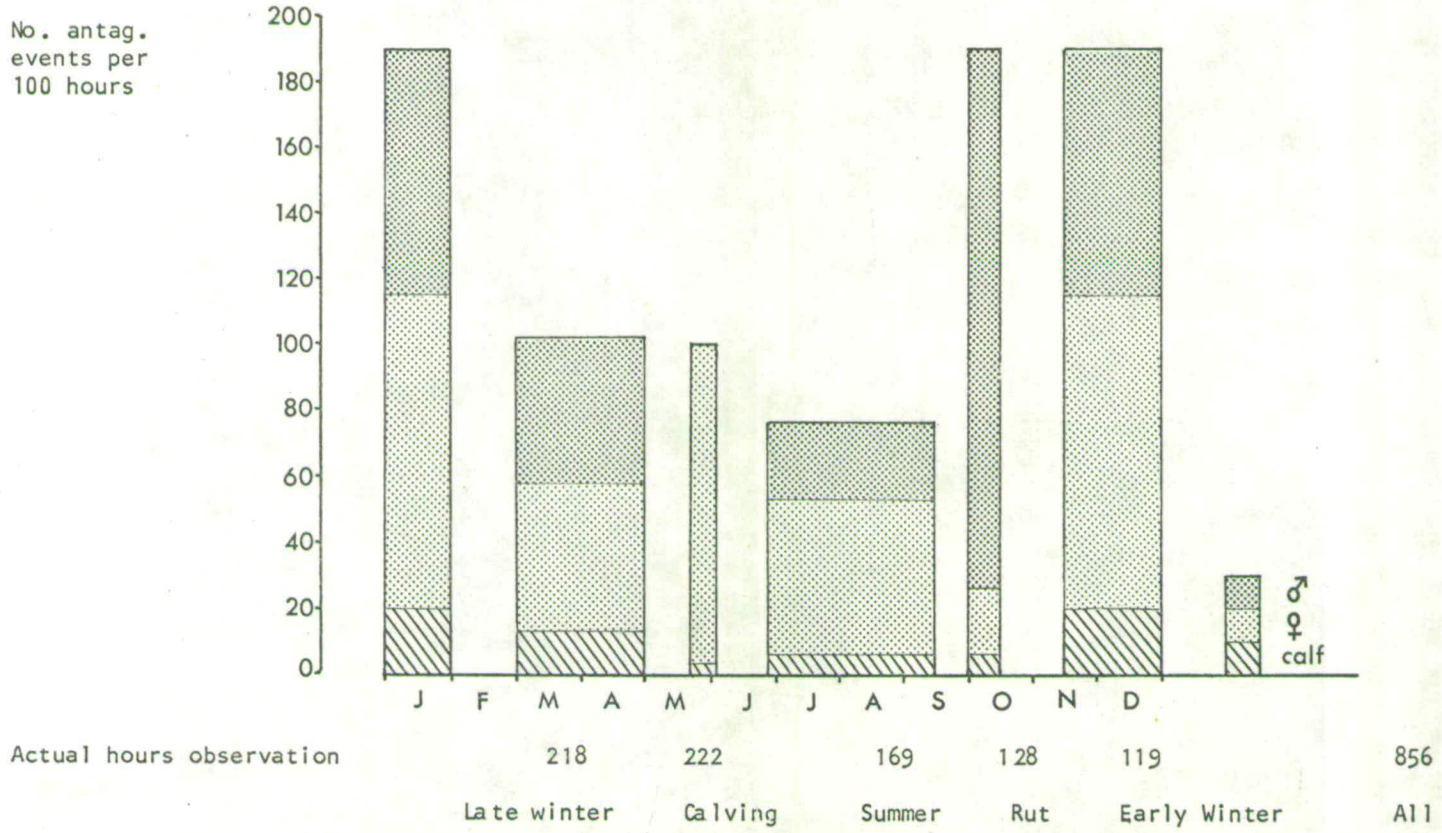
Observations at the end of June, one month after calving on Hardangervidda, showed that the mother no longer actively defends her calf. Indeed all animals at this time and throughout July, August, and September show the maximum degree of tolerance towards each other, even when they are massed together for movement, or under insect harassment.

The low frequency of antagonistic interactions in summer does not justify talk of a hierarchy at this time, nevertheless the interactions which do occur are clearly directed according to social rank. Encounters at this time are predictable on the basis of body size, and not on the development stage of the growing velvet antlers. Males therefore tend to be dominant to females, and females to yearlings in summer.

In this "velvet-antlered" stage use of the forelegs was twice as frequent as threats with antlers (Fig.5.8). Of the total 129 interactions recorded in summer, 79 (61%) involved rearing-up or foreleg kicks, and only 37 (29%) were antler threats (Fig.5.6). The use of antler threats at this time was particularly a feature of adult to calf interactions (14 out of 23 events), and less often foreleg kicks (6 out of 23 events), As in the calving season, adults did not rear up at calves; the single recorded incidence of this was when a female threatened to rear up at its <u>own</u> calf, after showing remarkable tolerance for several minutes in being struck on the head by continual "play" rearing-up from the calf. Antagonism between calves in summer was wholly restricted to rearing-up /

Fig. 5.9 The relative frequency of antagonistic encounters in reindeer at different seasons.

(Expressed as the number of antagonistic events recorded per 100 hours observation)



up and foreleg kicks.

5.2.5. Antagonism in the Rut.

By early October, antlers are fully grown and the mode of antagonism shifts from the predominant use of forelegs to almost exclusive use of the hard antler for threats and attack. Of the 242 antagonistic events recorded in the rut, only 8 (3%) involved use of the forelegs, and of these 6 were calf to calf interactions (Fig.5.6).

The dominance relationships between sex and age classes in the rut is broadly defined from males to females to yearlings to calves, and within these classes antler size is the key indicator of individual rank. Male yearlings (1½ years) which showed courtship approaches were dominant to females although their antlers were often no bigger than those of the females. Antagonistic events at this time are dominated by the rutting behaviour of the mature male. The ranking status between males at this time is formed, re-tested, and reinforced by displays, threats, ritual clashes, and fights (Ch.5.3.1.). No single factor could be isolated as the main determinant of male dominance, and thus rutting success; body size, antler size, and sexual drive, of which aggressiveness is a major part, were all positively correlated with age of the rutting male up to maturity. At the top of the hierarchy is found the large antlers, heavy bodies and full rutting repertoire of the mature males. Only if such a male became injured did his physical attributes not correlate with aggression and sexual interest /

interest. One large antlered male injured in the leg during the rut at North Ottadalen in 1969 took no further part or interest in competing for females.

The rush charge with antlers lowered was the commonest single antagonistic pattern seen in the rut (41% of all events) as dominant males chased off lesser ranking, usually younger, males who approached them or the females too closely (Fig.5.6). The antler-low threat is not used by rival males in the rut, instead rival males compete in direct antler clashes, or in the more violent pushing fights. These are described in the section on rutting behaviour (Ch.5.3.). The ritualised antler clashes are more than twice as frequent as the pushing fights (60 events v. 22 events).

Females in the rut occasionally antler threatened (6) or disputed with each other (5), apparently over grazing, and also antler threatened calves (12), particularly male calves who persisted in trial mounting attempts.

5.2.6. Antagonism in Winter

When heavy snow falls, normally in late October/early November, the deer react to the much reduced availability of food by a frequent interchange and possession of feeding craters according to social rank. The size of antler is a direct indicator of rank, so that when a male casts his antlers in winter, he becomes subordinate to the antlered females, except the very smallest or poorest-antlered females, in which case his greater body size will ensure superiority in an encounter. While the frequency of antagonistic encounters is high /

high, low intensity threats are most typical (Fig.5.8). Of the 448 encounters recorded from the thousands of encounters observed in winter, a simple walking approach and withdrawal was relatively common (21%) while the high intensity rush charges were infrequent (8% of events). Antler threats were the commonest type of antagonism in winter (37% of events). Of the 165 recorded antler threats, 141 were the antler-low threat with or without contact being made (type a) and the remaining 24 included antler hook (type c), antler shake (type d), and the head stretch (type e).

As younger males successively lose their antlers as winter progresses, there is a gradual increase in the amount of rearing-up and foreleg kicking which is seen. In early winter only 16% of male to male encounters involved use of the forelegs, while in late winter the majority of encounters between males involved rearing-up or foreleg kicks (58%). For calves by contrast, most early winter interactions between calves still involved use of the forelegs, while in late winter this was equalled by the number of antler threats observed (Fig.5.6). Clearly threats based on antlers are not a usual part of the calves' behavioural repertoire until it is well into its first winter.

The structure of the social hierarchy in winter is described in Chapter 7.2., and discussed in terms of possible differences between sex and age classes in nutritional intake and energy expenditure.

5.3. SEXUAL BEHAVIOUR

Throughout the period of antler growth in spring and summer, sexual behaviour in reindeer is not apparent. When the males begin to shed velvet from their fully grown antlers, they display the first signs of sex-connected behaviour, notably bush thrashing and antler sparring. The onset of oestrous in the female has been found to date from the time of velvet shedding, some 24 days and occasionally 36 or 48 days after (McEwan & Whitehead, 1972). The relationship between sex and antlerogenesis is thought to be more than coincidental. In ungulates, the male sex drive is controlled by the hormone testosterone (Fraser, 1968), and in several deer species it has been shown that rapidly increasing levels of this hormone as the rut approaches is associated with cessation of antler growth. Largely because both sexes of Rangifer carry antlers, Bubenik (1975 a) hypothesises that testosterone cannot be much involved in this process. However the rise in Rangifer male testosterone levels does appear to be correlated with final splitting of the velvet (McEwan, in press), while Meschaks and Nordkvist (1962) showed that the rapid fall in testosterone production in winter was associated with antler casting in reindeer males.

Reindeer females are known to be polyoestrous - if a female is not successfully copulated the first time on heat, she will come into oestrous at intervals until sired (Schmitt, 1936). These intervals may be as short as 10 days, but the average length is 22 days (Gorbunov, 1939). Recent work has shown that there is a long cycle of 24 days, and a short cycle of 10-12 days /

10-12 days which is often an inconspicuous "silent" heat (McEwan & Whitehead, 1972). In Scotland, experiments on the tame reindeer herd found that the interval between first and second oestrous averaged 23-24 days for 8 recorded intervals (H.M. Dott, pers. comm.).

On Hardangervidda, mature males start to shed their velvet at the end of August, females and younger males through September, with the peak of rutting in early October. Antler casting occurs from November to January for the mature males, and up to March or April for the younger ones. The male reindeer may be potentially capable of fertile insemination over all or most of the period in which he carries hard antlers, but his sexual behaviour is clearly concentrated into a two-to-three week period, the autumn rut, when mature females in the population are coming into oestrous.

The relatively simple act of mounting, entering and ejaculation by the male is preceded by a complex array of interwoven and repeated rutting behaviour patterns, which involve all modes of communication, visual, olfactory, auditory, gustatory, and tactile. Directly or indirectly these patterns tend to assist the progression towards successful copulation by a mature dominant male on an adult female who has come into oestrous. The rutting period of reindeer is notable for the conspicuous and incessant behaviour of the males in courtship displays and approaches towards females, aggressive displays and contests with rival males, and odour self-marking (Plates 20 & 21). The behaviour patterns characteristic of mature dominant males in /

in the rut are described in detail below.

5.3.1. Rutting Male Behaviour Patterns

(a) Standing Posture

The mature male ceases grazing for at least 2 weeks in the rut, and his main "activity" becomes a standing pose. The head is held slightly lowered, and as he stands his body may perceptibly rock gently and rhythmically to and fro (Plate 22). Although his head is fixed straight ahead and his eyes may be half closed, he appears to remain acutely aware of the proximity and sexual status of nearby animals. From this position he may suddenly trample his back legs forward and with back arched urinate (see c), or swing his head round towards a nearby female (see b), or rush charge at a subordinate male (see d), or other active behaviour, before lapsing back into standing. This standing posture is the basic pattern from which the other overt rutting patterns develop, and the posture may be held continuously for up to an half-hour. The posture appears to be specific to Rangifer and has been variously characterised as an "attitude of dejection" (Dugmore, 1913), and as "bush-gazing" (Bergerud, 1960; Lent, 1965a). As the pose represents a suspension of active rutting behaviour and not a cessation, it may permit a recovery of internal neural drives, allowing an active response to the surrounding sexual releasing stimuli.

(b) Head Swinging and Driving

The courtship approach of the rutting male towards the female has /

has been termed "driving" (Espmark, 1964a). With his muzzle stretched out and head held slightly askew, the male advances on the female from her side or her rear. As the female turns away the male follows her for a few seconds at a walk or trot, holding this driving position. As he drives his lips are pursed into an "O"-shaped mouth, through which he may flick his tongue repeatedly, or make low-pitched husky grunts, at one or two second intervals.

From a stationary position, a male leads into driving by swinging his muzzle up and round in an arc in the direction of the female. The head is held askew so that the dewlap (neck mane) is directed towards the female and conversely the antlers lean away from her. Head swinging represents a lead-in to driving of females by mature males and young males alike in the early part of the rut, but acquires greater significance as the rut develops and a mature male consorts or "tends" a single female. In such a consort pair the male often stands slightly behind and parallel to the female so that the effect of his head swinging is to bring his throat over the female's back. If the female's avoidance of this is minimal, the male will normally attempt to mount. As in many ungulates, the willingness of the female reindeer to stand and accept pressure on the back is a clear sign of an oestrous state (Barden, 1969).

As Pruitt (1960) has observed for caribou, the outstretched head of the male in his driving approach is similar to the head-stretch threat, which is occasionally seen in reindeer (re.Ch.5.2.1.). /

(re.Ch.5.2.1.). The non-oestrous female apparently perceives the male's approach as a threat in so far as she withdraws, but with decreasing intensity as her oestrous approaches. Head swinging and driving tests females' receptivity to a closer approach. Apart from this visual test a female's readiness for breeding may be apparent to the male through olfactory testing. As the male drives a female, his outstretched muzzle successively occupies the air space vacated by the female's rear as she walks or trots off in avoidance. As a female becomes more receptive the possibility for olfactory testing becomes greater, and the male is occasionally able to muzzle the perineum of the female he is driving and lick her. On other, similar occasions males were seen to sniff the rear of a lying female, or at the ground where she had been lying, or had urinated, and on two occasions at the stream of urine itself as it was passed by the female. The oestrous female is said to urinate frequently (Barden,1969). After sniffing, a male might continue to court the same female or would sometimes walk away.

Having smelled the perineum or urine of an apparently near-oestrous female a mature male often showed a characteristic response. He would stand for a few seconds, holding his mouth half open, eyes nearly closed, then slowly raise his head and muzzle up so that the mouth finally closed. A similar response has been recognised in many other ungulates and has been called flehmen (Schneider, 1930), lipcurl (Geist, 1971a), and olfactory reflex (Fraser, 1968). On only 2 of the 9 occasions when this olfactory reflex was recorded in wild reindeer /

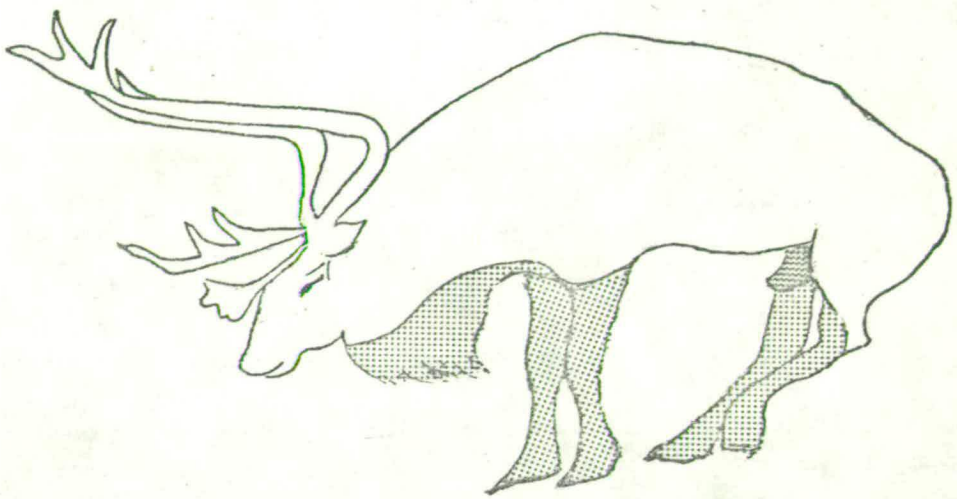
reindeer, did the male lift the upper lip and wrinkle his nose, while on the other 7 occasions raising the head with mouth half open was similar to the reflex described and illustrated for wapiti (Cervus canadensis) males (Struhsaker, 1967). This is the behaviour which Bergerud (1974a) saw in caribou bulls and called "yawning", which describes only its appearance. However I observed that the olfactory reflex of Scottish tame reindeer males, in response to the female perineum or urine in the rut, did often include a wrinkling of the nose.

(c) Hunching and Urinating

From a standing position, the male, keeping his head low, brings his hind legs forward in a rapid trampling motion towards his fore-legs so that his back arches and he urinates in spurts (Plate 23). This hunched position is typically held for 5-10 seconds, the hind legs are then returned without trampling to a more relaxed position for 20-30 seconds, before the male moves off or reverts to the standing posture. By lowering the rear quarters and bringing the hind legs forward, the penis is effectively brought into a more horizontal plane so that urine is propelled onto the front legs and dewlap, as well as dribbling onto the back legs. In this way a large area of the underside of the male is marked with urine (Fig.5.10). This self-marking is performed many times a day by the mature male and endows him with a powerful pungent odour.

The hunching behaviour has been variously described for Rangifer as "tramping" (Espmark, 1964a), hock rubbing (Bergerud, 1974a), and /

Fig. 5.10 Self-annointing with urine by the mature rutting male in the rut hunching posture.



Stippled areas are marked with urine.

and as the "horse-shoe" posture (Bubenik, 1975b). In calling it hock rubbing, Bergerud suggests that as well as urinating, the trampling motion of the hind legs, as they often cross each other, is rubbing the tarsal glands together. Mule deer (Odoicoleus hemionus) certainly rub the tarsal glands together, and usually urinate as they do so, especially rutting males (Linsdale & Tomich, 1953).

Espmark (1964a) noted that the hunched posture was most frequent when a rival male was in the vicinity. I also observed that hunching was a particularly common display before or after a confrontation with a rival male, but was as frequent amongst males in the vicinity of a female, or females, with no other males around (e.g. Plate 23). The fact that it occurred so frequently (see Table 5.4) and in various situations, not always accompanied by urination, suggests that it is an important visual display, as well as having the direct function of odour self-marking.

(d) Muzzling and Pawing

Infrequently, a mature male would stand muzzling at the ground for several minutes, often giving a few scrapes with a front hoof, then continuing nibbling and rubbing its muzzle on the ground at the same spot (Plate 24). Subsequent observations showed that muzzling was preceeded by or interspersed with hunching and urination, so that the male was nosing in his own urine patch. For Newfoundland caribou, Bergerud (1974a) claims that males smell or eat at the female's urine and may paw at this spot, whereas I found that males might sniff female urine /

Table 5.4 Relative frequency of male sex behaviour patterns in the rut.

Frequency of observation	Adult ♂ rutting patterns	Sub-acts	Frequency of observation
basic pattern	Standing pose		
100+	Swinging head up & driving	tongue flicking	21+
89+	Hunching and urinating	grunting	21+
85+	Charging subordinate ♂	sniffing ♀ perineum	45 (incl. 7 lickings)
82	Antler clash (60) & fight (22)	olfactory reflex	9 (5 from ♀ perineum, 2 from ♀ urine 2 from ground)
	rival ♂	pawing at ground	
36	Mounting attempts		18
35	Muzzling and pawing ground	muzzle-hindleg-antler rubbing	15
33	Bush-thrashing		
18	Female chases		
	Young ♂ patterns (esp. 1½- & 2½-year)		
64+	Swinging head up & driving		
51	Antler sparring		
27	Mounting attempts		
5	Fights		
(18)	Female chases		
Occas.	Bush-thrashing		
	♂ Calf rutting patterns		
	Mounting attempts		
	Participation in female chases		

urine patches and respond with the olfactory reflex (re. b above), but would not choose to paw or muzzle in them. Similarly, Espmark (1964a) observed reindeer males rubbing their noses in their own urine patches.

Unlike the hunching posture, muzzling at the ground did not appear to have any visual display significance, as it frequently occurred when a male was relatively isolated and not in the vicinity of other males or a consort female.

Of the 35 recorded observations of muzzling with pawing (Table 5.4), at least 15 events included some form of additional contact between muzzle, hind leg, and antler. Typically, the male would turn his head round from muzzling at the ground, lift up a hind leg, and rub his muzzle up and down the inside of this leg, often then turning the other way to repeat on the other hind leg, before continuing to nose the ground. Other contact patterns in this sequence included swinging the antlers down until the beam tips touched the muzzled patch, rubbing the antlers against a hind leg, or bringing a hind leg forward to rub or touch the muzzle, forehead, or antlers (Plate 24).

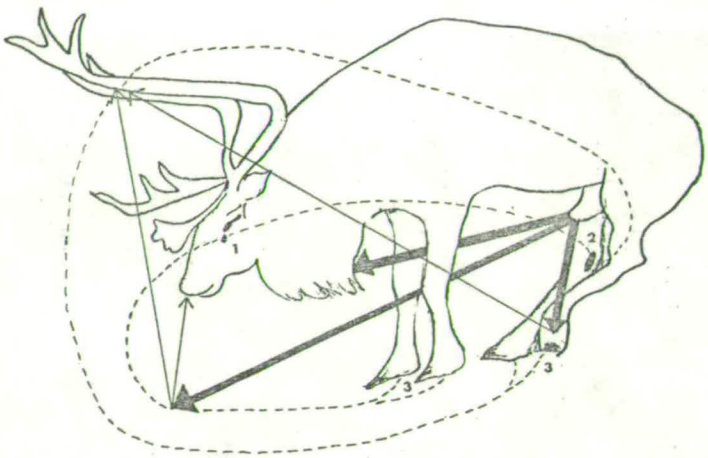
No two events of this type were identical. A particularly complete sequence lasting three to four minutes was recorded by assistant Anne Jackes; on 22nd September 1970 on North Ottadalen, a mature medium-dominant male was watched muzzling and pawing at the ground. He then turned his head back to rub up and down the hock of the hind leg, first with his nose, and /

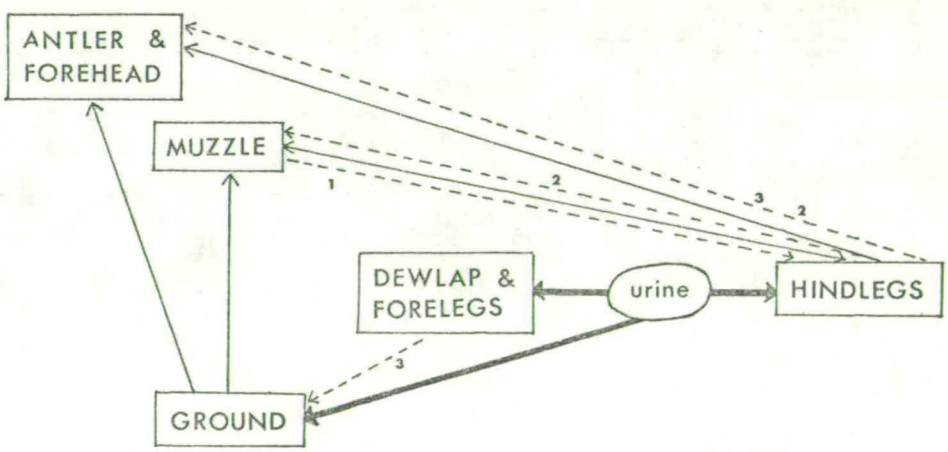
and then by swinging his head the upper part of the antler beam. He returned to muzzling the ground patch in front of him again for ten seconds, then nosed the hind leg again. This was repeated a third time before he went into the hunching posture and urinated. He then brought up his other hind leg and licked the front of his hock before muzzling the ground again. He turned to muzzle at this leg once more before finally walking off. On another occasion, also in the North Ottadalen rut, I observed a mature dominant male follow up hunching by giving two scrapes at the ground with a front hoof, and then muzzling there. For the next seven minutes the male nibbled and tasted the ground on this spot, pausing five times to rub his nose against his hind leg, and his hind leg against his face, forehead, and antlers, and three times momentarily rubbing his antlers on the ground. Following this he walked a few steps and lay down.

Muzzling of urine patches and the subsequent contact between muzzle, leg, and antler suggests that this behaviour is an extension of the self-marking process. The main pattern of hunching results in urine distributed over the hind legs, dewlap, and forelegs. Thereafter, muzzling and rubbing distributes the urine odour to the head and antler region. This is not recorded for caribou. The observed pathways of the transmission of urine odour in the self-marking process is shown in Figure 5.11.

This self-marking behaviour of reindeer males shows interesting differences with other deer species (see deVos, Brokx & Geist, 1967; etc.). Reindeer can be said to have a highly developed self-marking /

Fig. 5.11 The transmission of odour by the rutting male to various parts of its body by hunching, muzzling and rubbing.





Odour pathways

Direct urine marking (by hunching).
Urine transmission (by muzzling and rubbing).
1 Pre-orbital; 2 Tarsal; 3 Inter-digital.

self-marking process through hunching and subsequent muzzle contact, but unlike Cervus (Struhsaker, 1967; Lincoln et.al., 1970), they do not wallow in urine-soaked pits churned up by the antlers and hooves.

The use of secretion from scent glands has been verified in some deer species (e.g. roe deer (Capreolus capreolus) rub their forehead and pre-orbital glands up and down twigs as territorial markers (Tembrock, 1968), wapiti (Cervus canadensis) may rub their pre-orbital glands in wallows (Struhsaker, 1967)). Like Cervus the pre-orbital glands of mature reindeer males appear conspicuously enlarged in the rut, and may show some discharge, but unlike Cervus they do not rub the sides of their faces on the ground while muzzling. However, the possibility remains that odoriferous secretions from the pre-orbital glands, tarsal glands, and/or interdigital glands of reindeer are transferred to different parts of the males' body during the urine marking process (see Fig.5.11 and Ch.6.1.4.).

(e) Antler Clashes and Fights

Dominance in the rut carries with it the privilege of consorting with a near-oestrous female, and tending her until copulation is achieved. Before and during this tending phase males establish their dominance rank through hunching and broadside display-threats, antler clashes, and fights. The aggressive potential of a male is the ultimate basis of his rank in the rut, and is on display to other males through his antler size, body size, and behaviour.

For mature males of similar rank, antler clashes determine dominance. /

dominance. Often from a side by side position, the two combatants move their heads round together carefully until their antlers touch, then suddenly toss their antlers from side to side so that their antlers crash against each other loudly for 5-10 seconds. From this ritualised clash the participants are apparently aware of which one of them is dominant. The "winner" appears to be the one which walks or trots off first, often driving towards a female. If they move off together, side by side, they will lean their antlers in towards each other and clash again.

After indecisive clashes between two rivals, or at times of excitement, a more violent and less predictable fight occurs. The males join antlers, often at a run, and attempt to push each other backwards and off balance (Plate 25). Equally matched rivals will push each other to and fro, their bodies straining and hooves churning up the vegetation as they seek to gain the advantage. Eventually, one male is being pushed back at a run or falls to the ground, and the other misses no opportunity to rake the opponent with his antlers. Bergerud (1974a) records deaths of caribou males in rutting fights. In the 22 fights recorded in this study, I saw no deaths or even serious injury, although occasionally flanks would be hit by antlers or a foreleg caught up in the joined antlers. On one occasion the antlers of two males became interlocked during a fight and only after 20 minutes, long after they had given up pushing, did they manage to extricate themselves. Locked antlers are a known, although uncommon, source of mortality in wild reindeer males (e.g. Gossow, 1974).

Whereas /

Whereas these fights are the ultimate test of the strength of a rutting male, the antler clashes are three times more frequent (Table 5.4), and such ritualised clashes allow dominance to be decided without risk of injury to the participants. Indeed, the actual size and weight of the antler may be of more importance for the antler clash than it is for a real fight. The strength of the neck muscles, and the momentum (velocity x weight) of the antlers as they are simply and harmlessly shaken from side to side against an opponent's antlers, must be important in the animals' assessing rank from these brief clashes. The frequency of this behaviour pattern does not support the contention by Bubenik (1975b) that Rangifer uses antlers in a purely ritualised manner.

As part of the confrontation before a clash or fight, a mature male will sometimes paw the ground. This is not associated with the muzzling and pawing behaviour as described above (re. d), but probably represents overflow aggression at the challenging presence of a rival, as with domestic bulls. The pawing is not a common feature in reindeer males but is distinct when it does occur. For example, on 17th September, 1970, on North Ottadalen, two large males clash, they then walk off side by side and stop, standing parallel 10m apart - one male goes into the hunching posture and urinates, the other male paws the ground with a foreleg, and his rival then copies the act. With antlers leaning towards each other, they join in an antler clash - they then run off side by side, join antlers again, and fight vigorously until one is pushed right back and withdraws.

Often /

Often the sound of antler clashes and fights attracts animals, both males and females, to the area and results in periods of great activity with many further clashes, fights, driving and chasing of females, and mounting attempts.

The response of a mature rutting male to a lesser antlered male, usually a younger animal ($1\frac{1}{2}$, $2\frac{1}{2}$, or $3\frac{1}{2}$ years) is simple. The dominant male lowers his antlers and charges at the subordinate intruder who then retreats quickly. The dominant usually charges for 10 to 30m and then returns to drive a female. The dominant male tending a female seldom allows a subordinate male to approach closer than 10m. The posture and behaviour of the subordinate or younger male is important in this respect. If he appears to show little interest by keeping his head and antlers turned away, or by grazing, he may be tolerated by the dominant male, whereas if he presents his antlers forward or drives at a female in the vicinity, he is invariably charged at in attack. On the other hand, the mature males showed an inhibition against attacking male calves, even when a male calf was observed to direct persistent mounting attempts at its mother, who was being tended by the dominant male. Eventually it was the mother herself who antler-threatened and butted her own calf.

Young males of similar rank often indulge in prolonged antler-sparring contests together, where they twist their antlers together often wheeling round as they do so (see coverphoto, App.2). In the rut these sparring matches can develop into a pushing match, akin to the mature male fights, but without the /

the same level of aggression.

(f) Bush Thrashing

Thrashing of antlers in bushes or shrubs may be performed by any hard-antlered reindeer in early autumn, through the rut, and in winter, but it is performed most often in the rut and most vigourously by the adult males. The male lowers his antlers into a bush and then proceeds to "attack" by sweeping his antlers from side to side and up and down through the branches and twigs of the bush. With pauses, this violent thrashing may occur for several minutes before the male moves off leaving behind broken branches and stripped bark. It has been postulated that the single palmated brow-tine of the mature Rangifer male functions as a protective shield for the eyes during bush thrashing (Pruitt, 1966), and during antler-locking contests (Freeman, 1968), although an alternative theory claims that its main use is offensive - "the most dangerous part of reindeer antlers" (Bubenik, 1975b). Violent bush thrashing has the appearance of an aggressive mock fight. Espmark (1964a) similarly considers it "sham fighting" and found it most frequent in the presence of rival males, while conversely Lent (1965a) found it usually performed by mature caribou males in small groups without mature rivals, and in between bouts of driving females. I found it occurred in various situations not always with other animals in the vicinity, but where there was at least a moderate degree of sexual/aggressive arousal in the male. It was only common behaviour where suitable woody vegetation was available. In autumn, reindeer groups in North Ottadalen are often found near the treeline and thrashing of scrubby birch trees (Betula pubescens) /

(Betula pubescens) and juniper bushes (Juniperus communis) was common. In the low-alpine zone patches of shrub willow (Salix spp.) were commonly used as thrashing stocks. Where such shrubs were not available, rutting males occasionally thrashed their antlers in the dwarf birch shrub (Betula nana), and on two occasions at the ground vegetation so that lichen pieces were flung around.

Unlike Cervus males however, antler thrashing by reindeer was not associated with muzzling or pawing at the ground, nor was there evidence of either urination or ejaculation during bush thrashing, although this was looked for. It is uncertain whether bush thrashing by rutting caribou males has been observed to result in erotic stimulation. From Darling's (1937) observations on red deer (Cervus elaphus), Pruitt (1966) accepts the hypothesis that the hard antlers of Cervidae are erotic zones and states that for caribou "the erotic stimulation apparently occurs when the antlers are threshed in vegetation or when they are rattled against those of a companion" (my underlining). Bergerud's (1974a) evidence is similarly ambiguous when, in debating whether there is an erotic element in bush thrashing, he notes that "erection was not a common accompaniment of the display", and goes on to ascribe its function as assisting females in locating and distinguishing mature sexually stimulated males. That there is an erotic element in the use of hard antlers by males is undisputed. For reindeer, young males who deliberately twist their antlers together in a sparring bout in the rut, or in winter, often show some erection, and their less violent bush thrashing /

thrashing could conceivably have the same effect as sparring (re.Ch.5.3.3.). However, mature rutting males do not spar in this idle way together and their aggressive bush thrashing parallels their brief antler clashes and fights, with no erotic stimulation apparent in either case. Mock fights with scrubby vegetation probably function as a "self-rewarding" activity for the males, by providing a non-retaliatory outlet for their obvious aggressive drive. In the absence of suitable shrubs, Scottish reindeer males in the rut aggressively "bush thrash" against wire fences, wooden posts, bundles of hay, and young pine trees. Espmark (1964a) illustrates a male "sham fighting" a wooden fence. Graf (1956) considers that thrashing of vegetation is a visual and olfactory signpost of male territory in some species; but in the case of reindeer, although broken branches and stripped bark leave "signs", territorial significance is very doubtful since the reindeer group will generally have moved on by the next day.

Bush thrashing by female reindeer was observed on 10 occasions in the rut, varying from rhythmical side-to-side thrashing to a more deliberate rubbing and twisting of the antlers and forehead against the woody stands. Calves, particularly male calves, could also be seen rubbing their spikes up and down the woody stands from rutting time onwards. Occasionally thrashing by these younger animals or females would be interrupted to sniff or nibble where bark had been stripped off the stems.

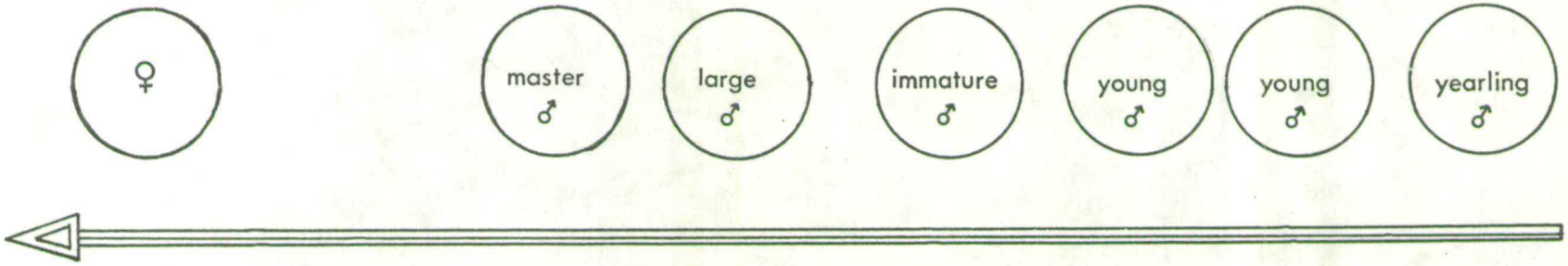
Bush thrashing also occurred in winter and was obviously socially /

socially facilitated, in that once a few animals had started rubbing or thrashing in the available Salix or Betula nana bushes above the snow, they were soon joined by other antlered animals, the females, young males, and spiked calves. Before the rut, bush thrashing, when it is performed, effectively, but it is thought, incidentally clears the antlers of remaining velvet strips (re.Ch.5.1.3c).

(g) Female Chases

Occasionally a female would be seen to react to persistent driving approaches or attempted mountings, especially those by young males or calves, by running out from the herd. She would then be followed by the males nearby, and in galloping or trotting over the terrain, other males would perceive this and join in the chase. The string of males behind the female would quickly sort themselves out in terms of dominance. The most dominant male would run immediately behind the female and not allow a lesser male to pass him, and so on along the line (see Fig.5.12). The only exception to this was the tolerance shown by a large male towards a calf who could run directly behind the female in such a chase. Clashes and fights between similarly antlered rival males were common in the course of such chases, and when a dispute occurred between the two leading males, the lesser males would rush forward so that the female would run on with increased speed. Up to 12 males have been seen running behind a female. In the excitement of the galloping chase wild running attempts at mounting were common, especially by the opportunistic young males, and even occasionally by the leading big male, but /

Fig. 5.12 Diagram of a rutting chase of a female by a string of males in order of their dominance rank.



but nothing resembling successful copulation was ever seen at such times.

It is the female who appears to have the controlling influence in these chases, as she alters her speed of running at will, and when she slows down and finally stops, the males quieten down, while the most dominant male immediately behind her will start to court her by head swinging and driving motions without her racing off again.

Often these chases would last up to 10 minutes by which time the female had covered many kilometres of terrain before returning to the area of the group. 18 such rutting chases were recorded on Hardangervidda, North Ottadalen, and Snøhetta (Table 5.4). Evidently, this behaviour has not been recorded for other reindeer or caribou populations. I would postulate that the normal function of such chases is that the female is advertising her near-oestrous state, and in the male rivalry that ensues, she becomes assured of the interest of a dominant rutting male as a tending partner.

(h) Mounting and Copulation

Mounting attempts on the female are not infrequently seen at any time of the day in the rut, either by the large dominant males, or when presented with an opportunity the young subordinate males and male calves. As with antler clashes, and fights, mounting attempts have a clear social facilitation effect in that other males will then often attempt mounting on other females. Mounting attempts, invariably unsuccessful, were /

were also frequent when a group were clumped together in response to an external disturbance.

After driving at various females earlier in the rut, the dominant male later consorts with a female and concentrates his courtship on her. These pairings are not stable pair bonds and may change from day to day, or even during the day, which allows a dominant male the chance to switch to another female who is coming into oestrous. The male is frequently "testing" the female he is tending by swinging his head across her back, nudging and licking her rear, as well as standing, hunching and urinating, and charging at subordinate males nearby.

The male seeks to mount the female by jumping up on his hind legs and clasping her flanks with his forelegs; then with thrusting movements he attempts intromission and ejaculation. The male's mounting attempt may occur from behind or, more usual with a tending female, from the side by swinging his head up and jumping up. If the male does manage to clasp, he may be able to stay on the back of the female for several seconds by running on his hind legs, even if she is pulling away from him. Occasionally a female's struggles result in her collapsing to the ground and/or the male falling off. The 20 mountings recorded where the male managed to clasp the female's back averaged 8 seconds (up to 22 seconds), but the female's struggles usually appeared to preclude the necessary intromission. Only 3 or 4 of these mountings were thought to be successful copulations, all by dominant males. In only one of these did the /

did the female remain wholly stationary, and in fact showed encouraging behaviour between mounting attempts by aligning herself with the male, rubbing her nose on the vegetation, and against his side (as described by Espmark, 1964a). The infrequency of such active oestrous behaviour by the female is discussed in relation to group composition and social organisation in Chapter 7.8. Following copulation the female stands with back slightly arched, emits some fluid from the vulva, and walks off stiff-legged for the first few steps.

There was no particular time of day when mounting behaviour was more frequent. In particular there was no evidence for an increase in sexual activity at dusk, as found by Espmark (op.cit.). The 106 records of mountings and mounting attempts in the rut (excluding male calves) showed a spread over the day, with apparent peaks between 1100-1230, 1345-1445, and around 1700 (Fig.5.13). The 3 to 4 known successful copulations observed were similarly spread over the day, both morning and afternoon.

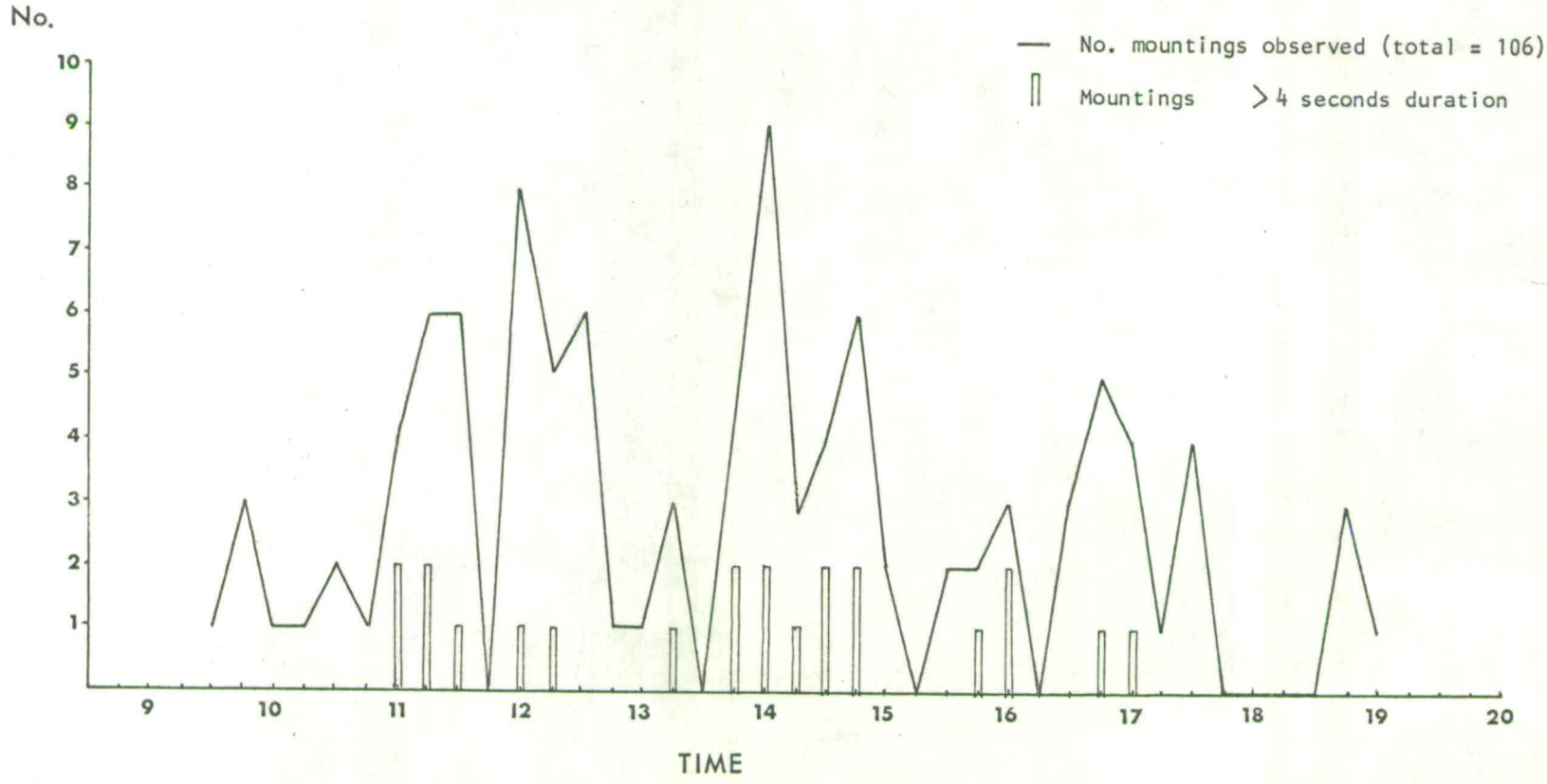
5.3.2. Sequence of Rutting Patterns

A sequence to explain the function and relationship of the behaviour patterns of the mature male in the rut is represented schematically in Figure 5.14. As has been described above, only the head swinging and driving of a male closely tending a female gives a direct lead in to successful copulation. His other distinctive rutting behaviour apparently both develops and /

Fig. 5.13 The daily timing of mountings by reindeer males in the rut.

Nb. of mountings observed in 1/4 hour intervals throughout the day in 4 rutting seasons:
(mounting by calves excluded)

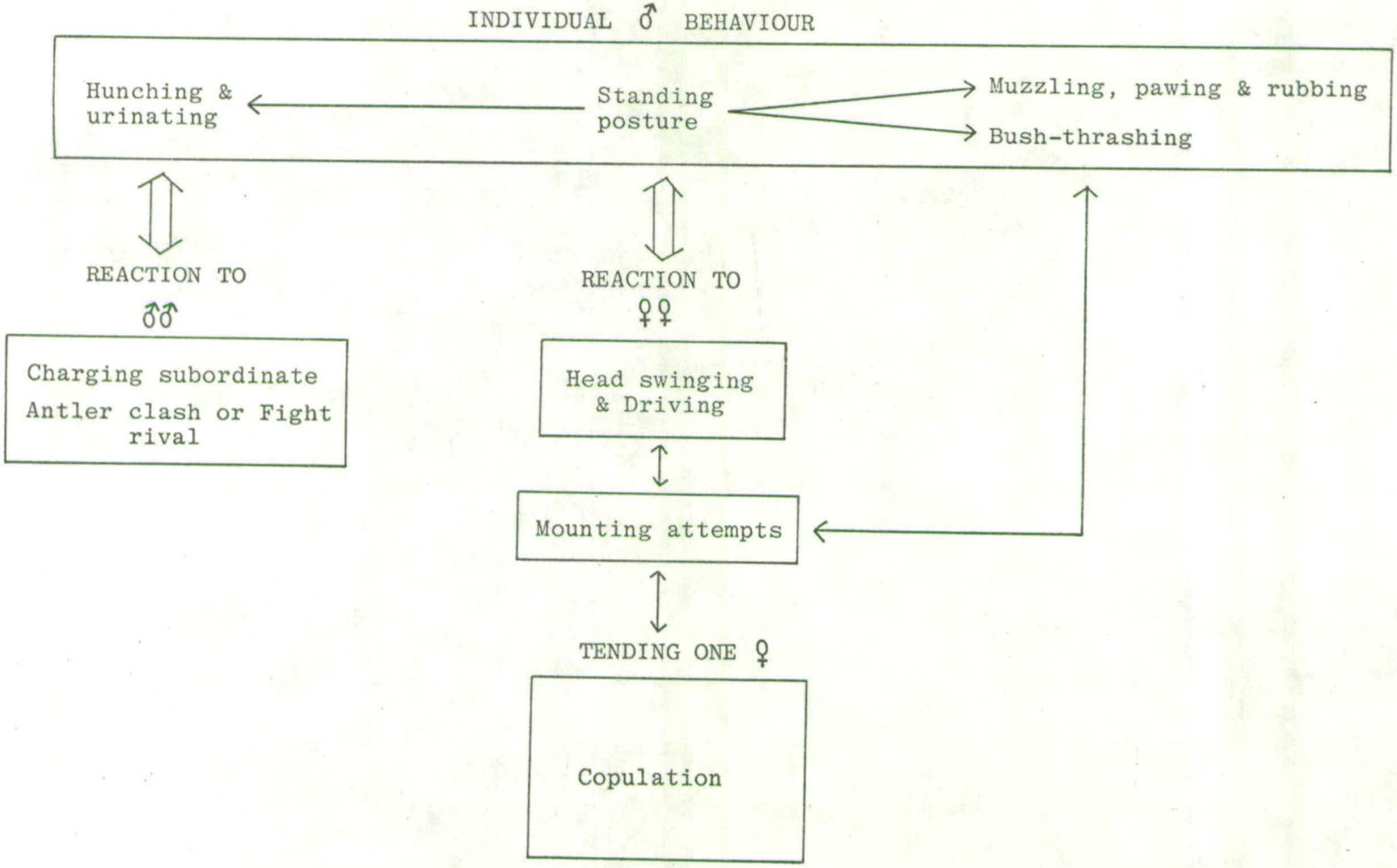
North Ottadalen, September 1969
Snøhetta October 1969
North Ottadalen September 1970
Hardangervidda October 1970



and satisfies his own inner sexual drives and acts as a sexual-aggressive display towards other animals in the herd, both males and females. These "displays" are not only visual through the adoption of special postures (e.g. hunching), but also have vocal and olfactory components, which may have a dual function in both intimidating possible rivals and stimulating females. Even the striking appearance of the mature male at this time, with the prominent white dewlap and neck contrasting strongly with the dark brown face, legs, and back, may have a double role in the attraction of females and the intimidation of rival males. In courting a female by driving, the male's head is tilted back and to the side, so that the antlers are less conspicuous but the dewlap is most visible to the female. Whereas in the common broadside position to a rival male, the head is tilted over so that the antlers loom even larger (Fig.5.15).

It is significant that in males of up to 3½ years it is only the basic driving approach and mounting behaviour which is performed (Table 5.4). The full rutting repertoire of the male is only developed with age. Where, however, adult males are not present, the younger males even with their basic repertoire can and do successfully serve the females. This was the situation on Hardangervidda in 1970 when adult males had been removed by hunting and it was at this time that an oestrous female was seen to take a more active role in displaying her readiness for mating (see h above). The normally passive role of the female at rutting time with minimal disruption to her on-going maintenance activities of grazing, lying /

Fig. 5.14 Sequences of rutting behaviour patterns of the mature male.



lying, etc., is illustrated in Figure 5.16. The observed relationships between rutting behaviour, group organisation, and sex and age structure in the population are discussed in Chapter 7.8.

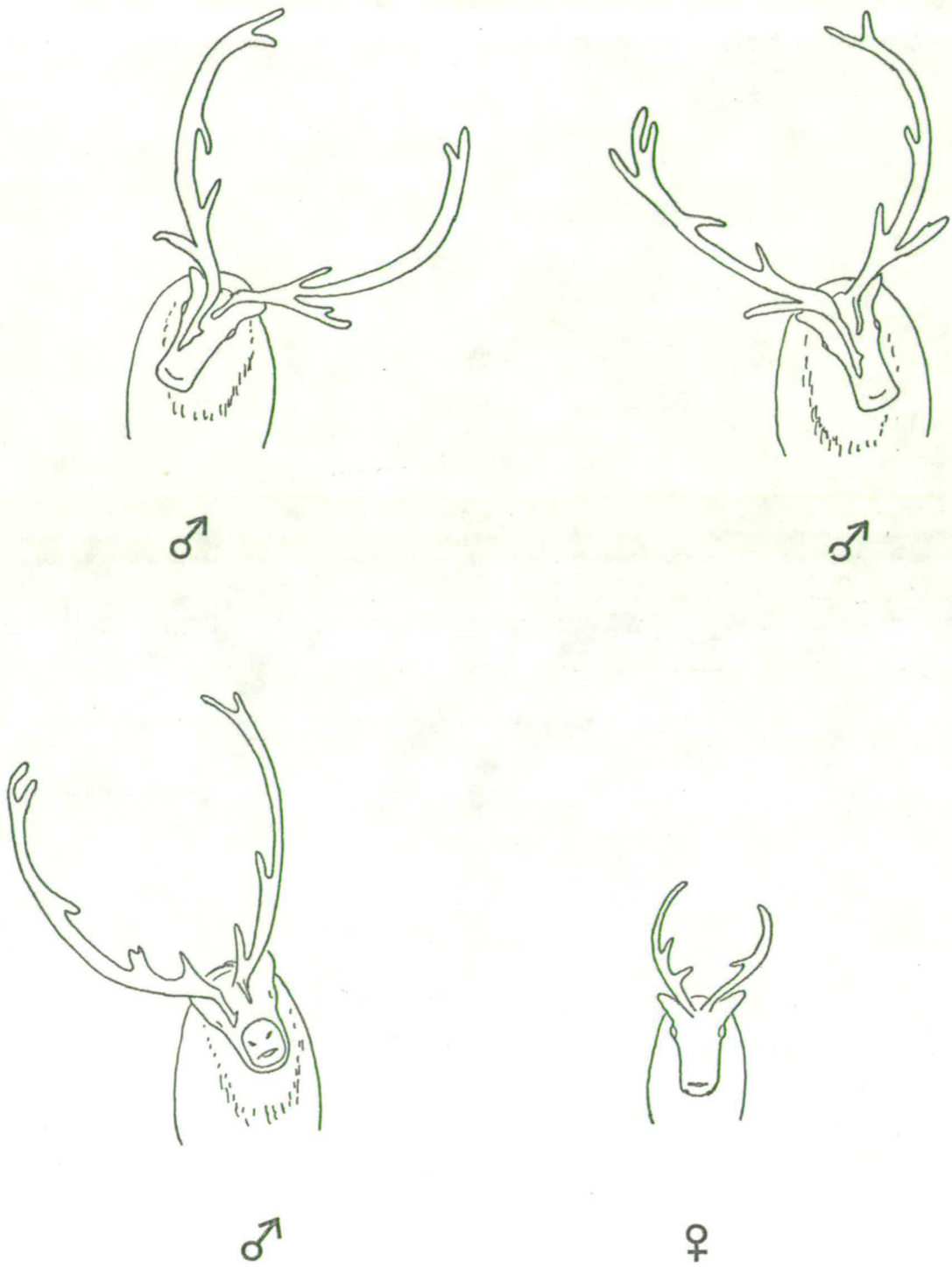
5.3.3. Sex Behaviour in Winter

"The sexual life of the reindeer
Is agile, athletic, and gay,
In the height of the Arctic winter
He tries to have it away;
But the females are too busy feeding,
They're not putting up any show,
Which accounts for the droop in his antler
And his fooling about in the snow." Anon.

Although the rutting period has no clear-cut boundaries, the obsessive persistence of the mature males in courting females, displaying and rivalling each other, drops off markedly in the third and fourth week of the rut. Females coming into oestrous in this later part of the rut are not pursued by the males with the same intensity or vigour as in the earlier part, and the display patterns such as the hunching posture are not exaggerated to their full extent. Within the space of a few days at the end of the season, a group's activity can have wholly reverted to peaceful grazing and lying periods, with only an occasional incomplete head-swinging pattern or mounting attempt seen in the course of the day, often by a younger male.

Such /

Fig. 5.15 Sketch of the tilting of the antlers of the rutting male; towards a rival male in broadside display, and away from a female being courted by head-swinging.

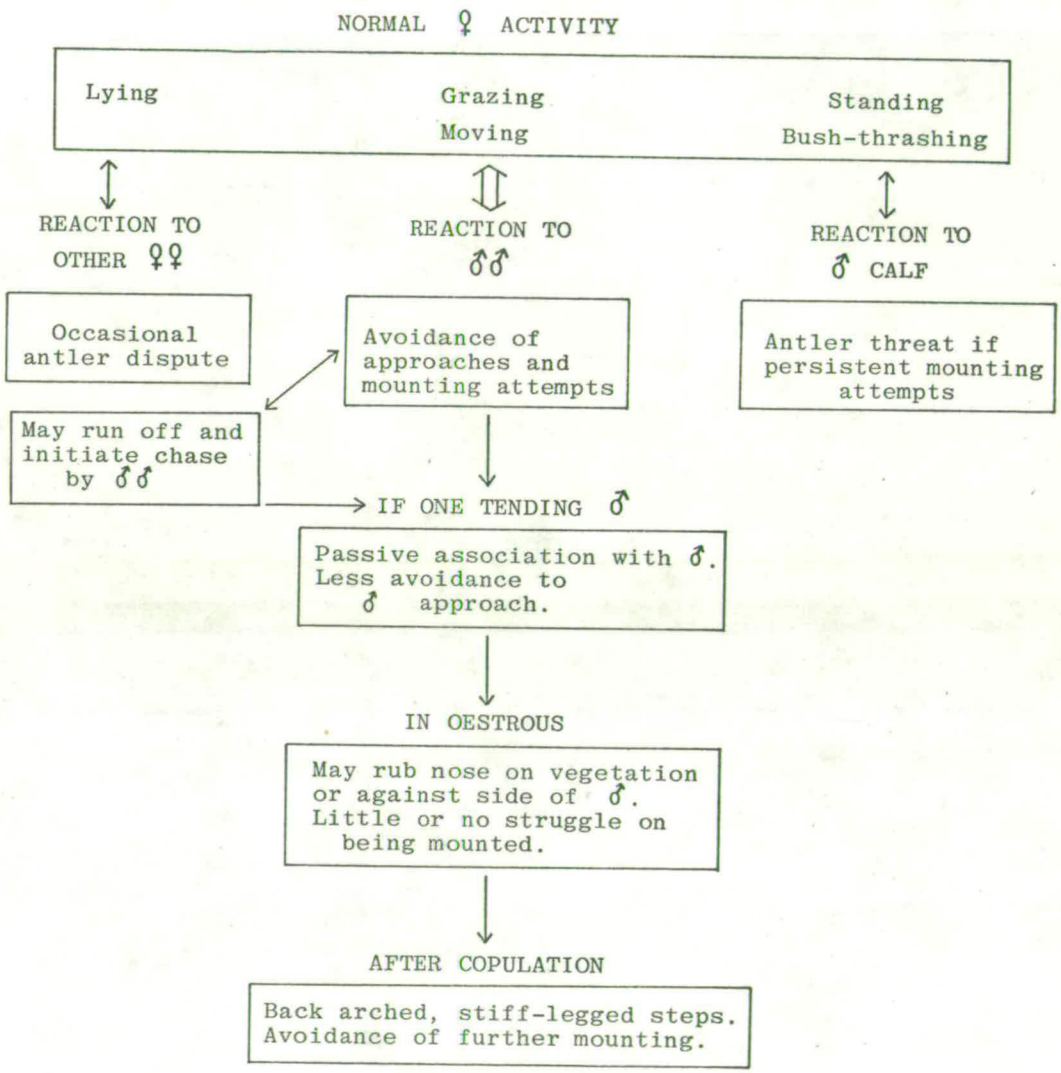


Such infrequent residual sexual behaviour may still be observed in the winter months. In early winter particularly, a male retaining its antlers (the younger males) may occasionally be seen to momentarily swing its head up with tongue flicking towards a passing female, or, especially if the group is crowded together, to make a rushed and indiscriminate mounting attempt at the female immediately in front of it. Unlike the sequences of behaviour in the rut, in no case was there any build-up or aftermath to these isolated events.

On two occasions, however, females were observed to be the instigators of sex-related behaviour in winter. On 22nd January 1970 a female was seen to run out from the group and in the course of three minutes of running interested 12 antlered young males and male calves to follow her. Apart from some mild sparring bouts between males there was no further action. Similarly one year later on 21st January, 1971, a female was watched rushing around, tail up and mouth open, "attracting" at least three young antlered males towards her, again without further developments. The conspicuousness of the vulva of this female and the similarity of her behaviour with a "rutting chase" suggested that she had not conceived at rutting time and her seasonally polyoestrus cycle was continuing.

In the second half of winter sex-related behaviour by the males was still observed but was not necessarily directed towards the females. A feature of winter behaviour is that individual males often associate together on a smooth snow slope /

Fig. 5.16 Sequences of adult female behaviour in the rut.



slope at the edges of the female-calf concentration and within such batchelor sub-groups sex-related behaviour is frequent. A standing male often invites sparring with a nearby partner by tentatively lowering his antlers towards the other (Plate 26). In the course of this prolonged rubbing and twisting of antlers partial unsheathing of the penis is common. One of the sparring pair will often break away to prance or kick its hindlegs in the air playfully, investigate other possible sparring partners, or even leap up towards the back of the nearest animal in a mounting attempt. The younger males who still retain antlers are invariably the instigators of all such sex-related behaviour and mounting attempts were seen to be most frequently directed towards the unantlered older males. As well as their subordinate social status, and leadership tendencies (Ch.6.3.), this represents a further way in which the older males are temporarily cast in the role of "females" at this time.

Such mounting attempts often stimulated a period of sexual behaviour among antlered males gathered in the vicinity. For example, on 23rd January 1971, an antlered male (estimated age 1½ years) tried to mount another. The male being mounted freed himself and antler threatened the first male who walked off then swung his head up in the driving position towards a passing female, before walking on and inviting sparring with a third antlered male. Meanwhile an antlered male had mounted an unantlered male and managed to hold on for 5-6 seconds. This type of undirected variable behaviour was typical of male sexual behaviour in winter.

The /

The relative frequency with which I observed these sex-related activities is shown in Table 5.5. Sparring is by far the commonest distinctive behaviour of the male in winter and while it can often be clearly seen to have associations with sexual gratification or arousal, it can also be seen to have elements of play, antagonism, and comfort (as discussed in Ch.5.1.3c.). The antagonistic element in antler sparring is most often seen when two male calves spar; as they push their spikes against each other with increasing strength a contest may develop until one breaks off and resumes grazing. By contrast, the relaxed antler sparring events of the $1\frac{1}{2}$, $2\frac{1}{2}$ and $3\frac{1}{2}$ year males can last for ten minutes or more with interruptions to graze or dig disinterestedly before joining antlers again. Sparring bouts, and on occasion bush thrashing where suitable shrubs occur, can take up a considerable part of the antlered male's time in winter, viz. 3% of the total herd activity time, and therefore at least 10% of the antlered male's time budget (Thomson, 1973).

The virtual restriction of sex-related behaviour in winter to the males who have still to cast their antlers, is a clear outward sign of the effect of the hormone testosterone on both rutting behaviour and antler status. As the level of testosterone falls, the antlers are cast (Meschaks & Nordkvist, 1962). For red deer males Lincoln et. al. (1970) have described the rut as a form of hyper-sexual activity of limited duration which is directly hormonally controlled, whereas male libido (the ability to copulate) can linger on for six months and is as much dependent on experience and opportunity, as on hormones. /

Table 5.5 Observations of sex-related behaviour in the winter months (November-April).

Type of behaviour	No. of observations	Remarks
Head swinging/driving	11	From antlered ♂ towards ♀ only. Rarely followed directly by mounting attempt.
Mounting attempts	47	From antlered ♂ towards ♀ ; unantlered ♂ ; other antlered ♂ ; or calf.
Female Chase	2	♀ running hard caused interest of ♂♂ but no follow-up.
Antler Sparring	200+	Prolonged and frequent sparring bouts by antlered ♂♂ in winter.

hormones. Like red deer, reindeer females are seasonally polyoestrus and will come into heat at regular intervals until conceived. However, it is unlikely that the male libido, even for young males, lasts as long in reindeer as is supposed in red deer. Meschaks and Nordkvist (op.cit.) found acute regression in the germinal epithelium of reindeer testicles in November, one month after the end of the rut, and by Christmas time this rapid regression process was complete. Similar study on the physiology of caribou reproduction found that spermatogenesis extended from September to December (McEwan, 1963, in Dauphiné & McClure, 1974). However, the occasional late-born calf, as late as September according to Holthe (1975), indicates that at least some males must remain capable of fertilising an unconceived female in mid-winter, into the month of January. From behaviour observations I would assume that these are young antlered males.

5.4. MOTHER-INFANT BEHAVIOUR

"The fawn is like most of the deer well-developed and strong at the time of its birth, so that when but an hour or two old it can, with rather awkward strides, follow its mother."

A. Radclyffe Dugmore, 1913.

The second phase of the breeding cycle, giving birth to the young, occurs some 7½ months after the females are conceived in the autumn rut. The adult male, having played his role in promoting the survival of the species, takes no further part in the breeding cycle, and indeed males are normally absent from /

from the calving area. Every productive female is responsible for bearing, grooming, nursing, sheltering and defending its own new-born calf. The bond of intimate contact between mother and young becomes gradually weaker as the calf becomes less physically dependent on the mother for food and protection, and develops secondary social relationships with other animals of the herd.

Although "maternal drive" is a frequent behavioural expression and suitably illustrates the intensity with which a mother ungulate cares for its young, there is no simple parallel with the male sex drive. Whereas the rutting behaviour of males is closely linked to testosterone levels, maternal behaviour is dependent on no single physiological mechanism but on genetic and experiential factors also (Fraser, 1968). Although the hormone oxytocin is a key substance in parturition and induces milk let-down, neither it nor any other hormone can induce maternal care. Mothering ungulates commonly show individual variation in their maternal behaviour, and an individual's performance can improve with experience, (Fraser, op.cit.). In this study wild reindeer mothers showed particular individual variation in their pre-parturition behaviour, the amount of licking given to the neonate, their willingness to be suckled, and the degree of aggression towards other mothers and their calves.

5.4.1. Pre-Calving Behaviour

The arrival of groups of females and yearlings on the calving grounds /

ground is soon followed by their thorough dispersal, with much wandering of individuals, pairs, and groups between successive snow-free grazing areas. The pregnant females in particular (still retaining their antlers) appear particularly active and will often walk or trot away from a group. In doing so they may gratuitously become leaders as all or part of the group attempt to follow. For example:

a) One antlered female walked away from a group of 15 and was followed by 6 yearlings and 4 females, leaving behind 3 females and 2 yearlings.

b) Three antlered females were alternatively trotting and walking over the snow, the one in front often stopped to sniff the ground, look around, and in passing by a lying group of 7 yearlings and 3 yeld females, one of the yearlings got up and followed the 3 antlered females.

c) One single antlered female joined 2 female-calf pairs then walked away again after two hours.

d) An antlered female was seen running from a group then after a pause the rest of the group ran after her.

e) An antlered female trotted away from a group of 8, going back the way the group had come and often sniffed in their tracks. At 300m away it was followed by a yearling, and further behind 3 yearlings and one female. The same antlered female one hour later was lying alone on a bare patch and for several hours until nightfall it often got up, turned round, and lay again, indicative of imminent calving.

While /

While this restless moving behaviour of pregnant females could be interpreted as a desire for seclusion, it was also observed that some females would simply choose to be left behind on the grazing area which a group had moved from, either because they had just calved or were about to. For example, on North Ottadalen on 9/5/1970 a herd of 120 moved off after a lying period and left behind 8 females, all with new-born calves. On two other occasions, a female was seen at the rear of a moving group still attempting to keep up while the front hooves of its unborn calf were clearly visible from the vulva. Similarly, on 9/5/1971 to follow a herd of 300 containing many pregnant females was to see calving in progress as individual females dropping their calves were left in the wake of the herd.

From these observations it was clear that the pre-partum behaviour of mountain reindeer was variable. While a few females appeared to seek seclusion for calving, most showed no such motivation and either gave birth with other deer around or were fortuitously left behind as the group moved on. Bergerud (1964) and Lent (1966) similarly believed that caribou females did not actively seek seclusion for calving, while Espmark (1971a) found that many mountain reindeer gave birth in the company of others, whereas all woodland reindeer females sought seclusion.

5.4.2. Parturition

In domestic ungulates the increasing restlessness of expectant females /

females is thought to be evidence of a build-up in labour pains (Fraser, 1968). Espmark (1971a) has described labour in reindeer as the frequent alternation of lying and standing, the decline and cessation of grazing, intermittent groaning, and tossings of the head towards the hind quarters. Of the three parturitions I recorded fully in this study, the females showed some of these signs of discomfort both before and after giving birth, but none of the violent contractions described by Bergerud (1964).

1. Hardangervidda, 23rd May, 1970

At 11.45 a.m. a female walking over the snow with a group of 45 twice paused to splay its back legs apart and turn its head around towards its rear where the front hooves of the foetus were clearly visible (Plates 27-29). The yearling behind her sniffed the female's rear on one such occasion. Variously walking and trotting she then moved off at a tangent from the group towards a small bare area some 50m off, stopping twice en route in apparent labour contractions. On reaching the site the female lay down, two minutes later she stood up and seconds later the calf slipped out (12.09h) (Plates 30 & 31). The female immediately lay again and in the next hour, during which the calf was more or less constantly licked, she got up 19 times to stand for a few seconds, turn around, and lie again. The yearling who had accompanied the female and had lain watching the birth got up to graze and after four minutes had moved away back to the group. After two hours the female began grazing again in the close vicinity of its calf, and some three hours after the birth, the placenta was passed which /

which the female started to eat.

2. Hardangervidda, 23rd May, 1970

A herd of over 120 ending their lying period were moving off from the area leaving behind two females and a yearling. One of these females was seen getting up from lying whereupon a calf slipped out (21.37h). The female immediately began licking the calf. Eleven minutes later the yearling lying some 20m away got up and walked slowly off to join the herd now grazing 200m away. The mother remained lying licking its calf, getting up 21 times in the next hour as darkness fell.

3. Hardangervidda, 24th May, 1970

A female lying on a bare patch separate from a group of 10 grazing and lying animals was seen to stand up with the fore-legs of the foetus clearly visible, then lie down again. While lying the back of the female looked hunched, the head would sometimes be stretched forward, and on occasions she would alternately stretch out and bend her legs. She was also seen to frequently open her mouth (groaning?) and to prick her ears forward. Each time the female got up (7 times in the 8 minutes preceding birth), more of the calf would be visible. By 10.29h half the calf had emerged and as the female lay down the calf's head appeared to be striking the ground rather heavily. The female rose once more, turned round and with all but the hind legs of the calf out, and in the process of lying once more, the calf dropped to the ground. The female lay and immediately began licking the calf and apparently ingesting the white amniotic threads around it. Ten minutes later a yearling from the /

the group walked by the mother-calf pair and urinated 2m away without interest or concern by the female. As the yearling then grazed to within 1m of the pair, the female turned its head for a moment towards the yearling then back to licking the calf. After this yearling had moved off, a second yearling came up five minutes later, gazed at the mother-calf pair for a minute, then walked off. This female showed no signs of post-partum discomfort and got up only 6 times in the hour following birth. After four hours it was seen to graze again and shortly after the placenta was passed.

The three births recorded above took place in the morning (10.30), at noon (12.09), and in the evening (21.37). Other known births on Hardangervidda and North Ottadalen occurred around 7.00, 10.30, 11.30, 12.00, 17.00, and eight between 10.30 and 14.30 (Table 5.6). Considering these and the thirteen times documented by Espmark (1971a), it can be said that calving in reindeer is associated with no particular time of day. Parturition in mammals has been said to be usually associated with an animal's resting period (Slijper, 1960). The observed reindeer births were certainly associated with females in a lying herd or single lying females, but since lying periods alternate irregularly with active periods at calving time (Thomson, 1971), it would not be expected that any particular time of day would be associated with parturition.

The position of the mother at the moment of delivery is also highly variable. In the three parturitions described, all females /

Table 5.6 Parturition and first occurrence of certain behaviour in calves and mothers.

	Observation No.									
	1	2	3	4 to 11		12	13	14	15	16
Location	H'vidda	H'vidda	H'vidda	North Ottadalen		N.Ottad.	N.Ottad.	N.Ottad.	N.Ottad.	H'vidda
Date of birth	23.5.70	23.5.70	24.5.70	9.5.70		8.5.71	9.5.71	9.5.71	9.5.71	28.5.71
Time of birth	1209	2137	1030	1030 to 1430		c.1700	c.1030	c.1130	c.1200	c.0700
Calf behaviour	Time after birth in minutes (m) and hours (h)									
Calf attempts to rise	3m	4m	5m	-	-	-	-	-	-	-
Calf up on back legs	14m	>30m	22m	-	-	-	-	-	-	-
Calf stands on four legs	27m	>60m	35m	-	-	-	-	-	-	-
First lying suckling	34m	-	29m	-	-	-	-	1h	-	-
Calf walks	40m	-	45m	-	-	-	-	-	-	-
Calf sleeps	1h 40m	-	1h 25m	-	-	-	-	-	-	-
First side-suckling attempt	2h 15m	-	4h 10m	-	-	-	-	-	-	-
First successful side-suckling	2h 50m	-	4h 30m	-	-	-	c2h 30m	-	-	-
Calf runs	5h 40m	-	6h 30m	-	-	-	-	-	-	-
Calf nibbles vegetation	6h	<24h	7h	-	-	-	-	-	-	-
Mother behaviour										
Position of female at birth	standing	lying → standing	standing → lying	-	-	-	-	-	-	-
Female recommences grazing	2h	>1h	4h	-	-	-	-	-	-	-
Placenta passed	2.9h	>1h	4.2h	2h,2.5h,3h,>5h		-	3.5h	2.5h	-	-
Female and calf leave place of birth	8.5h	40h	24h	9h,9h,19h,19h, 24h,24h,24h		-	0.8h	-	-	-

females were spending most of their time lying, and at the moment of delivery one female was standing contracting, another was in the process of getting up, and the third in the act of lying down. Other observers of reindeer and caribou find that females may be standing (Slijper, 1960; Lent, 1966), lying (Pruitt, 1960; Kelsall, 1968; Espmark, 1971a), squatting (Grimmer, in Lent, 1966), or in the process of getting up from lying (Bergerud, 1964).

The female's choice of snow-free ground for delivery of the calf is a more regular feature. Although snow covers more than 50% and up to 80% of the ground at calving time in the mountains of south Norway (Plate 39), no calves were known to have been born on snow. Of nine known parturition sites all were situated on snow-free ridges or terraces on flattish dry ground, typical of the sites that reindeer will lie on at this time. The vegetation in these areas allows the mother to feed after a few hours without the calf having to move with the mother in search of grazing. However, occasions must arise when a female in labour is unable to reach a snow-free patch. For example, Lent (1966) records two caribou females giving birth on a snow slope in the midst of snow storm. A photograph in Baskin (1970) shows a standing female delivering a calf onto snow. In this study mothers and their calves of a few days old were seen to settle on snow, but only when the weather was warm and sunny.

The time taken for the female to pass the placenta (after-birth) is relatively long in reindeer. I noted that the placenta was passed /

passed 2.0, 2.5, 2.9, 3.0, 3.5, 4.2, and over 5 hours after the calf was born (Table 5.6). This is within the range of 1½ to more than 7 hours found in reindeer by Espmark (1971a), but is considerably longer than the few minutes reported for caribou (Pruitt, 1960; Kelsall, 1968). Lent (1966) found that the range of variation in caribou was from a few minutes up to a maximum of two hours, whereas this maximum for caribou is around the minimum time so far recorded for reindeer.

Reindeer mothers were seen to pass the placenta in the course of grazing and immediately start eating it, taking some ¾ to 1 hour to ingest it fully. Occasionally a female would not remove all the placenta, and this was particularly likely if she was disturbed by the presence of interested ravens or gulls on the ground nearby. Usually after a few charges at such birds she would move off with her calf and leave the placenta to these scavengers (Ch.5.4.5.). It may be hypothesized that ingestion of the placenta has evolved so that the relatively quick disposal of the bloody placental remains minimises the risk of attracting scavengers such as ravens and foxes, which are potential predators of the young calves.

Another difference apparent between calving reindeer and caribou is that the time taken for a reindeer mother to move away with its calf from the site of parturition is longer than for caribou. On Hardangervidda and North Ottadalen, mother and calf pairs left the area of birth 50 minutes, 8½ hours, 9 hours (2 pairs), 19 hours (2 pairs), 24 hours (4 pairs), and 40 hours after the time of birth (Table 5.6), and the shorter /

shorter of these times was as a result of disturbance from ravens, gulls, or a passing herd. Similarly Espmark (1971a) records mothers leaving the site of parturition at 10, 18, and 30 hours, and 2 mothers on the initiative of their calves at 3 hours and 6 hours. Undisturbed caribou mothers on the other hand move off when the calves are 1-3 hours old (de Vos, 1960; Pruitt, 1960; Kelsall, 1968), and not more than 4 hours (Lent, 1966). The longer time in reindeer would not appear to be due to any slower development of the reindeer calf's faculties (see Table 5.6). The difference may be related to the more extensive and prolonged migratory behaviour of barren ground caribou. Caribou migration does not cease when the animals reach the calving ground and mothers will pause for only a few hours after calving before continuing their movement. Reindeer mothers on the other hand when finally choosing to leave the parturition site would invariably join up with other mother-calf pairs, and these nursery groups so formed would be characteristically stationary for a few days.

5.4.3. Maternal Care

The mother begins licking its calf all over immediately after delivery. An hour or more of concentrated licking is interrupted only by short pauses when the mother licks her own hind legs or body, or occasionally holds her head up in a yawn. In the first hour of its life a calf is constantly active and appears particularly stimulated by the mother's licking. Within the first few minutes it struggles to rise, and by 15-20 minutes it can usually stand on its back legs while kneeling on its forelegs /

forelegs. In this position it may succeed in suckling from the udder of the lying mother, while the mother concentrates licking on the calf's rear. The calf manages to stand on all four legs at about half an hour old although at first it may be knocked down again by the force of its mother's licking. By one hour old the calf can normally stand for over one minute and has taken its first few steps (Table 5.6).

Thereafter there are longer pauses in the mother's licking and the calf now sleeps for short spells. By this time licking has become concentrated on the calf's anal and head regions (Plate 33). Whenever the calf is licked or muzzled by its mother it is stimulated to activity and similarly when the mother stands up the calf invariably gets up and rubs itself against the legs of its mother, while thrusting its head up in search of the mother's teats. Especially if the calf has successfully suckled the lying mother a few times (Plate 34), the first successful bout of suckling from a standing mother may not occur for two to three hours or more. By this time the mother has begun grazing around the calf, frequently turning to sniff or lick the calf which responds with 3 - 4 minute bursts of activity followed by 10 - 20 minutes of resting and sleeping.

By the age of 5-7 hours the calf makes short runs around the mother and begins its investigation of its physical environment by tentatively pawing at the ground or nibbling on the vegetation. In immediate contact with the mother the calf is still frequently licked on the rear, stomach, and face, and always /

always on the rear when it moves into the standing suckling position (Plate 35).

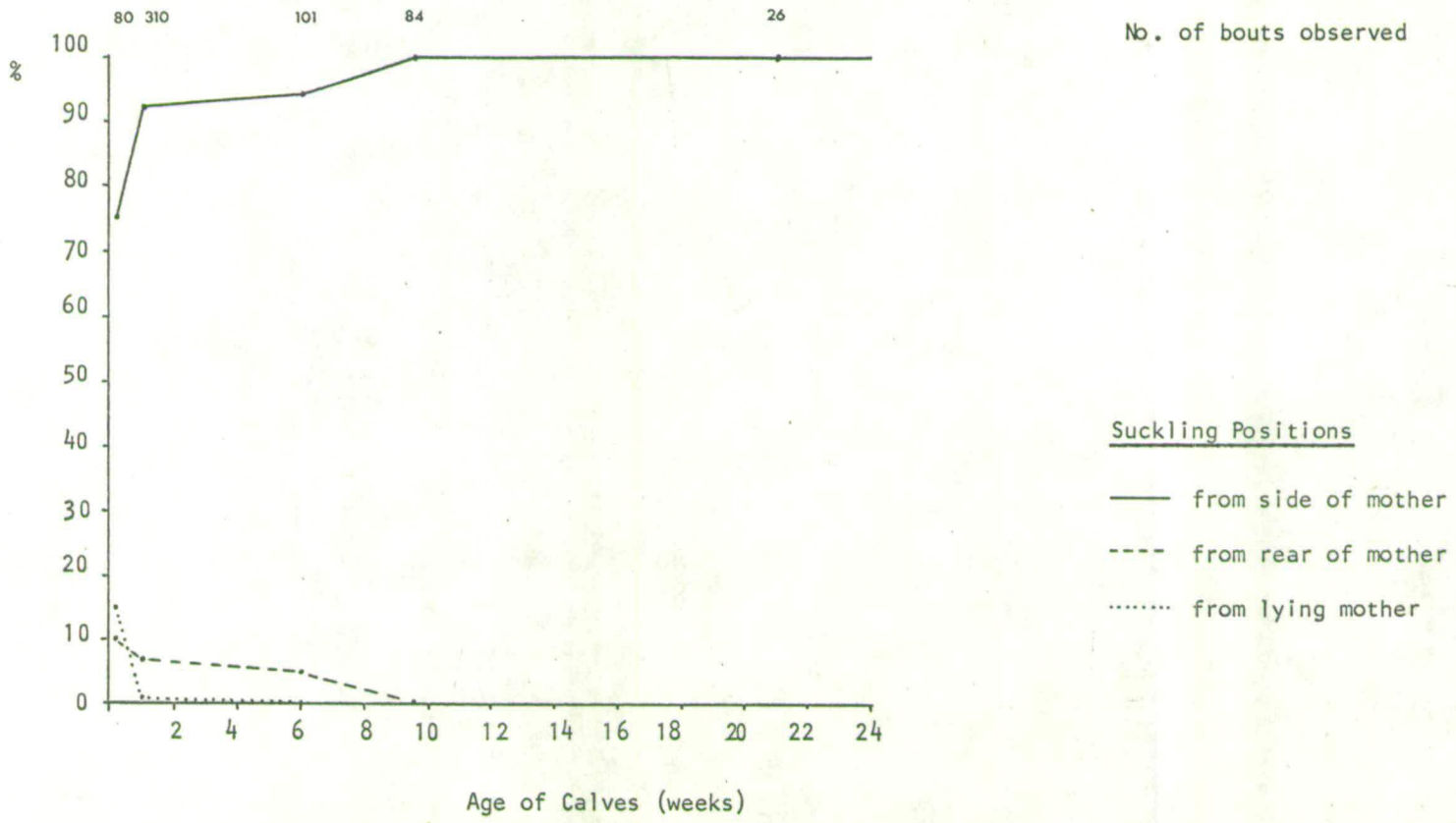
Licking of the neonate is common to all ungulates, and from studies on sheep, various functions have been ascribed to the licking (Fraser, 1968), all of which seem likely for reindeer also. Licking is thought to clear off the amniotic mucus from the new-born lamb, and check body heat loss as the fur dries. Licking orients the lamb's response of turning to the mother, and by licking the posterior it is guided to the mother's udder. Apart from stimulating the neonate, licking may furnish a quick and effective basis for maternal fixation by olfactory and gustatory means. Baskin (1969) states that the ability of the female to distinguish the smell of her own calf commences after the first suckling and suggests that it is the smell of her own milk which renders the calf recognisable. How a female would recognise the smell or taste of her own milk is not suggested.

5.4.4. Suckling

There are three types of nursing position in reindeer. By far the commonest position is from the side whereby the calf stands parallel and opposite to the mother with its head in under the udder, while the mother licks the calf's rear (Plate 35). This position accounted for 92% of the 310 successful suckling bouts recorded for calves 1-10 days old, becoming the only suckling position for older calves (Fig.5.17). Suckling from between the hindlegs of the mother was sometimes attempted /

Fig. 5.17 Relative frequency of different suckling positions with age of reindeer calves.

(Expressed as % of total number of successful suckling bouts observed)



attempted while the mother was grazing or standing and accounted for 7% of successful bouts for calves 1-10 days old. Suckling from the lying mother (Plate 34) was a feature only of some calves a few hours old, usually before the side position had been successfully mastered(Fig.5.17).

Suckling bouts were timed at four different calving seasons, and showed no significant differences between ranges or years. The mean duration of complete suckling bouts for calves 1-10 days old was 80.8 seconds ($\pm$9.7) for 134 events (Table 5.7). Suckling from the common side position lasted significantly longer than suckling from between the hind legs of the mother (mean 84.8 v 25.5 seconds; Table 5.8). In the hind leg position there is no opportunity for the mother to lick its calf's rear, so that the mother either continues grazing, taking a few steps occasionally, or stands and eventually terminates the bout at an early stage. Hind leg sucklings were significantly more frequent on Hardangervidda than on North Ottadalen (Table 5.9). This is thought to be due to the females on Hardangervidda being in poorer condition than those on North Ottadalen, spending less time indulging their calves and more time on active grazing. Hardangervidda calving females spent 54% of their time on grazing and 1% on idle standing, whereas their North Ottadalen counterparts spent only 36% time on grazing and 6% on idle standing (Gaare, Skogland & Thomson, 1970; Thomson, 1973; Fig.3, App.4). In their first day of life, mothers usually stand and allow their calves to suckle until the calf itself decides to terminate the event (58% of all events), whereas from the age of 1-10 days old significantly /

Table 5.7 The duration of successful suckling bouts for 1-10 day old calves on North Ottadalen and Hardangervidda in 1970 and 1971.

	No. of bouts	Mean duration (secs)	t- test Significance
North Ottadalen 1970	53	77.6	N.S.
Hardangervidda 1970	51	88.5	
North Ottadalen 1971	6	62.5	
Hardangervidda 1971	24	76.0	
All	134	80.8 ± 9.7 (at 95% confidence interval)	

significantly fewer bouts are calf-terminated (41%), 45% of events on North Ottadalen and only 22% on Hardangervidda (Table 5.10). By the age of 4 weeks a calf-terminated event is exceptional. Not surprisingly, sucklings where the mother terminates are significantly shorter in duration than when she allows the calf to suckle until satiated (mean 71.7 v 98.8 seconds for calves 1-10 days; Table 5.10). Suckling is usually initiated by the calf moving in to suckle the standing or grazing mother who then stops grazing to turn and lick the calf. Occasionally, however, the female may be seen to initiate the bout by muzzling or licking its lying calf, standing orienting itself for the calf, or licking the calf's rear to encourage it to suckle. On one occasion a female was seen to get its young calf up by gently prodding it with a front hoof. This is illustrated by Espmark (1971a). Occasionally while nursing the mother's hind leg would be raised slightly to allow easier access for the calf. Espmark (op. cit.) mentions also that the female may bend her hind legs and thus lower her udder to facilitate suckling for a young calf.

Milk feeding is a frequent event in young calves, and was estimated to occur on average every 40 minutes in the calf's first week of life. Typically suckling occurred as the female rose from a lying period; after a period of temporary "separation" while the female was grazing; through social facilitation in the nursery group when a calf saw nearby calves suckling; or following a disturbance to a nursery group. At the moment of alarm itself, however, females were seen to refuse to nurse their calves. This may be related to the physiology /

Table 5.8 Comparison of the duration of successful sucklings from the side of the mother and from between the hindlegs of the mother for 1-10 day old calves.

	Type of suckling position	
	from side	from hind legs
No. of bouts	115	10
Mean duration (secs)	84.8	25.5
t- test significance (t = 5.53 at 15 d.f.)	$P < 0.001$ ***	

physiology of the hormone oxytocin which is required for milk let-down but is blocked by adrenalin (Fraser, 1968). Calves older than one week would often push against the mother's udder while suckling. This "bunting" is thought to mechanically stimulate the process of milk flow from the udder (Zaks, in Lent, 1966).

After observations of calves up to 10 days old, the next observations in the field were made when the calves were 4-8 weeks old by which time mothers and calves were integrated into the large mixed herds of early summer, and their suckling behaviour considerably altered. Suckling bouts were much less frequent, and were invariably initiated by the calf only, often with persistent strong bunting at the mother's udder. The mother usually turned around to sniff the calf's rear momentarily, but rarely licked, and always terminated the bout, on average after half a minute (48 bouts averaging 30.2 seconds $\pm$ 3.1, Fig.5.18). Also multiple sucklings were common in that when a calf went in to suckle a female another calf on observing it would often move across to join in. Occasionally a third and even fourth calf moved in to attempt to suckle from the same female. Females appeared to differ in the degree to which they tolerated this intrusion, and bouts would often end chaotically with the female clambering away from calves on all sides. Of the 220 suckling bouts recorded for calves after the age of 1 month, 82 were multiple bouts (37%), and 16 of these involved 3 or more calves. Multiple suckling was at its highest frequency in the massed post-calving herds with calves 4-8 weeks old (45% of recorded bouts), with a mean number of 1.52 calves /

Table 5.9 The relative frequency of suckling between the hindlegs of the mother for 1-10 day old calves on Hardangervidda and on North Ottadalen.

	Number of suckling bouts	
	from side	from hindlegs
North Ottadalen (1970 & 1971)	248	4
Hardangervidda (1970 & 1971)	110	17
χ^2 significance (χ^2 = 20.26 at 1 d.f.)	$P < 0.001$ ***	

calves per suckling bout (Fig.5.19). Espmark (1971a) also found that this "thief-suckling" was commonest amongst reindeer calves of 4-8 weeks. Interestingly, it was not attempted by caribou calves of this age at Prudhoe Bay, Alaska, nor is it reported for caribou elsewhere, with the exception of one such event described on Newfoundland (Bergerud, 1964). The incidence of multiple suckling would seem to be one of the few behaviour patterns which distinctly differ between reindeer and caribou (see Ch.9.4.). Since it is the calf which initiates suckling from a strange mother, it is clearly a difference which arises at an early stage in the ontogeny of Rangifer behaviour.

Weaning is a difficult term to define for reindeer. For at least some mother-calf pairs successful suckling events (averaging 20 seconds) can be recorded with reducing frequency throughout summer, autumn, and winter (Fig.5.18). Espmark (1975) found that the parturient female aggressively drives off her yearling, and that there were no indications that the social bond between mother and yearling was re-established in summer. However I have observed yearlings suckle lactating females in the calving season and summer, and often simultaneously with a calf or calves (Table 5.11). Whether these yearlings have re-associated with their mothers or are thief-suckling can only be surmised. In the sedentary Cairngorms herd it is known that animals in their second and even third year often remain associated with their mothers, even to the extent of an occasional suckling bout (Plate 40; and M. Utsi, pers. comm.).

5.4.5. Defence of the Calf /

Table 5.10 Comparison of the duration of successful suckling when the mother terminates and when the calf terminates the bout, and its frequency between different ranges for different ages of calves.

	Termination of suckling		
	by mother		by calf
No. of bouts (for 1-10 day old calves)	64		44
Mean duration (secs)	71.7		98.8
t-test significance (t = 2.44 at 68 d.f.)		$P < 0.02^{*}$	
Number of bouts (for < 1 day old calves)	16		22
Number of bouts (for 1-10 day old calves)	112		64
χ^2 significance (χ^2 = 5.16 at 1 d.f.)		$P < 0.05^{*}$	
No. on North Ottadalen (1-10 day old calves)	61		50
No. on Hardangervidda (1-10 day old calves)	51		14
χ^2 significance (χ^2 = 8.80 at 1 d.f.)		$P < 0.01^{**}$	

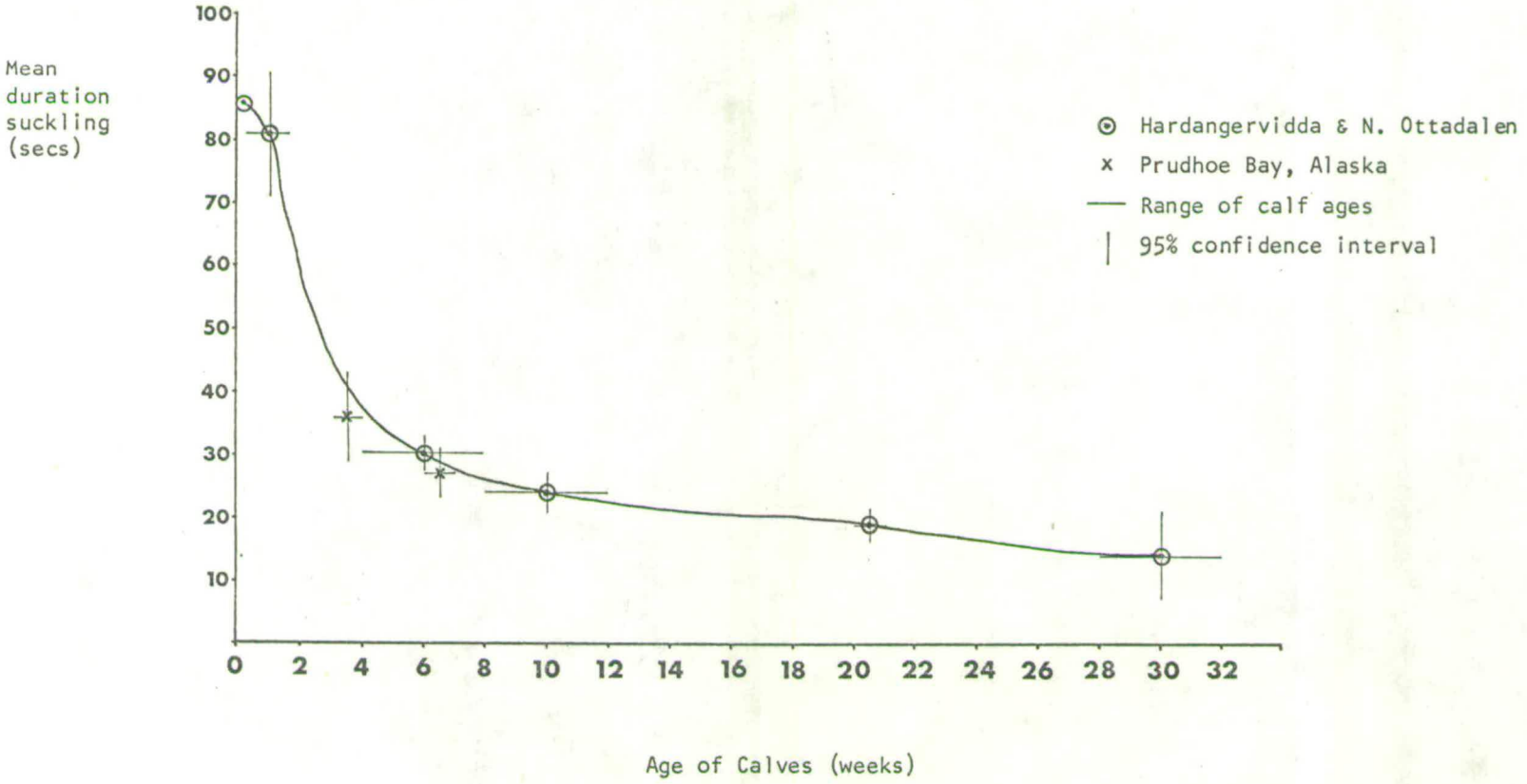
5.4.5. Defence of the Calf

An almost universal feature of maternal behaviour in mammals is the way in which the mother protects its young from potentially dangerous influences in the environment. For reindeer, young calves are kept relatively isolated from other animals, including other calves initially, by the antagonism shown by the mother towards any deer which approach the pair too closely. Antlered threats, foot jabs, and rush charges are commonplace amongst mothers in recently established nursery groups. The greatest intensity of maternal "aggression" is directed against yearlings or other calfless adults with a gradual increase in tolerance towards other mothers and calves (re. Ch.5.2.3).

This readiness of the mother to protect its calf is also evident whenever scavengers or potential predators display any interest. Ravens and gulls are particularly attracted by the placenta when it is passed by the female and will settle on the ground nearby, then walk up closer. The mother reindeer frequently pauses from chewing on the placenta or caring for the calf to look around at the intruders. When, as commonly happens, a bird walks up to within 5-10m the female will break off and rush charge at the intruder, often in time to charge at a second bird even nearer the placenta and her young calf. With the usual persistence of the scavengers the anxious mother invariably abandons the placenta and leads its calf away from the site.

At /

Fig. 5.18 Mean duration of suckling bouts with age of reindeer calves.

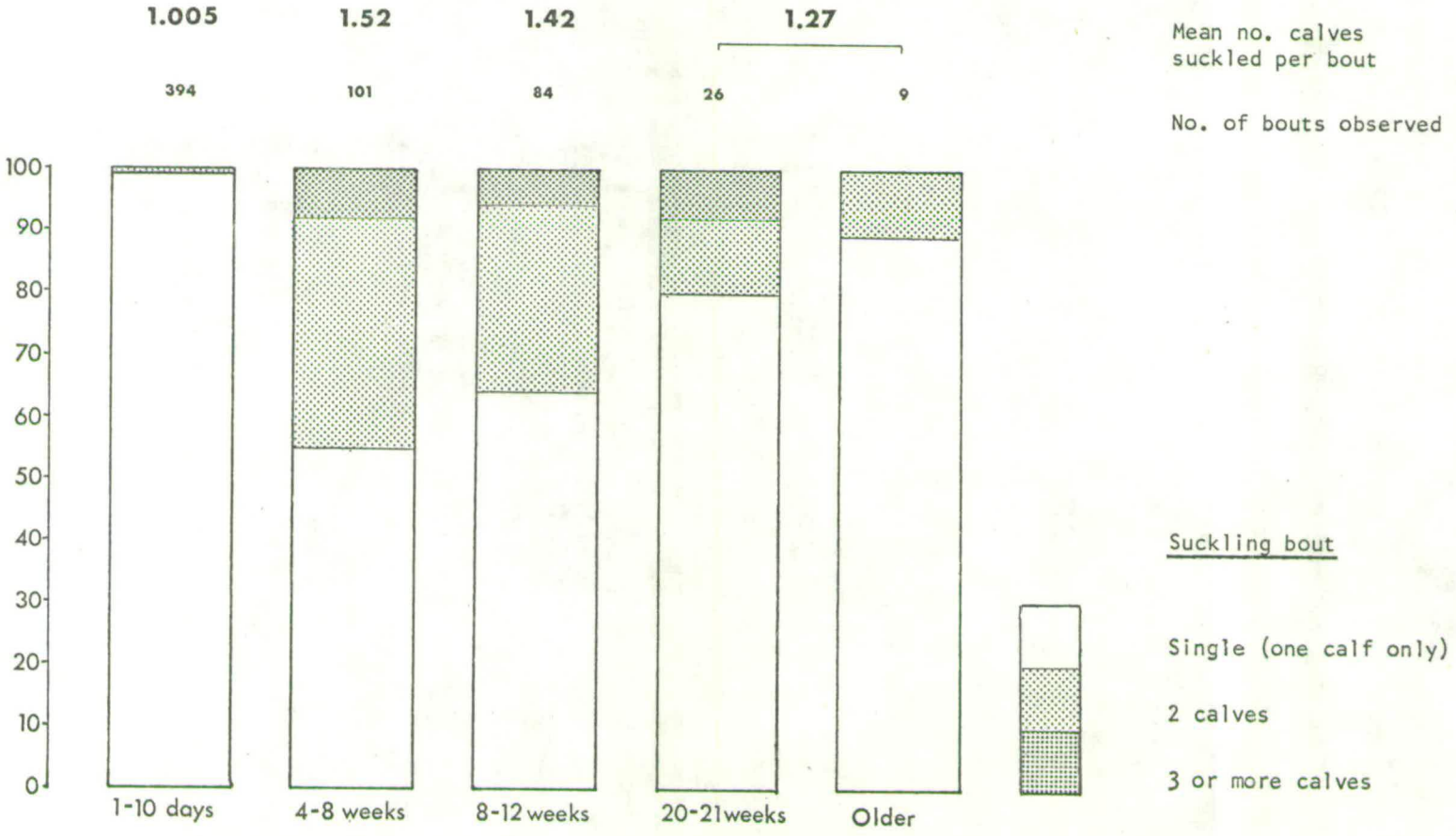


At other times too the mother stands by its calf whenever it sees or hears the call of ravens overhead. The greatest concern was shown when a golden eagle flew over a female and calf. The mother did not run initially but stood directly over its calf, and when the eagle made a swooping low dive the female reared up on its hind legs, kicking in the air with its forelegs towards the attacker. This defence against an eagle has also been recorded for a red deer hind with a young calf (MacNally, 1968). From the response of reindeer groups in winter to foxes, there is little doubt that the mother female would similarly stand its ground and charge or kick out at any fox which ventured too near its calf. Rush charge and kick was precisely the response of two male tame reindeer when approached too closely by a dog (Gaare et.al., 1970). The observed incidence of active defence by reindeer against small predators within and outwith the calving season is shown in Table 4, Appendix 6.

The reaction of mother females to human disturbance was more variable. If suddenly alarmed a female would usually make off with a slow exaggerated springy gait with tail flag erect, pausing and turning back frequently, if its calf was too young to keep up. Only on one such occasion when a female turned back to face its calf did it appear to bob its head towards it. For caribou mothers on the other hand head bobbing is known to be a common "attraction pose" to induce a following response in their calves (Pruitt, 1960; de Vos, 1960; Lent, 1966; Miller & Broughton, 1973). While retreat is the usual form of defence behaviour in both reindeer and caribou, caribou mothers /

Fig. 5.19 The incidence of multiple sucklings in reindeer, involving simultaneously more than one calf per suckling bout.

(Expressed as a % of total suckling bouts observed)



mothers have been known to stand their ground and rush charge at humans who have approached closely with the intention of gathering the young calf for weighing and ear-tagging (Lent, 1966).

5.4.6. The Mother-Infant Bond

The observed association of mother and young is clearly dependent on mutual recognition, and this appears to be established at an early stage. My observations suggest that olfactory, visual, and auditory communication all play a role in individual recognition, and that the female in particular becomes adept at recognising its own calf within 1 hour or so of birth. The constant licking of the calf in its first hour is probably essential behaviour in establishing the mother's attachment to the infant. For domestic sheep it is thought that licking for 20-30 minutes establishes attachment and the basis for the mother's recognition of its lamb, and for goats 5 minutes of contact is said to be sufficient to ensure olfactory imprinting (Fraser, 1968). How long it takes the calf to recognise its mother is less certain. Baskin (1969) claims that the time required for mutual recognition between reindeer female and calf is 5-6 hours. However, I observed that where several births had taken place on the one site, young calves of a day or two old would commonly approach females other than their mothers and be rejected as soon as the female had sniffed the strange calf's rear. Such rejection could take the form of antler threats or foot stabbing (Ch.5.2.3.), and would continue as long as the calf sought association with a female other /

Table 5.11 Recorded instances of suckling by yearling reindeer.

Date	Approx. age of yearling	Location	Success	Duration (secs)	Remarks
25/5/71	12 mths.	Hardangervidda	?	10	Y. only on apparently unantlered yeld ♀ .
25/5/71	12 mths.	"	?	40	Y. only on apparently unantlered yeld ♀ .
14/7/70	13-14 mths.	"	?	?	Y. and calf.
14/7/70	13-14 mths.	"	yes	5+	Y. only.
14/7/70	13-14 mths.	"	no	-	As Y. in to join calf, ♀ moves away.
15/7/70	13-14 mths.	"	yes	10	Y. joins calf who had suckled 5 secs.
16/7/70	13-14 mths.	"	no	-	As Y. and calf in to join 2 calves, ♀ moves away.
16/7/70	13-14 mths.	"	yes	8+	Y. and calf.
1/7/71	13-14 mths.	"	yes	?	Y. and calf.
2/7/71	13-14 mths.	"	yes	20+	Y. joins 2 calves then a second Y. joins.
20/7/71	13-14 mths.	"	yes	25	Y. only.
4/8/70	14-15 mths.	"	yes	10+	Y. and calf.
4/8/70	14-15 mths.	"	yes	15	Y. only.
5/8/70	14-15 mths.	"	yes	20+	Y. and calf.
5/8/70	14-15 mths.	"	yes	5+	Y. and calf.
5/8/70	14-15 mths.	"	no	-	As Y. in to join calf, is repulsed by ♀ .
5/8/70	14-15 mths.	"	yes	10+	Y. only.
6/8/70	14-15 mths.	"	no	-	As Y. in to join calf, ♀ moves away.
7/8/70	14-15 mths.	"	no	-	Y. is repulsed by ♀ .
4/9/70	15-17 mths.	"	yes	7+	Y. and 2 calves.
16/9/70	15-17 mths.	North Ottadalen	yes	9	Y. only.

other than its mother. Such negative re-enforcement of the mother-calf bond could occasionally be seen to confuse the young calf and it would subsequently back away in fright from the approach of its own mother.

While the olfactory check of sniffing a calf's rear or muzzle appears to be the ultimate determinant of a mother re-establishing contact with its calf, visual and auditory cues may also be seen to play a role. Young calves may be darker or lighter in colour than the normal deep reddish-brown, while a few are born grey or white. When a mother female seeks to re-establish close contact with its calf, it will sniff only calves of a similar colour and size to its own, and ignore or directly threaten any others without first sniffing. Similarly calves have been seen to approach females which look similar to their own mothers, whether in regard to coat colour or antler status.

Vocal communication also played an obvious role in re-uniting a temporarily separated mother and calf pair, as well as being used to maintain on-going contact in a moving group or herd. The extent to which the female grunt and the calf bark (a low-pitched bleat) are used, or are capable of being specifically used, for individual recognition has been intensively studied by others without conclusive results. Ericson (1975) considered that female grunts and calf bleats serve as alerting signals which are more likely to produce response amongst temporarily separated pairs, but actually played little or no role in individual recognition as such. Espmark (1971c) and Lent /

Lent (1975) on the other hand concluded that both mothers and infants can respond selectively to each others' vocalisations, and it was my impression also from observation in the field that this usually occurred.

The olfactory, visual and auditory bases for individual recognition do not in themselves describe the mother-infant bond. The strength of association between mother and young is most clearly evident when it is inadvertently broken. Where a calf is lost or dies the mother will return to the site, frequently grunting, looking around, and searching. Searching behaviour may be continued into the second day of the mother's loss. Suckling events undoubtedly have a strong reinforcement on the bond. Whenever a temporarily separated mother and calf pair become re-united, and following a brief olfactory identification check by the mother, a suckling occurs. Baskin (1969) has suggested that the pressure of milk in the mother's udder causes her to search for her calf, while the calf experiences increasing hunger and therefore incentive to locate the mother. However, I observed that reinforcement of the bond by suckling often occurred regardless of how soon the previous suckling event had taken place.

Physical contact between mother and the young calf would also seem to act as a positive reinforcement of the bond. Their early close association involves much licking and sniffing of the calf, while the calf variously muzzles, nudges, or clambers over its lying mother. The mother's licking of the calf becomes restricted after a few days to licking of the calf's /

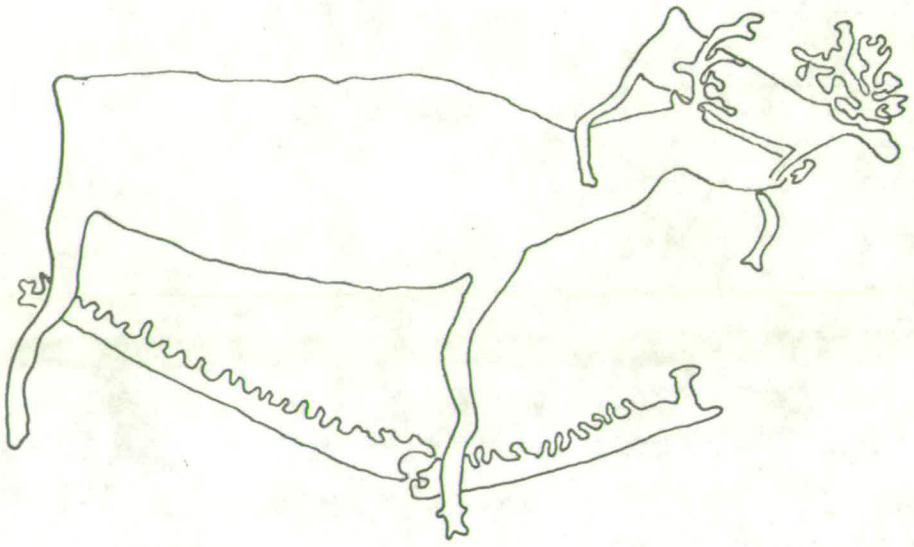
calf's rear during suckling, which in turn gives way to a perfunctory sniff.

The maternal care of the reindeer female, encompassing as it does provision of milk, shelter, protection from predators, and leadership, enables the growing calf to explore and develop its potential within a relatively safe environment. Miller and Broughton (1973) observe that the large post-calving aggregations and rapid movement requires a strong maternal-filial bond in the species.

Even in winter when the calf is capable of providing entirely for itself, the bond is operative in that the calf can still benefit from its mother's experience in leadership and, if necessary, by sharing her feeding crater (Ch.7.2.). If wild reindeer were in small permanent groups there is little doubt that the mother-young relationship would be the basis of social organisation with groups structured on the successive generations of mothers and young, as in the small stationary Cairngorm reindeer herd. However, the changing size and composition of wild herds indicates that familial relationships may have no lasting place in the social organisation. The mother-infant bond ultimately equips a calf for anonymous independent membership of the herd. Group "members" associate together through temporary common needs linked to a general sociality and social facilitation of activity (Ch.6.2.). Dominance and leadership are expressed and accepted, not on the basis of kinship or age, but from anonymous strangers, or at the best temporary associates. However, total anonymity in /

in a wild population may not always apply. There is some indication from ear-tagging and radio-tracking of barren-ground caribou in Canada that long-term social bonds between individuals in a group may exist (Parker, 1972; Miller et.al., 1975; & see Ch.7.1.3.).

CHAPTER SIX SOCIAL BEHAVIOUR



Stone-Age rock engraving, over 3m long, of reindeer and boats at Zalavruga, Vyg Delta, White Sea Coast, U.S.S.R. (from Maringer & Bandi, 1953).

CHAPTER SIX SOCIAL BEHAVIOUR

"The war of each against all is not the law of nature. Mutual aid is as much a law of nature as mutual struggle.... Many striking illustrations of social life could be taken from the life of the reindeer...."

Prince Peter Alexeivich Kropotkin, 1902.

In many ethological studies, the social behaviour of a species is represented as the sum of behavioural interactions between individuals in a population, with particular emphasis on reciprocal interactions between two individuals stressing dominance/subordination relationships, the mother-infant relationship, and the sexual relationship of male-female. I have chosen to describe such paired interactions in the previous chapter on individual behaviour, while patterns which involve several animals or the whole group interacting together, are described here as social behaviour. This includes the reindeers' gregarious habits, social facilitation, leadership and its associated roles, and play behaviour. This is preceded by a review of the various ways in which reindeer are able to communicate with each other.

Recent work on a range of higher animals, notably birds, primates, and still more recently ungulates, suggests that description of reciprocal relationships alone is an inadequate way to represent or understand the social organisation of a population. Easily observed interactions, such as antagonistic /

istic patterns, are invariably stressed at the expense of group phenomena such as spacing, sociality, or leadership. Crook (1970) compares this approach with trying to understand a football game by merely studying the paired interactions between players. The positioning and roles of supporting players would go unrecorded, and thus the strategy and co-operation of the team as a whole would not be understood.

Moreover, social behaviour alone does not define the social organisation of a population, since behaviour patterns are the framework within which the animals respond to their biological and physical environment. To continue Crook's analogy of a football game, the performance of the team is not only dependent on the rules and on individual capabilities but on the circumstances of a changing environment, e.g. tactics of the other team, state of the pitch, etc. The ways in which the social organisation of reindeer populations in southern Norway were seen to be moulded by snow cover, food availability, windchill conditions, insect harassment, the type of habitat, and other environmental factors, are evaluated in Chapter 7.

6.1. COMMUNICATION

"No form of social organisation would exist if there were not a communication system of some sort between the members of the society". R.F. Ewer, 1968.

Communication has been defined as any stimulus arising from /

one animal and eliciting a response in another (Scott, 1956). The gregariousness of reindeer and their synchrony of activity could not be achieved except by a constant perception of the behaviour of others. This awareness and response to what other animals are doing is assisted by behaviour specifically intended to signal an individual's intentions; for example, a threat signal from a dominant to a subordinate, a courtship signal from a male to a female, an alarm signal from an alerted animal to other animals in the group, etc.. As well as perceiving the signal, the receiver's response may depend on its perception of the status of the sending animal, e.g. whether it is a dominant, leader, or calf. On several occasions animals were observed to ignore the behaviour of a calf or yearling, when it appeared to display all the behaviour indicative of alarm, or when attempting to act as "leader".

Many behaviour patterns which appear important for communication between reindeer serve dual purposes; a directly functional one and a communicative one. For example, the act of grazing not only satifies nutritional requirements, but appears to express a state of calm (i.e. non-alarm) in the animals. As Pruitt (1960) observed, "silhouettes of feeding caribou tend to elicit feeding in nearby animals and thereby reduce alarm or wariness". In the same way, the hunching posture of rutting males serves as a urine self-marking process, but is also recognised as a threat display by rival males (re. Ch.5.3.1.). This last example is typical of a behaviour pattern which has become "ritualised" in that the functional behaviour has developed through evolution into a more effective communicative signal.

Communication /

Communication is not limited to the visual mode, since reindeer have an interesting range of scent glands, a small repertoire of vocalisation, while physical contacts play a role in the reproduction cycle. The role that scent plays in communication now requires further research through behavioural and physiological trials on captive reindeer, if the relative importance of different modes of communication is to be fully assessed. However, I have listed various ways in which I believe reindeer communicate their intentions or moods to each other, and thus maintain a complex social organisation (Table 6.1.). Within each of the four modes of communication, visual, tactile, acoustic, and olfactory, the communicative patterns function mainly to signal alarm, aggressive intent (threats), sexual responses, mother-young relations, or for on-going contact within the herd.

6.1.1. Visual Communication

The range of postures and movements by which one reindeer is seen to influence the behaviour of another, or others, was the most easily recorded aspect of communication in the field study. Visual communication has a vital role in all parts of the social organisation, but particularly in antagonistic and alarm behaviour.

A distinction can be made between behaviour which is communicative, and behaviour patterns which have a specialised signal function, and may have become more conspicuous through ritualisation. For example, social facilitation of activity, whether /

Table 6.1 Communication in reindeer - Some possible signalling patterns.

Mode	Type	Pattern	Function or Response
VISUAL	Morphology	White rump and white underside of tail.	Following response when alarmed (and in play).
		White mane and neck contrasting with dark back, face and legs.	Indicates sexual-aggressive potential of rutting male.
		Light pelage areas, e.g. legs and rump.	Assists contact and orientation at night.
		Antlers.	Important in indicating social rank, sex.
	Postures	Head down, grazing.	Indicates calm, lack of tension.
		Head up, staring.	Indicates suspicion or alarm, and orients others.
		Urination position held.	Alarm pose, releases same behaviour.
		Standing position of female.	Calf moves in to suckle.
		Standing position of female.	Rutting male moves in to mount.
		Hunching posture of rutting male.	Display threat to rival males and to impress females. Self-rewarding behaviour also?
	Movements	Head up quickly.	Indicates alertness.
		Slow head bobbing.	Indicates uncertainty or curiosity, and orients others.
		High-stepping gait, with tail up.	Indicates surprise and alarm and movement away. Others follow and may copy.

(over)

Table 6.1 (continued)

Mode	Type	Pattern	Function or Response
VISUAL	Movements (continued)	Flight running.	Releases flight in others.
		Play running and leaping.	Invites play, releases play mood in others.
		Leader's movements.	Following animals watch and copy leader in front.
		Walking approach. Rush charge. Antler low. Antler shake , or hook. Head stretch. Intention to rear-up.	Avoidance is taken by a subordinate or there is a dispute.
		Rutting males move side by side before a clash.	Broadside display threat, antlers leaning in.
		Pawing at ground by rutting male.	Threat before and between clashes.
		Head swinging of rutting male.	Avoidance by female if not ready for mating.
		Driving with tongue flicking.	" " "
		Female's fast running in the rut.	Induces following by males.
		Young male lowers antlers to another.	Invitation to spar.
		Movements of young calf.	Releases licking by mother female.

(over)

Table 6.1 (continued)

Mode	Type	Pattern	Function or Response
TACTILE	Contact	Mother female muzzles lying calf.	Calf gets up to follow or suckle.
		Licking of calf's rear by female.	Stimulates suckling by calf.
		Suckling of the udder by calf.	Releases licking or sniffing of calf's rear and genitals.
		Mother/Calf contacts; licking, muzzling, contact with lying, etc.	Maintains mother/infant bond.
		Rutting male licks rear of female.	May stimulate female, and degree of avoidance by female indicates readiness to mate.
		Female muzzles side or flanks of male.	Indicates readiness to mate and releases mounting behaviour by male.
		Mounting of female by the male.	Releases struggle by the female unless willing to mate.
		Antler sparring by young males.	Erotic stimulation for both.
		Antler dispute or fight.	Pushing fight determines dominance.
		Antler clash by rutting males.	From contact of antlers males can usually determine dominance.

(over)

Table 6.1 (continued)

Mode	Type	Pattern	Function or Response
ACOUSTIC	Vocal	Mother female grunt. Calf blat.	To maintain contact and especially when searching for each other.
		Rutting male grunt.	Threat to males and to impress females.
		Alarm grunt.	By female, to indicate alarm and releases alertness in others.
		Blowing air through nostrils.	On scenting danger, and releases alertness in others.
		Involuntary belches, grunts, snorts, etc.	Adds to in-group feeling of herd, especially when lying ruminating.
	Mechanical	Clicking of feet while walking.	To maintain contact and gauge individual distance at night.
		Clashing of antlers by rival rutting males.	May attract other males and females.
OLFACTORY	Scent Glands	Inter-digital glands - scent trail from hooves.	To follow scent trail and copy activity over the trail. Fright bound leaves warning scent. (Equivalent of caribou excitation leap).
		Caudal glands - tail erected.	Tail erected on alarm - running or high-stepping gait spreads alarm scent.
		(Rutting male only) Pre-orbital gland rubbed on hind leg. Tarsal gland rubbed together in hunching posture, and on face and antlers. Inter-digital gland applied to antler. Circumoral glands ? on muzzle rubbed on leg.	Rutting scent of male may influence other males, females, and be self-rewarding. Muzzling and pawing in urine patches with subsequent muzzle - leg - antler contact may mix gland scents with urine scent.

(over)

Table 6.1 (continued)

Mode	Type	Pattern	Function or Response
OLFACTORY	Urine	Self-marking by rutting male.	Rutting male in hunching posture ejects urine on hind legs, forelegs, and dewlap - subsequent contacts spread scent.
		Female urine in the Rut.	Smell of female urine or perineum releases olfactory reflex in rutting male, and driving and licking towards female rear.
		Calf scent.	Female identifies own calf by sniffing its rear or muzzle.

whether of grazing, lying, speed of movement, etc., would not be possible without visual contact and communication between the reindeer, although these activities are not signals as such. On the other hand, the sight of an animal running will not produce unease or flight in other animals of the group unless the animal observed is in alarmed flight itself. Play running with tail up by calves or adults can (to the human observer at least) look identical to the real flight behaviour but it is perceived differently by the animals themselves. Play running or leaping will often instigate a similar mood in other animals who react in their own way and do not merely imitate the particular play pattern of the instigator. Again, the behaviour is communicative, without having a specialised signal function.

On suspicion of possible alarm an animal will bring its head up suddenly from grazing to stand and stare, and this elicits a similar response in the nearby reindeer. As one or more animals return their heads to grazing the others follow suit. If a reindeer remains suspicious it may lower its head as if grazing, then suddenly raise it again for a further look at the possible danger. If a potential predator is then 'caught' moving, the suspicion is confirmed and the herd becomes fully alerted. This movement of the head appears to have become ritualised into a slow head-bobbing motion only infrequently seen by animals who appear puzzled by some unusual feature, such as a peculiarly shaped rock on the skyline, an ice crossing, etc. In caribou a ritualised head-bobbing motion is commonly used by mothers to elicit a following response in /

in their young calves (Pruitt, 1960; de Vos, 1960; Lent 1966). However, the occasional head-bobbing of reindeer may be a direct visual technique to assess the distance and size of an unusual feature in their environment, as occurs in other animals such as cats, owls, and wader birds (J.D. Lockie, pers. comm.).

When a reindeer is alerted it will frequently urinate in the normal stance with its back legs apart, and will then continue holding the pose as an alarm posture which other animals see and copy (Plate 12). In caribou this alarm signal has become ritualised in that unlike the normal urination stance, only one hind leg is spread out, and urination need not occur (Pruitt, 1960; and my observations, Prudhoe Bay, 1972). The exaggerated high-stepping gait with tail up is another instance of a specialised and ritualised alarm signal, and is common in reindeer.

Antagonistic behaviour between individuals appears to be entirely based on visual communication, in particular by threat signals (described in Chapter 5.2). Leadership is another important aspect of social organisation where the mode of communication is predominantly visual, although not exclusively so (Thomson, 1972). Communication in the reproductive phases on the other hand, merely includes visual components, some of them as ritualised signals (Table 6.1.), but scent, voice, and touch all play an important and integrated role at calving and rutting times.

Visual /

Visual communication is not confined to particular movements or postures. It has already been noted that the way an animal is perceived in regard to antler size, sex, and body size, indicates its social rank in the hierarchy or its capabilities as a leader. Light and dark contrast in the pelage may also play a role in communication. Observations at dusk suggest that the white rump area and feet may assist animals in keeping together and orienting themselves at night. The contrast between light and dark on the coat is particularly noticeable on mature males at rutting time; the size of the male's white neck and dewlap and the contrast with the dark face, back and legs, may, as well as the antlers, be a component in the display of his sexual-aggressive potential (e.g. Plates 22, 24 & 25). These and other probable signals in the visual mode are listed in Table 6.1.

6.1.2. Tactile Communication

Communication through physical contact occurs at both phases of the reproductive cycle. The mother-infant bond is thought to be partly formed and maintained by their frequent contacts in the first week of life. In particular, when the female licks or muzzles its lying calf, the calf will get up to suckle or follow the mother. Licking of the calf's rear stimulates the calf and induces it to suckle, while conversely contact by the calf on the female's udder prompts her to turn and lick the calf's rear and genitals. The female's licking of the young calf's rear also involves ingestion of the excreta. This gustatory (taste) stimulus possibly also plays

a /

a strengthening role in the mother-infant bond.

In the rut, the female will generally avoid contact by the male but as her oestrus approaches the male may have more success in attempting to lick the female's rear. This may conceivably stimulate her further (as well as providing a gustatory stimulus for the male). Mounting attempts, where the male rides over the back of the female and attempts to clasp her side firmly, directly tests her readiness for mating (confirmed by Barden, 1969). An oestrus female has been seen to contact a male by rubbing her muzzle on his side and flanks, as well as on nearby vegetation - this stimulated the male to mount.

Other significant contacts are made with the antlers. The young antlered males, especially in winter, are often seen to derive erotic stimulation from their prolonged sparring contests together, and one male may be seen to invite such a contest by slowly lowering his antlers towards a partner. Antler disputes on the other hand, including fights in the rut, function to determine dominance based on which animal is assessed to be the stronger. Ritualised antler clashes during rutting are similarly intended to determine dominance but achieve this without pushing, as animals guage the weight and strength of their opponents as their antlers are shaken together briefly (Ch. 5.3.1e).

6.1.3. ACOUSTIC COMMUNICATION

Vocalisation is reindeer is particularly significant in mother-calf /

calf relationships. When the female and calf become temporarily separated the female can be heard grunting while the calf responds with a flat-sounding bark or blat. Mother and calf appear to be able to recognise and respond to each other's calls. The evidence from acoustic research on Rangifer calls is conflicting, but observation and playback experiments mostly support this opinion (Espmark, 1971c; Ericson, 1975; Lent, 1975). In the large mixed herds of early summer the females and calves would call to each other constantly while the herd was on the move, apparently to help them to maintain contact. In one such aggregation of 10,000 animals on Hardangervidda in August 1970 the combined sound of the mother and calf calls from several kilometers made a dull incessant roar (Thomson, 1971). The female/calf calls were seldom heard by late summer.

The vocalisation of the mature male is even more confined in time, to the rut. While driving a female or while standing, the male often emits a husky call from the throat which may draw a reply or challenge from a nearby male. It may also have a role in stimulating the female. I believe also that the deeper the grunt of a particular male, the more dominant he is likely to be. Because the sound emanates from the pharynx as in a cough, and not through the nostrils, the male rutting call has been termed a husky rattle (Espmark, 1964a), while Bergerud (1974a) has described it as 'panting'. It has the sound however of a grunt (Lent, 1965a, and this study).

Reindeer /

Reindeer have a vocal alarm signal which appears to be used sparingly. When alerted at close quarters a female may grunt once or twice, and may then move off as leader of the herd. Other sounds were heard when reindeer scented danger, such as man, and blew out the scented air loudly through the nostrils. Such a snort also appeared to alert and orient others. Further investigation might show a limited range of alarm sounds for different situations and different intensities of alarm.

Apart from these "voluntary" sounds, reindeer produce a variety of involuntary belches, grunts, and snorts, especially when they are lying ruminating, and such sounds may add to their in-group feeling, or have a reassuring effect in the herd. This is also Ericson's (1975) opinion. Similarily, the characteristic clicking sound in the feet while walking, now thought to be produced by the interplay of the sesamoid cartilages (Lent, 1975), may be of importance in maintaining herd cohesion and guaging individual distance, especially at night. Another non-vocal sound which may have communicative properties is the loud crashing sound heard when two rival males in the rut clash their antlers together. Other reindeer males have been seen to be attracted to the area by the sound alone. Lent (1975) has also observed this, and considers whether bush thrashing has a similar attractive effect.

In his recent review of acoustic communication, Lent (op. cit.) notes that the repertoire of acoustic signals in Rangifer is limited /

limited compared with other ungulates, and relates this to the use of predominantly open habitat and corresponding dependance on visual and olfactory communication.

6.1.4. Olfactory Communication

This mode of communication is least amenable to field study alone. However, I have observed behaviour strongly suggestive of communication by smell. This is considered here in relation to the presently known physiology of scent glands (Quay, 1955). A controlled programme of research on the role of scent glands in reindeer is presently being undertaken (Y. Espmark, pers. comm.).

Scents which act as chemical signals are called pheromones. Pheromones may have an immediate releasor effect, for example as an alarm substance or sex attractant, or they may have a primer effect in which case they alter the subsequent behaviour or physiology of the receiving animal. For example, the male smell synchronises the time of oestrus for several domestic ungulate females (Fraser, 1968). As well as sending a signal, pheromones can transmit information to conspecifics on the sex, age, and physiological status of an individual (Tembrock, 1968).

Cervidae have ten different sites where there are glands capable of producing scent. For Rangifer four of these gland sites have been shown to produce secretions. These are the pre-orbital glands, inter-digital glands, tarsal glands (Quay, 1955), and caudal glands (Lewin & Stelfox, 1967). The site of these glands was shown in Figure 5.11. From behaviour observations /

observations it might also be supposed that reindeer have circum-anal glands, circum-oral glands, and possibly a forehead gland between the base of the antlers, but these have not so far been established.

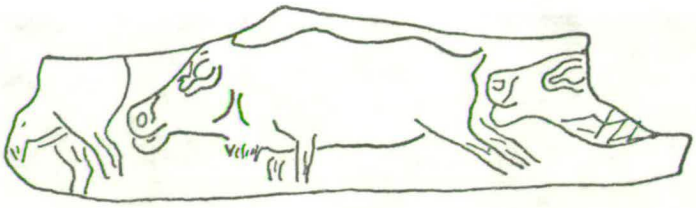
The inter-digital glands, or hoof glands in Rangifer, lie in the skin between the toes of the hoof of both hind and forelegs, and were first mentioned in the literature by Caton in 1877. Quay (1955) has described the complex cytochemistry of the secretory cells in the gland, and suggested that they may function to leave a trail scent. My observations confirm that reindeer can follow the trail of others who have gone before without visible orientation. In many situations in summer and the rut animals were seen to catch up a herd by frequently pausing to sniff the ground. On tracks across snow in late winter, not only could following animals keep to the same trail by sniffing the tracks, but could apparently copy the activity of the leader animal or animals who had already passed out of sight. This olfactory facilitation of activity is fully described in Thomson (1972). Scent from the inter-digital glands following the excitation leap of a caribou is said to be detectable even by a human observer, and other caribou reaching this same spot react with fright (Pruitt, 1960).

The secretion from the hoof glands of the hindlegs has been described as a sticky viscous yellowish mass (Zhigunov, 1968). While the antlers are growing in summer a reindeer may often be seen to bring up a hind leg and turn its head so that the velvet antler tips contact the hoof. Espmark (1971a) notes that /

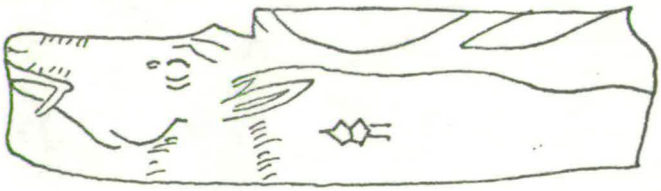
that Lapp reindeer herders believe that secretion from the hoof glands aids growth of the antler. Some Lapps also believe that the position of tines on the antler beams is determined by the placement of inter-digital secretion (E. Gaare, pers. comm.). During the muzzling and pawing behaviour of rutting males, contact between the hard antler and the hind hoof may add inter-digital gland scent to the self-marking process, as described and illustrated in Chapter 5.3.

The pre-orbital gland in reindeer is situated immediately in front of each eye, and in mature males particularly becomes conspicuous in the rut. This gland seems to be depicted on some prehistoric engravings (Fig. 6.1). Quay's (1955) description of the gland structure was made in April when the gland does not appear to be particularly active. If the pre-orbital gland has a role in olfactory communication in reindeer it is not as obvious as it is in some other Cervids, e.g. rutting red deer males may be seen to rub their pre-orbital gland over vegetation and in wallowing pits, while roe deer males rub pre-orbital secretion on twigs. The bush thrashing of reindeer males might leave traces of pre-orbital scent on bushes, but unlike more territorial Cervidae it is not believed that such bushes in any way act as territorial markers (re. Ch. 5.3.1.f). However, in the self-marking process of a rutting male, the hind leg is occasionally brought forward to rub the face, and could conceivably collect pre-orbital secretion (Ch. 5.3.1.d). A more speculative possibility is that secretion from the pre-orbital gland may serve to intimidate a rival in the course of antler clashes and /

Fig. 6.1 Pre-orbital gland evident on pre-historic engravings of reindeer on bone.



The Cave of Massat (Ariège)



La Madeleine (Dordogne)

(Sketched from Graziosi, 1960)

and fights between rutting males. In the male red deer at least 12 separate components have been analysed in the secretion from this gland (Müller & Lemperle, 1964).

The tarsal glands are situated on the inside of the hocks near the bend of the hindleg, and there is a conspicuous growth of longish, pale hairs at the site of the gland. Quay (1955) notes that there are differences in the thickness of the gland cells between sexes and ages of reindeer. Müller-Schwarze (1967) found that frequent sniffing of the tarsal gland by black-tailed deer occurred when a newcomer was introduced to a group. Chemical extractions from the glands used subsequently in behaviour trials showed that individual recognition from different tarsal odours was possible (Müller-Schwarze, op.cit.). In the closely related mule deer, scent from the tarsal glands is used as a threat with flaring of the tarsal hairs to allow passage of the scent (Linsdale & Tomich, 1953), and as an alarm scent on disturbance (Nichol, in Mykytowycz, 1970). No observations were made in this study to suggest that there could be similar functions for reindeer, but controlled experiments would be required to test the possibility. However, it need not be that the glands in all Cervidae serve the same function for all species (Quay, 1955), and certainly some gland sites are vestigial depending on species.

I have observed rubbing of the muzzle over the tarsal gland area by reindeer males in the rut, which, as with other glands, may mix scent into the urine marking process. Also during the hunching posture itself the trampling movements of the back legs may effectively rub the opposite tarsal glands together, /

together, and this may conceivably mix tarsal scent with the urine odour. This behaviour is also observed in mule deer (Linsdale & Tomich, op.cit.).

Caudal glands on the tail of Rangifer were not discovered by Quay (1955) in his investigations, but have since been described by Lewin and Stelfox (1967). These glands have an obvious signalling function in indicating alarm in reindeer and the spreading of this scent is facilitated by observable behaviour. On alarm, the reindeer's tail is raised, and greatly alarmed or surprised animals move around in a high-stepping gait, presumably to increase the intensity of the visual signal and to more effectively distribute scent around nearby animals, before the herd makes off with their tails raised.

The possibility of there being other active scent glands in reindeer cannot be ruled out. Behaviour in both phases of the breeding cycle suggests some possibilities. From the muzzling of the rutting male in urine patches, and his subsequent rubbing, and from the frequent nose to nose contacts between mothers and their infants, one can suppose that circum-oral glands may occur. In Cervus and Odoicoleus spp., where these glands occur, rubbing their muzzles on territorial signposts (Graf, 1956) may be parallel behaviour to the reindeer male nosing its urine patch and then its hind leg.

The sniffing by a mother female on the rear of calves to identify her own, poses the question whether this is achieved from the excreta scent alone, or whether there are anal or circum-anal glands present. The same question applies to the olfactory /

olfactory reflex of rutting males on smelling the female's perineum, i.e. whether in the reindeers' "world of scent" there is also scent from anal glands.

Urine is undoubtedly the main vehicle of scent transmission in the rut. The self-marking behaviour of the male has been fully described in Chapter 5.3.1. The powerful scent of the rutting male is very obvious to a human observer, and may function as a pheromone for both females and other males. In sheep it has been demonstrated that oestrus of ewes can be synchronised by the primer effect of the smell of the ram (Fraser, 1968). Reindeer males performing urine self-marking may also boost their own aggressive-sexual drive by the performance and result of the process. The behaviour may be self-rewarding as well as an external signal. Ewer (1968) notes that "any form of behaviour which discourages a rival may at the same time increase the self-confidence of the animal that performs it, and the smell which acts as a threat to a stranger may also function in this way", and quotes the African elephant smelling its own temporal gland. Smelling of the female's urine or perineum in the rut by mature reindeer males does appear to increase their general sexual motivation, and this includes occasional licking of the female's perineum or tasting of the urine. There is an immediate released response to the oestrous female odour in the form of an olfactory reflex by the male (re. Ch.5.3.1b).

In conclusion, much still remains to be investigated about the types and importance of olfactory communication in reindeer. This study offers a contribution in that it can verify the social /

social function of glands in reindeer, in particular a trail scent from the inter-digital glands and alarm scent from the caudal glands, while pre-orbital, tarsal, and inter-digital glands may be utilised alongside the urine self-marking process of the rutting male. Other behaviour observed suggests the possibility of there being other glands present, in particular around the anus and the muzzle.

6.2. GREGARIOUSNESS

"Where a species is of social habit I would emphasise the necessity of taking sociality fully into account..... it is the very foundation of red deer existence."
F. Fraser Darling, 1937.

Many theories have been put forward on the adaptive value of sociality or group living as opposed to isolated living, but a general principle is still no clearer now than it was when Kropotkin (1902) declared his views on the sociability of animal life. In Rangifer the question is an important one, and as such is comparable to other grazing ungulate species on open habitat, such as wildebeeste on the African savannah, saiga on the Russian steppes, or the original herds of buffalo on the American prairies.

The survival values for social grouping most often hypothesised for vertebrates are that group animals are less subject to predation than isolates; a good food source discovered is shared by all; reproductive activities are facilitated; and group living stimulates greater or more effective activity (Etkin, 1964). /

(Etkin, 1964). However, since one can observe grouping tendencies to some degree in most animals it may be equally valid to consider why some animals do not form large groups. This might include the converse of the above reasons and include conspicuousness in regard to predation, exhaustion of a food supply, territorial reproductive behaviour by individuals or pairs, and the difficulty of maintaining contact in a closed habitat, such as forests. The general reasons propounded for the adaptive significance of group living are not therefore wholly convincing.

However, without hypothesising cause and effect, it would appear that an empirical relationship exists between group size and openness of the habitat for the Cervidae. Species in open habitats, such as reindeer, tend to live in large groups, while forest-living deer such as moose (Alces alces) or roe deer (Capreolus capreolus) live solitary, in pairs, or in small groups. This relationship would even seem to apply for populations of the same species in different habitats; for example, it is well-known that populations of red deer (Cervus elaphus) on open moors and hills gather in larger groups than their forest or woodland-living counterparts. Recent analysis for ungulates in Africa points to a relationship, not only between group size and habitat, but also between the species feeding style, type of breeding group, extent of sex-segregation, body size and degree of dimorphism (Jarman, 1968). A hypothesis is developed for antelope species in particular, stressing the links between group size and cohesion, the availability of food items in the habitat, and anti-predator behaviour (Jarman, 1974). A similar integrative analysis for deer would undoubtedly /

undoubtedly help to evaluate the factors which influence the gregariousness of reindeer.

From observation it is clear that mountain reindeer show marked affiliative responses towards each other at most times of the year, and that this sociality appears to be as much a need as, for example, is mobility. Reindeer generally seek each others' company and maintain a close synchrony in behaviour and movement. Russian biologists have similarly remarked on this 'yearning for company' in reindeer (Naumov, 1933), which Baskin (1970) has considered to be an unique characteristic of the species.

The neuro-hormonal basis for this affiliative behaviour is not known, but is clearly very strong as it is not easily swamped by other internal drives or external pressures. Even at calving time, when affiliative responses are at their lowest, the pregnant female will often remain with a group up to the point of calving, and may even attempt to keep up with a moving group at the stage when the neonate's legs are emerging from the vulva. Within one or two days after birth the female again seeks contact with other animals, particularly other mother females. Yearlings which are hounded out of nursery groups seldom elect to move away altogher, and if they do, they will join with other yearlings and yeld females. Similarly, the vigorous rush charging of young subordinate males by mature males in the rut does not negate affiliative tendencies, and both types of male remain associated with the group. The affiliative tendencies of reindeer are at an obvious peak in early summer (see Ch. 7.1.2. and Fig. 7.2), when the animals mass /

mass closely together in herds of thousands, with few antagonistic interactions evident.

The only occasion when reindeer were consistently seen to move apart from a group was when a particular individual had been wounded or was lame.

6.2.1. Searching Behaviour

Perhaps the clearest proof of the strength of affiliative behaviour in reindeer is seen when animals lose contact with a group. Such animals become hyperactive, restless and search constantly for other deer. For example, in mid-summer, a female with a calf at heel was seen to be very alert and stopped to look round frequently, sniffed at the ground, frequently gave the alarm-urination posture, while her calf merely grazed. Eventually the female lay down but got up within a minute and trotted off again with the calf following. Whereas the calf appeared relaxed, and grazing in the secure zone around its mother, the female appeared insecure without the herd. On another occasion a female with a similarly-aged calf was trotting, stopping every now and then to look around; eventually she met up with and joined another female and all three moved off in the direction of the herd 3km away.

This searching behaviour may even be shown by small groups in summer. For example, in early July a group of 21 became separated from a herd of 700 after swimming in a lake, and led by a mother female with a calf at heel showed typical searching behaviour; stopping, looking, sniffing the air, trotting on again /

again, etc..

The restless behaviour evident is identical to that normally seen by mother females or calves who have become separated from each other in the quickly moving herds of summer. On one occasion a lone 3-month calf which had been calling and showing searching behaviour, became alarmed as I came into view at 50m. When I adopted a "four-legged" stance with arms down and occasionally moving my head up and down, the calf approached to within 10m, and when I lay down the calf did likewise. The calf seemed to be anxious for company of any sort and for the next half hour it lay 10m off and ruminated, before it finally made off when I attempted to approach closer.

6.2.2. Social Facilitation

An important consequence of group living in reindeer is that animals emulate each other so that a co-ordinated group activity is evident. This tendency for mutual stimulation so that animals do the same thing at the same time has been termed allelomimetic behaviour (Scott, 1956), which includes both imitation - the direct copying by an animal of another's behaviour however unusual or unlikely a pattern; and social facilitation - where there is a mutual stimulation or synchronisation of normal activity such as feeding, resting, walking.

Social facilitation is highly developed in reindeer which results in well defined herd periods of grazing and lying irrespective of the number of animals involved (Gaare, Skogland & Thomson, 1970; Thomson, 1971; Thomson, 1973; Apps. 1, 2 & 3).

At /

At the commencement of the activity recording it was thought that in large herds synchronisation of activity might not occur (Thomson, 1969). This was proved not to be the case on 22/1/70 when a herd of 1150 switched from 95% active at 1230 h. to 100% lying at 1300h. The possibility of rapid transition in a herd is illustrated elsewhere (e.g. Figs. 5, 7 & 8, App.1; Fig.9, App.2; Fig.3, App.3). Similarly in early summer, movement of animals is socially facilitated so that even in herds of thousands each animal relates its speed to those around it, so that at times sections of the herd will move faster or slower while remaining as one massed unit changing its shape and direction in amoeba-like fashion (e.g. Fig.6, App.2).

The extent of synchronisation of activities in a herd of reindeer was seen to depend more on the spacing distance between individuals than on the actual size of herd. Social facilitation works quicker and more completely when animals are closer to each other. Where a large stationary herd becomes very spread while grazing, such as in a valley bottom in late summer, or scattered over available grazing ground in late winter, then some contact between individuals is lost and sub-groups of liers and grazers may be detected within the herd. When two separate groups meet and coalesce there is a tendency for animals to continue the feeding-lying rhythm they had formed in their original group, until after a few hours they synchronise into a common group activity.

Social facilitation is weaker when different sex and age classes behave differently, and in such circumstances groups can split up and segregation occur. For example, on the Hardangervidda winter /

winter range from March onwards pregnant females show a tendency to start trekking westwards, followed by other females and young animals, whereas the males which are present show minimal tendency to move at this time. This results in an increasing segregation of sexes such that by May males may be virtually absent on the calving grounds (see Ch.7.4.). After calving, by contrast, affiliative tendencies are high and as nursery groups begin to move about the terrain they meet and coalesce, and are joined by calf-less adults to form the large integrated post-calving herds of early summer. For caribou, Bergerud (1971) similarly considers that the post-calving herds are formed by the natural tendency of the females to aggregate after calving, and not as a response to insects, which may not have emerged by then, nor as a result of mechanical funnelling by topographic barriers, which had been suggested by Kelsall (1968). Lent (1966) considered that individuals which show synchrony in their activities tend to form groups, and while this holds true for reindeer in some situations, my observations suggest the converse is more often true in that it is the attraction of animals for each other which results in cohesive groups, which then display a synchronised activity through social facilitation.

6.3. LEADERSHIP AND SOCIAL RESPONSIBILITY

"When elk cows got ready to cross a swollen stream in their spring migration, a mature elk cow would be in the leading role. Most significant was that she determined the place and time to cross.....". Margaret Altmann, 1956.

A basis for the definition of leadership is normally sought within the confines of allelomimetic behaviour in so far as animals may be unequally stimulated so that one tends to lead and others to follow (Scott, 1956). Clearly, the leader-follower relationship is a two-way relationship in that as well as requiring an animal willing to take the initiative, it equally requires that the rest of the group must be willing to follow. In reindeer, leadership is typically seen at times of alarm when the group bunches together and one animal moves out to direct the pace and direction of travel away from the alarming stimulus (Photo 36). One quarter of all disturbances causing a herd to move together resulted in such clear-cut leadership (Thomson, 1972). Naumov and Baskin (1969) note that in semi-domestic herds in Russia it is the experienced older females who tend to be the most wary, alert, and whom the herd were willing to follow. (My emphasis.). I observed that immature individuals such as calves and yearlings were much less 'respected' by the herd at times of alarm and even if they were the first to take fright and run out from the group, it was typically an adult female who would eventually emerge to lead the herd away in a controlled manner (Thomson, op.cit.). Of 98 events where the leader was classified in both alarming and non-alarming situations, a female led the group on 78 occasions, and only on 5 occasions a juvenile. Of the remaining 15 leadership events, 2 were by males in hard antler and 13 by unantlered or velvet antlered males (Table 3, App.6). Females show the highest degree of leadership, juvenile animals the highest degree of 'followership', and males the highest degree of individualism. Males in hard antler are typically less socially facilitated, and may show a reluctance both to lead /

lead and to follow. However, when unantlered, the males behave much more like the females and can be seen at the head of mixed bands of unantlered and antlered males in winter, or of integrated groups of females, juveniles and males in spring and summer.

Through following experienced leaders, particularly in critical situations such as eluding a predator, moving across an ice-covered lake, or choosing a crossing place for swimming a river, the capabilities and experience of the leader animal becomes the 'common property' of the group. Those animals which adopt the temporary role of leader are also those which are most prepared to face or defend against potential predators; which remain alert for longest after an alarm; and which bring up the rear or edges of an alarmed herd and look back frequently at the source of alarm (Thomson, op.cit.). The security of the herd is undoubtedly increased by the behaviour of these experienced, socially responsible animals, notably the adult females, in guiding, protecting, and directing the movement of others when necessary. In reindeer, leadership and its associated roles are evidently the basis for a group process of great survival value. A full description and discussion of leadership and its associated roles is given in Thomson 1972 (App.6).

6.4. PLAY

"Joy is a condition which induces play actions." N. Bolwig, 1963.

Play in reindeer is readily recognised by a variety of unstereotyped actions, particularly gambolling, bucking, kicking, prancing /

prancing, running and chasing. It is most often seen by young calves but is also a feature of yearling and adult behaviour. The mood of one animal in giving a few hind leg 'bronco' kicks, or two animals alternatively chasing each other, can spread to others through social facilitation, so that several animals or the whole group may indulge in playful prancing, bucking, and running for a few minutes.

While play is usually easy to recognise, it is difficult to define. Play in mammals is said to be typified by the exaggerated fragmentation or repetition of behaviour acts which generally occur in efficient ordered ways in other contexts where there is an obvious goal (Loizos, 1966). Schein (in Hafez, 1969) considers that play in cattle is engaged in solely for the sake of the activity itself. In observing reindeer at play, particularly adults, it is indeed often hard to avoid the conclusion that the animals are spontaneously reacting to favourable circumstances, and are expressing a 'joie-de-vivre'. This is not to say that play is without function.

6.4.1. Calf Play

For young calves of one- to two-weeks old play is a regular feature of their short active periods. Even before a calf is fully one day old it can be seen testing its physical capabilities by playful bounds, leaps, and runs in the immediate vicinity of its mother. Over the next few days play is gradually extended into a variety of bucking (kicking up the hind legs, bronco-style), leaping (bounding off the hind legs), stotting /

stotting (bouncing on all four legs) and prancing (high-stepping) behaviour, interspersed with long fast runs at top speed with tail held up, running out from the mother and back again in loops or figure-of-eights. Other spontaneous activity of the young calf arises as responses to its physical and social environment. Calves may be seen making tentative pawing motions towards the ground or snow without necessarily making contact, and such investigative behaviour is often interspersed with playful leaps. On one occasion a calf was seen to paw towards an unusually white boulder embedded in the ground, and twice in summer calves were seen pawing at the surface of open water. Similar playful and exploratory behaviour occurs in calves of caribou (Lent, 1966) and domestic reindeer (Espmark, 1971a).

When in a nursery group, a calf's play runs inevitably brings it within the range of other females and calves. For the first few days of their life and up to a week-old, mothers follow their calves with concern, and ward off strange calves so that contact between the calf and other animals, except the mother, is kept to a minimum. As the mother becomes less concerned and the length of the calf's runs extends, the number of contacts between calves increase. Bucking and leaping by one calf often induces play actions in another. A calf running at top speed may be joined by one or more calves and a 'chase' develops. When two calves stop and face each other they appear hesitant and uncertain. One or both may head-bob, buck or leap on the spot, and tentatively interact, by one of them kicking towards the other or rearing up on hind legs without contact, before /

before they run off together in play, or back to their respective mothers. For barren-ground caribou calves over the age of 4 days, de Vos (1960) records play by running after one another and mock battles.

The frequency of the various types of individual and social play in reindeer calves under two weeks old in nursery groups may be compared with the play of calves one to three months old in the summer herds (Table 6.2). Already by the age of two weeks play between calves is common, so that there is no increase in the proportion of social play at this later age. This is apparently different to woodland-type caribou in Newfoundland where play between calves did not occur before the age of two weeks (Bergerud, 1971).

Play responses towards or with the mother are uncommon in young reindeer calves (2% of play types) but become more common in summer (21% of play types; Table 6.2). On eight occasions in summer, mother females were seen to become infected with the play spirit exhibited by their calves, and would indulge in a few playful leaps or bronco kicks of their own. On four occasions, calves were seen to playfully contact the mother by slow pawing and butting, by clambering over her back while lying, and twice with trial awkward mountings directed onto the mother's head or flanks. This incipient sexual behaviour was also a feature of male calf behaviour in the North Ottadalen rut, by which time the mounting attempts had acquired the correct orientation and some degree of intent (see Ch.5.3.). Similarly, by early winter calf-to-calf interaction involving rearing up or kicking had evolved into sufficient effectiveness and reason (competition for grazing spots) for it to be no longer classified /

Table 6.2 Play behaviour by calves under 2-weeks old in nursery groups, and 1-3 month old in summer herds.

Type of play	Recorded instances of play types	
	Calves < 2 weeks	Calves 1-3 months
Individual Play		
lone running	37	18
leaping and frisking	25	19
pawing ground/snow/water	4	3
play with object	-	1
Total	66	41
Play with other calves		
chasing	12	3
confronting with head bobs	8	4
confronting with rearing/kicking	6	7
Total	26	14
Play with adults		
running/leaping with mother	1	8
kicking at mother	1	2
mounting mother	-	2
running/leaping with yearling	4	4
Total	6	16

Comparing the incidence of individual play, play with other calves, and play with adults (figures underlined), suggests significance heterogeneity between the two ages of calves:

$\chi^2 = 8.89$ at 2 d.f.; $P < 0.05^*$.

classified as play.

Play would appear to have an important learning function for the calves. From an early age the calf is developing and testing its physical capabilities by gambolling, bucking, and leaping. Play running with tail held high, to and from the mother, directly parallels real disturbance flight when animals move off with a high-stepping gait, or run at full speed with tails held high in alarm. Also, through playful investigation of its physical environment, the calf develops its grazing and pawing behaviour which is to become essential for its survival in winter. Through playful confrontations with other calves the calf develops secondary social relationships, in particular it learns the antagonistic patterns of threat and withdrawal which later gradually acquire significance. Similarly the mother's tolerance to tentative mounting attempts allows the male calf to develop its "performance" without the competition characteristic of the real situation. Loizos's definition of play is therefore particularly relevent to play in reindeer calves, as it alludes to the way in which play is a learning process in that patterns occur which are later used in ordered meaningful contexts.

6.4.2. Adult Play

Calf play diminishes in frequency throughout the summer, autumn and into winter, but even as yearlings in the following spring there is still a greater propensity to play than is found in fully adult reindeer. The recorded instances of play amongst calves, yearlings and adults over the four main seasons is shown /

shown in Table 6.3. At least 72% of all play events recorded were performed by calves, which is seven times more than occured in either yearlings, adult females or males. When these events are adjusted for the differing proportion of classes in the herd it can be calculated that, for equal numbers of animals, calves evidenced at least 17 times more play than their mothers over the year (Table 6.3.).

Adult play was found to be seasonal. Females played mostly in summer and autumn in association with their calves, while male play was a feature of the winter period. By adjusting the observed incidence of play for varying hours of seasonal observation as well as the class proportions, this varying propensity for play at different seasons by different sexes can be illustrated (Fig.6.2). By late winter, and in spring, play by adults of either sex was at its most infrequent, although yearlings will still play at this time, either with the new calves or with each other. For example, on 10/5/70, on North Ottadalen, two yearlings associated with the nursery group were seen playfully chasing each other. At first the 'knobber' yearling male was being chased by a spike-antlered yearling female, running with tails up at full speed over the hard crusted snow, occasionally slowing into a springy trot; after several hundred metres the female turned and as it ran back it was now chased by the yearling male. After five minutes of this unusual play chase, including running together, they returned to the group and began grazing.

Play by yearlings and adults is usually characterised by the exaggerated individual acts of leaping, frisking, and bronco-kicks /

Table 6.3 Play by calves, yearling and adult reindeer at different seasons.

	Calving	Summer	Autumn	Winter	All	Herd structure[1]	Adjusted play events[2]	Ratio[3]
	Recorded play events at different seasons							
Calf	98[a]	75	23	13	209 (72%)	26%	209	(17.4)
Yearling	9	6	3	12	30 (10%)	21%	37	(3.1)
Female 2-year+	2	10	10	6	28 (10%)	41%	12	(1.0)
Male 2-year+	-	1	2	19	22 (8%)	12%	48	(4.0)
Unclassified adult	-	2	-	1	3 -			
Whole group	2	5	5	11	23 -			
No. hours observation	222[b]	161	136	336	855			

1. Estimated herd structure in summer, 1970 (Table 3.6).
2. Play by other classes adjusted to calf proportion in the herd to indicate propensity to play (3).

a. Underestimate - not all calf play recorded.

b. Calves not in view for the full 222 hours of reindeer observation.

kicks, and on occasion (23 observations - Table 6.3) this developed so that nearby animals or the whole group became infected with the spirit of play. For example, on Snøhetta on 20/10/69, as a group of 48 reindeer moved off mid/high alpine rocks onto a patch of snow, a 2½-year male started chasing a 1½-year male, not rushing at it antagonistically, but dodging playfully like a calf; this enlivened animals nearby so that within a few minutes the whole herd were rushing about on the snow patch with bucking and leaping, and mock presentation of antlers towards each other. On another occasion, at Hardangervidda, on the evening of 6/8/70, a herd of 800-900 which had earlier been mildly harassed by insects, moved over wet flats, and as calves began racing about with tails up, they were joined by many yearlings and females running, bucking, leaping, jumping to the side, and even backwards. After a few minutes these animals raced across to join the others which had now moved on to drier stonier ground and begun peaceful grazing and walking without play. Half an hour later, on reaching a flat area once more, some calves and adults began playing again.

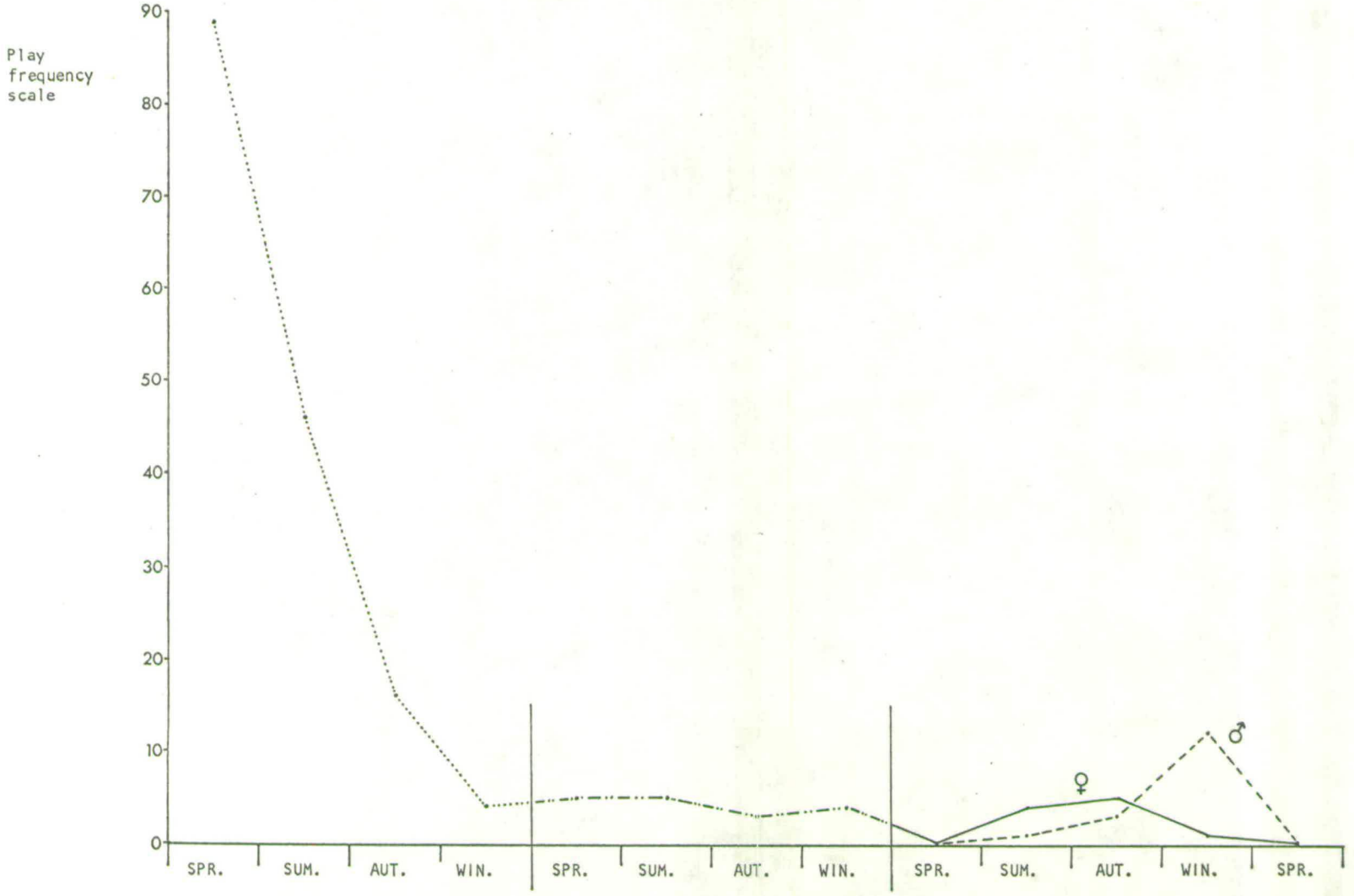
There are surprisingly few records of play in adult caribou. Edwards and Ritcey (1960) record that mountain-living caribou in British Columbia attracted to patches of snow in hot summer weather would occasionally play there.

6.4.3. Play Situations

No two adult play events were entirely identical, either as individual behaviour or as a group. However, situations in which /

Fig. 6.2 Propensity for play amongst calf, yearling and adult reindeer at different seasons.

(Expressed as records per 100 hours observation, after adjustment for varying herd proportions - Table 6.3)



which play occurred or did not occur had certain features in common. Play was not seen in stressful situations, or where motivation for other behaviour was high. Thus at times of insect harassment or predator disturbance, play was not seen, and it was most infrequent during late winter migration and on calving grounds pre-calving.

In summer, play by both calves and adults most commonly occurred on flat expanses of either hard snow or wet boggy flats. On such terrain animals appeared stimulated by their ability to move quickly and without restriction, and play behaviour would often develop. Hafez (1969) observes that cattle will often play when they are faced with a novel but not wholly unknown object or environment, such as moving into a new field. The observed tendency for reindeer to play on snow patches, or on marshy areas or on entering birch woods at rutting time, or when running down a steep snow slope in winter may be related.

Low or falling temperatures also seemed to play a role in stimulating reindeer to play. For example, in summer when temperatures fell in the late afternoon after a day of insect harassment, play was often observed. On days too cool for insects in summer (below $7^{o}C$) play occurred at any time of the day. In winter, one could gain the impression that the animals were 'breaking the monotony' of their regular static grazing and lying periods by indulging in a burst of activity. However this behaviour may have functioned to increase their bodily warmth or relieve stiffness after their stationery activities since it had a tendency to occur in cold and sunny weather /

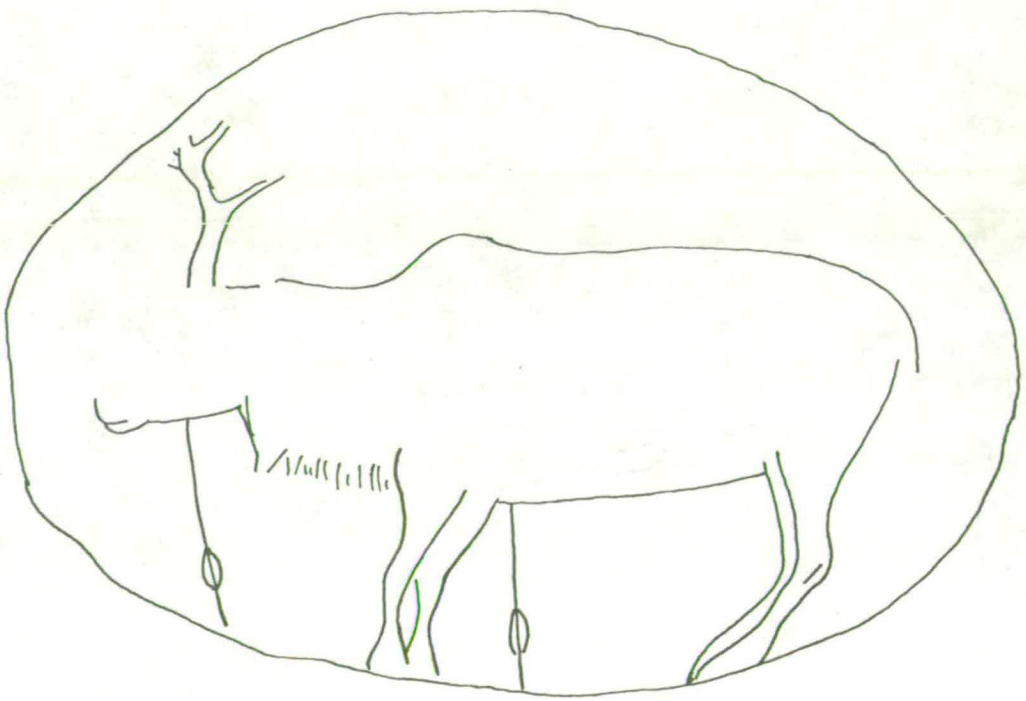
weather (below -15°C). Similarly, in summer after heavy rain or after swimming animals would often break into a run with elements of playful-type behaviour evident (bucking, leaping, etc.). While such behaviour may have been initially stimulated by the cooling effect of the water, it appeared essentially playful, and quite distinct from the windchill behaviour of animals under blizzard conditions in winter, which occasionally also included elements of running and leg-kicking (see Ch.7.3).

The function of play in adult reindeer is therefore more difficult to define than for calves. In many situations it was hard to escape the conclusion that the animals were reacting positively to a feeling of well-being in a suitable environment, and possibly expending surplus energy. In cattle, well fed healthy animals play more often than poorly fed or sick ones, and more frequently in good weather (Brownlee, 1954). Geist (1971a) considered that play was related to body condition for mountain sheep, and that a population on a good range showed more calf play and longer nursing times than on a poor range. Detailed quantitative study would be required to determine whether the incidence of play, particularly by adult reindeer, could be used as a behavioural criterion in comparing the condition of animals of different populations. No obvious differences in the frequency of play was recorded from different ranges in this study.

CHAPTER SEVEN SOCIAL ORGANISATION AND THE ENVIRONMENT

"Traces of the reindeer have been found all over Eastern, Central and Western Europe, as far south as Northern Spain and even on the Riviera. In the eastern alpine region it penetrated as far as Trieste and then kept to the north of the Danube and Black Sea."

From 'Art in the Ice Age' by J. Maringer and H.-G. Bandi, 1953. Late Palaeolithic - 20,000-10,000 B.C.



Engraved pebble (actual size) from the Cave of La Colombière, France.(from Graziosi, 1960).

CHAPTER SEVEN SOCIAL ORGANISATION AND THE ENVIRONMENT

> "A major objective in the study of mammalian societies is to develop an understanding of the way in which, through evolution, species characteristics and environmental forces have interacted to shape the structure and dynamics of these diverse and complex systems."
>
> Crook, Ellis & Goss-Custard, 1976.

While observing and classifying reindeer social behaviour and group activity under varied circumstances, it became progressively evident that many aspects were a direct or indirect response to the prevailing environment. As Ewer (1968) remarks "the social order is not a thing-in-itself, but a complex interaction of the animals with each other and with the environment". On Hardangervidda and the other mountain ranges seasonal and daily changes in snow cover and food availability, winter winds, plant phenology, insect harrassment, predator and human disturbance, resulted in quantifiable responses from the reindeer herds. The influence of these environmental factors are individually discussed in this Chapter. In general it can be said that the individual and group response to these factors had survival value, notably through energy conservation measures, avoidance measures, and other suitably flexible behavioural responses.

7.1. SOCIAL STRUCTURE

The way in which an animal population is split into sub-units; the /

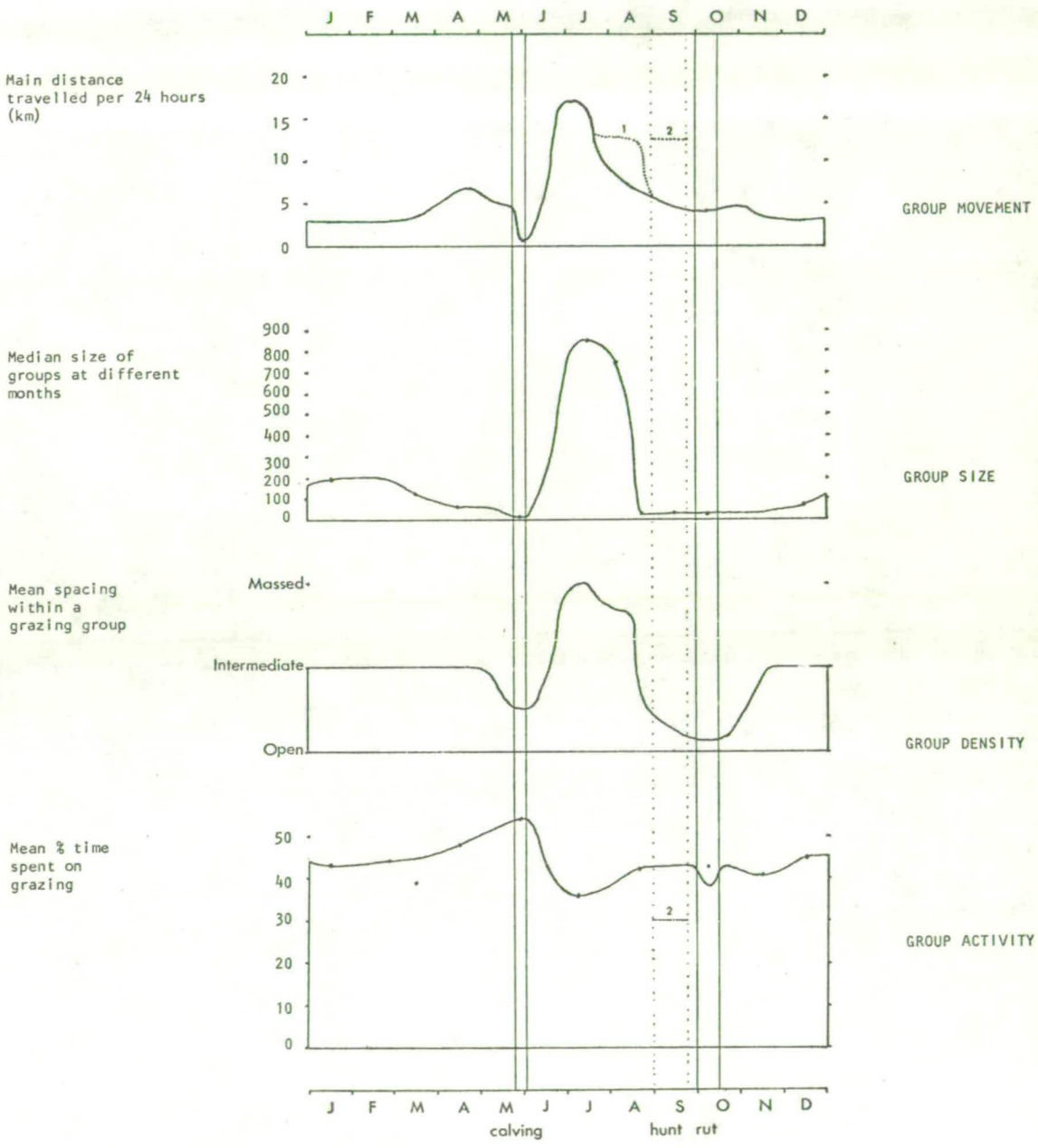
the extent to which animals of differing sex and ages associate in these groups; the extent of daily travel; and the amount of time spent on different activities, may be thought of as the social "building blocks" or structure on which the social organisation is based. Reindeer exhibit particularly marked seasonal changes in these general parameters of social structure (Fig.7.1.). These are now quantified and discussed before analysing in detail some of the specific links between reindeer behaviour and environmental factors.

7.1.1. Group Movement and Distribution

The geographical distribution of reindeer on Hardangervidda has been shown to be seasonally predictable (Gaare, Skogland & Thomson, 1970; Thomson, 1973; Skogland, 1974). On a day-to-day basis also the distance moved over the terrain is seasonally characteristic. To consider extremes, whereas the post-calving herds of early summer readily shift 15-20km in the course of grazing during the day, at calving time nursery groups of mothers and their calves may move less than 1km for several days. This seasonality of movement is summarised in Figure 7.1.

The movement of animals in a herd is not normally in one consistent direction and there is also variable movement taken by individuals in moving or stationary groups. While the activity study recorded times for walking, trotting and running which reflect the amount of energy spent by an animal in moving at that time, it does not reflect the distance a group /

Fig. 7.1 The seasonality of social structure of reindeer on Hardangervidda.



1. On days of insect harassment.
2. Effect of the hunt.

group as a whole would have travelled. For example, in the April migration the 10% time on movement is largely spent on a slow westerly trek between grazing areas so that the herd may shift up to 6-7km per day; on the calving grounds animals spend 12% time on moving and shifted 4-5km on average; whereas in the rut the approximate 20% time spent on moving included male charges at subordinates, courtship approaches and chases, but by the end of the day the group as a whole was unlikely to have drifted further than 4km.

At any one time of year the daily distance covered was either fairly constant, or variation could be attributed to specific environmental influences. For example, the 24-hour movement of rutting groups at North Ottadalen in 1969 (to the nearest 0.5km) was 4.5, 4.0, 4.0, 5.0, 2.5, 4.5, 3.5, 5.5, 4.0, 4.0, and 2.5km, a daily average of 4.0km. In winter by contrast, movement could be minimal for several days averaging 1-3km daily, then a sudden change of area made. For example, two groups of 90 and 100 animals on Snøhetta in November, 1969, spent four days shifting only 1-2km each 24 hours, then moved off during the night to a new grazing area 7-10km away. Similarly, on Hardangervidda in March 1971, 400 reindeer had been relatively stationary for three days of cold, sunny and calm weather but started to move more as temperatures decreased and winds developed, until finally, in two herds of 300 and 100, they were moving 8km per day into the wind.

The long-ranging, post-calving movement of the massed herds in late June/early July occurred irrespective of weather conditions /

conditions except that movement was directed into the wind (see Ch.7.6.). From this post-calving peak of movement, summer herds increasingly dispersed into smaller units which moved a variable distance over the terrain. On warm days of insect activity, the deer would move faster and longer into the wind in search of insect-relief habitats such as snow fields, hill tops, lake sides, or as a last resort by milling together (see Ch.7.7.). On cool or wet summer days without insects the groups would seldom move more than a few kilometres in the course of grazing.

The seasonal movement pattern for most of the population can be characterised as a regular deliberate shift of range in April from the wintering area to the calving grounds, long ranging movement after calving in early summer, insect-induced movement in summer, and short local movements only at calving, rutting and in winter. The geographical distribution of animals on Hardangervidda in relation to this movement pattern is shown on a map (Fig.11, p.37, App.3). This distribution and movement pattern was basically similar in subsequent years also (see Fig.1, Skogland, 1974).

7.1.2. Group Size and Individual Distance

Up to 90% of the Hardangervidda population has been observed in two or three massed herds of thousands on days in July and August, whereas a few months previously in late May the deer had been distributed over the calving ground in hundreds of small and uncohesive units. Such differences in the size and /

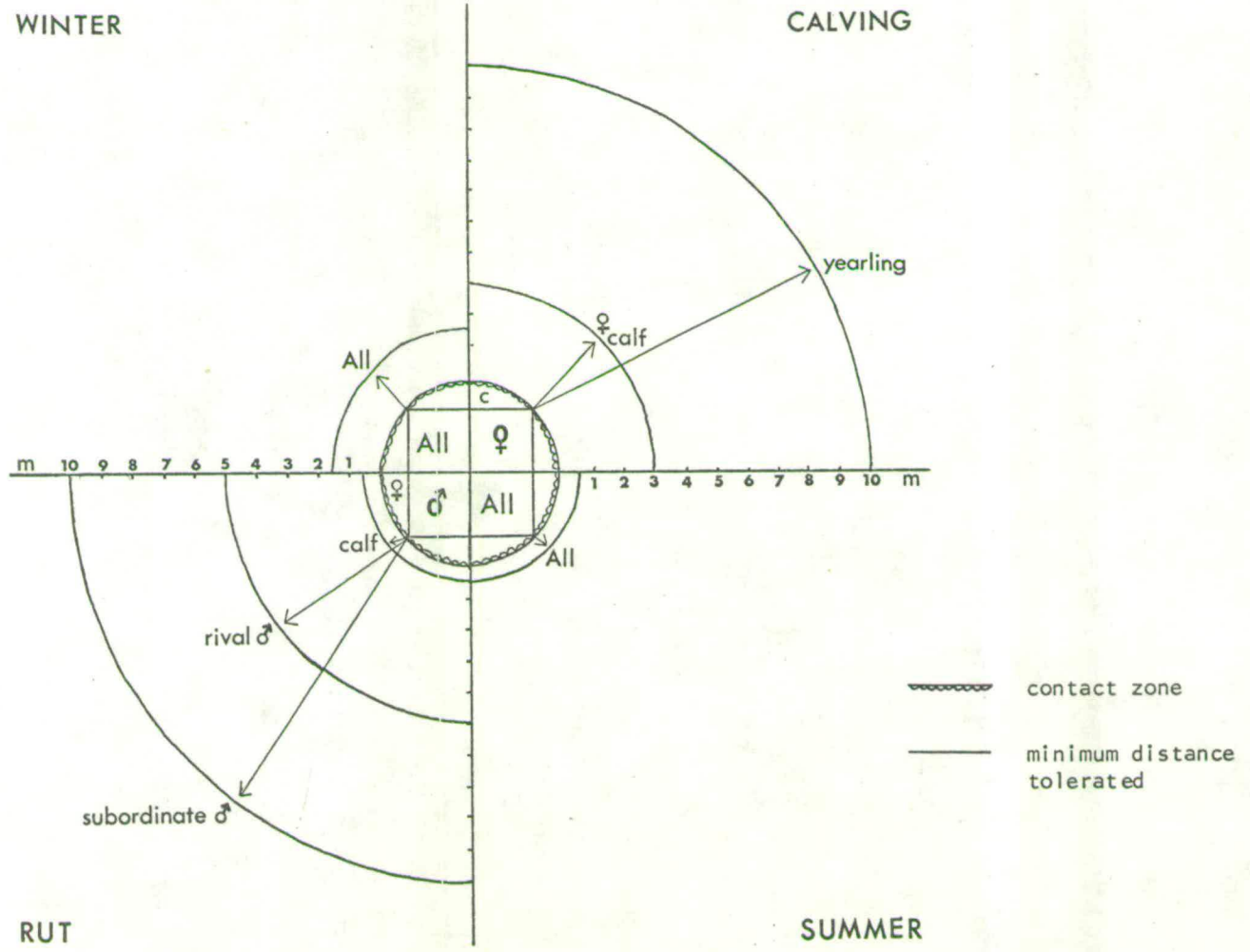
and cohesion of groups represented the extremes in what was a regular seasonal pattern. The number of groups of different size categories observed on Hardangervidda at different months throughout the study period was recorded (Fig.5, p.17, App.2), and the proportions of size classes summarised for the four main seasons (Fig.2, p.9, App.3). From this the median size of group at different months has been calculated, and the seasonal pattern, consistent in both study years, illustrated in Figure 7.1. The maximum size of aggregation did vary between the years. In particular, an assemblage of 10,000 deer seen on 4th August, 1970, could not be repeated the following year because of the reduction in the population from 14,600 to 6,000 after hunting in autumn 1970. Nevertheless, aggregations of up to 2,000-3,000 were observed in early July, 1971, followed by their break-up and dispersal over the range in late summer. Observations on Hardangervidda in 1948 can confirm this pattern of herds up to 4,000-5,000 being common in early summer followed by a dispersal in the "mushroom season," when a single female and calf, or female, yearling and calf, can be seen ranging together (Wildhagen, 1948).

The parameter of group size was seen to be directly influenced by factors related to spacing. When deer associated closely together in a group they would show a greater synchronisation of activity, and thereby more readily and more often coalesce with other groups. Also, a group in the process of moving over the terrain functioning as a cohesive unit was more likely to meet with other groups so that there was the possibility ultimately /

ultimately of forming large herds. The spacing within a group was seen to be partly a function of the activity of the animals within the habitat, and partly due to the affiliative tendencies of animals at that time (see Ch.6.2.). Animals in a stationary grazing herd tended to spread out from each other so that loose sub-groups would form which could ultimately lose contact with each other. This could also happen with a large herd when situated in an area with only small localised grazing sites, as is common in late winter. Conversely in stressful situations, such as an alarm or in strong winter winds, or under insect harrassment, all animals in the vicinity would clump together and a strictly cohesive unit form. The typical spacing of animals in undisturbed grazing groups at different times of the year is illustrated in Figure 7.1. The group density or spacing shows a clear relation to group size and movement.

The minimum distance which animals choose to keep from each other at different times of the year is often, if not always, the determinant factor in group spacing. This minimum or "individual distance" can be defined as the distance which one animal will tolerate another of its own species or group without taking avoidance or antagonistic action. It is thus a quantitative parameter of the affiliative tendencies of different classes of reindeer at different times of the year (Fig.7.2). For example, a dominant male in the rut, especially when tending a single female, will not tolerate the approach of a subordinate male closer than approximately 10m. Similarly, a mother female in a nursery group at calving time will charge at /

Fig. 7.2 Individual distance of reindeer at different seasons (estimates).



at any strange animals around, particularly yearlings and other calf-less adults, while it shows an increasing habituation to other mothers and their calves and co-exists with them in the nursery groups. By contrast, the same animals in the massed herds of summer commonly graze at a distance of less than 1m from each other with only infrequent antagonism. In winter, on the other hand, an approach closer than 1-2m in the course of grazing usually results in a withdrawal, threat or dispute. Individual distance amongst lying animals in both winter and summer is often less than during grazing, although actual bodily contact while lying is unusual. For the female, the individual or contact zone is reserved for its calf, while in the rut the male courtship patterns are aimed at temporarily eliminating the natural individual distance between the female and himself to permit the brief act of copulation.

While group spacing, as determined by individual distance and the response of animals to a benign or stressful environment, can largely account for the main seasonal trend in group size (Fig.7.1), groups of varying size characteristically do occur at any time of the year, or indeed on the same day. There is clearly a large element of chance in the precise size of a group due to a variety of accidental or "random" factors. For example, I have observed animals become separated from each other while swimming, or running over the terrain after swimming; while grazing around different sides of a knoll or hill; as mothers trot away from the summer herd in search of their calves; or as animals move off in opposite directions following a herd lying period. The extent of daily change in the /

the size of a group with animals leaving and new animals joining may be so considerable, that it is only with the more sedentary groups in winter that any constancy in size from day to day can be considered as the norm.

7.1.3. Group Composition and Segregation

At very few times of the year can the sex and age composition of a reindeer herd be considered to be characteristic of the entire population to which it belongs. Only in the rut with a complete mixing of animals is there a greater justification for considering this to be so, but then group sizes are relatively small and therefore unrepresentative (Ch.3.4.3.), apart from which there may be characteristic differences in the composition of the various rutting groups (Ch.7.8.).

The variable degree of segregation of males makes the prediction of group composition difficult for most times of the year. In winter all-male groups occur as well as integrated herds of females, young, and males, usually but not always occupying different parts of the same range. I observed all-male groups on Forelhogna and Snøhetta in winter, and they are known to occur on Hardangervidda, notably in the northern Hardangerjøkulen region (local information). Females on Hardangervidda are concentrated on the eastern winter range, together with calves, juvenile animals including many second and third year males, and a variable number of older males. In the winter of 1970/71 /

1970/71 on Hardangervidda, mature males were present in the female-young herds in approximate number to their proportion to the population; whereas in the previous winter a greater degree of segregation had occurred. The difference between years was still evident by calving time when males comprised approximately 10% of all adult reindeer present on the calving grounds in 1971, whereas in the previous year only 1% were males.

After calving the large herds of early summer comprised a relatively high proportion of males in both years (i.e. c.15%), and were clearly totally mixed herds. However, not all males in the population need be present in these large herds since small batchelor groups may still be observed in the mountains of western and northern Hardangervidda at this time (Kjos-Hanssen, 1974). Also, in mid-July 1970, I observed a herd of 200 reindeer on Fagernut which comprised around 80% males, and another small group of 10 males in early July, near Tinnhølen (map on Fig.2.4). These males may have recently moved from a wintering area in the north into the central summer range, and certainly in both instances these male groups were quickly dissolved as they integrated into the large mixed herds. Although males tend to be in the van of the quickly moving herds of early summer, with mothers and their calves in greater proportion at the rear (Fig., p.29, App.3), this does not appear to lead to the formation of separate male and female herds in summer. This contrasts with the situation on the summer tundra range of the Alaskan North Slope when each time after insect harrassment had subsided, the caribou herds readily /

readily segregated themselves into male groups and female-calf-yearling groups (Table 5, p.160, App!7). In equivalent periods without insect harrassment on Hardangervidda there was no evidence of a similar dispersal of animals on a segregated basis.

The mechanics of segregation in Rangifer are little understood. On Hardangervidda in summer, Wildhagen (1948) often observed 2-3 males associating together in the mixed summer herds. I also observed this, and noted that they would remain in sufficient synchrony with the rest of the herd to avoid becoming a separate group. In winter, by contrast, males showed less tendency to synchronise their activity with the majority, and this, coupled with their tendency to gather apart and indulge in sparring and sex-related behaviour, could often leave them on the periphery or at the rear of the herd when most animals moved on to the next grazing site. In March/April, with pregnant females displaying a distinct urge to lead off on westerly migration, and males displaying least tendency to move, a progressive differentiation in group composition and ultimately spatial segregation was seen to occur (Ch.7.4.).

The factors responsible for a complete or partial segregation of males soon after the rut and in early winter were not observed. Pruitt (1959) has demonstrated that the areas inhabited by caribou male groups in winter have greater densities, depths and/or hardness of snow cover than the areas occupied by the female groups, and attributed this to the males' greater threshold /

threshold of tolerance to these snow characteristics which can inhibit feeding. Paradoxically, one hypothesis for segregation amongst red deer in Scottish mountains in winter is that the males seek lower ground on account of a lesser tolerance to winter storms and blizzards than the females (A. Jackes, pers. comm.).

It might be considered a definite advantage to mature reindeer males who have cast their antlers (and therefore are low in social rank) to over-winter in separate areas and so avoid the competition for grazing spots with the higher-ranking antlered females. However, mature males in winter do not invariably segregate, and even in the all-male groups observed in winter there were invariably present some younger antlered males who would readily capitalise on their dominant status during grazing periods.

The occasional identification and association of like-with-like did not only apply to the sexes. Different classes of animals were particularly associated together on the calving grounds resulting in segregated groups. Pregnant females often showed minimal tendency to associate with any group, and especially if it was comprised of yeld females and yearlings. However, after calving, the same females as mothers voluntarily associated together into nursery groups. Pruitt (1960) suggested that caribou females form into maternity bands, false nursery bands, and nursery bands at calving time. For wild reindeer on Hardangervidda and Ottadalen, nursery groups appeared to be the only relatively stable identifiable units at this time.

In /

In species where group sizes are smaller and more constant, the association of female and young of overlapping generations is apparent, e.g. red deer (Darling, 1937); white-tailed deer (Hawkins & Klimstra, 1970); mountain sheep (Geist, 1971). In wild reindeer and caribou, the formation of hugh aggregations and the coalescing and splitting of groups means that even the basic mother-infant relationship may be difficult to maintain, as seen by the number of mothers and calves in summer who become temporarily or seemingly permanently separated from each other. However, recent studies on barren-ground caribou in Canada have produced evidence of long-term social bonds between individuals. Results from a massive ear-tagging programme showed that in 13 instances migratory caribou from the same small group, tagged at the same time, were shot together over 12 months later. Nine of these 13 long-term bonds were between males, and in 4 of these cases two adult males were shot together more than 3½ years after tagging (Parker, 1972). Radio-telemetry studies on a different population found that particular caribou individuals in post-calving herds tended to seek association with each other, and would return to the same small cohesive group after hours or even days of separation (Miller et.al., 1975).

With reindeer I have observed that where a group remained relatively constant in size and composition over several days or weeks, then animals did at least develop temporary associates. For example, in winter a deer might be seen to capitalise on its dominance over another by following it around during grazing (Ch.7.2.). Further work is now required on the nature of association in groups of reindeer, to determine whether /

whether group composition is a random insignificant reflection of the individuals in that particular area, or whether familial relationships or associations between unrelated individuals are commoner than is presently supposed.

7.1.4. Group Activity

The co-ordination of activity by animals in a group results in well-defined group active periods of grazing and moving, alternating with lying periods of rumination and rest. Daily and seasonal variation in group activity and records of the time spent by animals on different activities over the day was a main feature of study, and is reported and illustrated fully in Gaare, Skogland & Thomson (1970); Thomson (1971, 1973); and Gaare, Thomson & Kjos-Hanssen (1975) (Apps. 1, 2, 3 & 4).

It is clear that a change in activity is an animal's immediate response or first line of defence to a slowly or suddenly changing feature of the environment. Whereas a group cannot instantly change its size or composition, the animals within the group can readily graze more, lie more or move more, depending on the prevailing circumstance. Activity is controlled by two basic cycles; a short-term rhythm of alternating periods of feeding and rumination, and a longer-term response to the 24-hour light cycle, particularly evident in early winter. Superimposed on this basic pattern, group activity is attuned to seasonal factors of the environment, such as variation in food quantity and quality and their relationship with snow cover. Upon this framework, daily activity of groups can vary instantly as a direct response to rapidly changing factors of the environment, such /

such as disturbance, high winds in winter, or fly harrassment in summer. The effect of such environmental factors on activity is particularly considered in Thomson, 1973 (App.3). Their effect on other aspects of the social organisation is described in subsequent sections of this chapter.

The activity of reindeer is thus a seasonally variable matrix of regular and irregular responses. In early winter, groups of whatever size and composition display identical patterns of activity closely tied to the time of day, namely an active grazing period in morning and afternoon, and a 2-2½ hour lying period in the middle of the day. Moderate levels and intensity of disturbance have no lasting effect on this regular pattern (Figs.5 & 6, pp.64-66, App.1). At other times of the year activity periods are less tied to the time of day so that one group may be grazing while another group in the same area is lying. If two such groups coalesce, a mixed activity pattern initially prevails as animals continue on their previous rhythm, until a unified group activity is gradually re-asserted. Mixed activities within a group were also a feature of animals in darkness. On summer nights, particularly after long-ranging movements during the day, animals would become stationary at night with lying the predominant activity. However, some grazing, standing and walking about would also occur and not until daybreak were the animals in a large herd able to visually contact each other and so fully synchronise their activity pattern again (e.g. Fig.8, p.25, App.2).

Illustrated examples and descriptions of the daily activity patterns /

patterns of groups throughout the year are given in Appendices 1, 2, 3 and 4. The relationship between group activity, in particular the mean time spent on the major activity grazing, and other aspects of social structure, is indicated in Figure 7.1. The recorded activity time budget and its seasonal variations is analysed in relation to energy expenditure in Chapter 8.

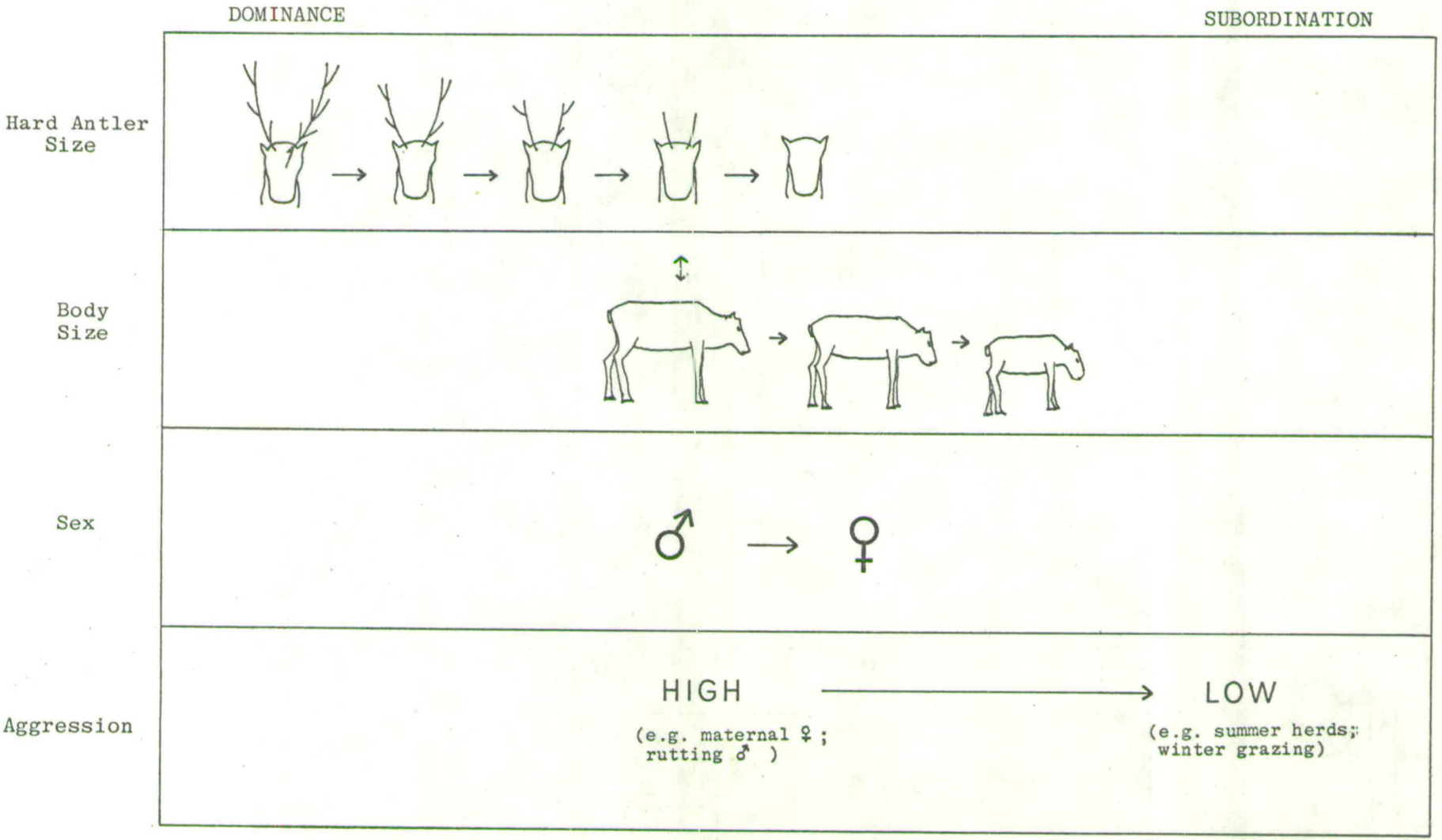
7.2. SOCIAL HIERARCHY AND WINTER GRAZING

> "In the rut the bulls are male, but the cows are male in winter." J. Stalker, an old reindeer herder at Nome, Alaska (in Henshaw, 1968b).

The frequent interchange of feeding craters in winter is governed by the social rank of the individual reindeer which are feeding. In Chapter 5 the range of approach, threat, and attack postures used in conflict situations were described, and how the social rank of an animal can be recognised particularly by the size of its hard antlers, as well as its body size, sex, and aggressive motivation (see Fig.7.3). A relatively high degree of aggression is characteristic of rutting females and mother females at calving, but is not normally a feature of winter grazing antagonism. The observed changes in social rank for different types of reindeer between successive seasons is summarised and illustrated in Table 7.1.

In early winter, soon after the rut, the mature males cast their antlers and become subordinate in antagonistic encounters with /

Fig. 7.3 Criteria of social rank in reindeer.



with antlered animals. Thus the antlered females and young males become the dominant classes during the winter. Only the smallest and poorest-antlered females and calves are unable to assert dominance over the unantlered but mature males. Espmark (1964b) found similar changes in social rank from rut to winter for semi-domestic reindeer in Sweden.

From hundreds of encounters recorded in winter, and thousands more observed, it became quickly clear that the stature of the antlers was crucial in determining the outcome of confrontation between two animals, whether in overt confrontation through a direct threat or attack posture, or merely passive approach and withdrawal. Animals have been assigned to eleven distinguishable classes to facilitate the illustration of the hierarchy so found (Table 7.2). Using an artificial points system to classify these classes according to the possession and size of their antlers, their body size and sex, a tabular prediction of social rank may be made, and this is found to be close to the actual performance of these types of animals in winter (Table 7.2).

The importance of antler size in determining rank was only modified where sex or body size could outweigh a minor antler superiority. Thus a well-antlered female would normally be dominant to a lesser-antlered young male, but would be subordinate to a young male of equal antler stature. Unantlered males, although the largest bodied animals present, tend to be subordinate to all other adults, except those females with especially poor antlers and the few females which are unantlered. For /

Table 7.1 Changes in the social rank of reindeer classes over the year.

Social Rank	Rut	Winter	Pre-calving	Post-calving	Summer
HIGH RANK	Master ♂	Young (antlered) ♂	Pregnant (antlered) ♀	Antlered mother ♀	
	Lesser ♂	Well-antlered ♀		Unantlered mother ♀	
	Young ♂	Poor-antlered ♀		Antlered ♀	
	♀	Mature (antlered) ♂	Unantlered ♂	Unantlered ♂	Velvet antlered ♂
	Calf ♂	Unantlered ♀	Yeld (unantlered) ♀	Unantlered ♀	Velvet antlered ♀
	Calf ♀	Calf	Yearling	Yearling	Yearling
LOW RANK					Calf
Main Determinant of Social Rank	Rutting ♂ Aggression (and antler size)	Antler Size	Antler Size	Maternal ♀ Aggression	Body Size
No. of recorded antagonistic encounters	242	448	221		129

For calves of both sexes, their much smaller body size determined that they played a subordinate role in any encounter. Occasionally a well-spiked calf was seen to poke an unantlered or poor-antlered adult in the rear, but would retire immediately if it was threatened or butted in reprisal.

The only areas of overlap in what appeared to be an essentially linear hierarchy based on antler size for the eleven distinguishable classes of animals, was between antlered females and young antlered males; between unantlered males and small poorly-antlered females; and in the calf segment where possession of spikes did not necessarily ensure dominance within calf-to-calf encounters. Disputes were much less common than approaches or threats (re.Ch.5.2.), and tended to be most frequent in these overlap areas and between animals of very similar status within the same "class".

The relative ranking order of individuals does not remain static throughout winter but alters particularly as more and more males cast their antlers, until only the youngest males ($1\frac{1}{2}$ and $2\frac{1}{2}$ years) retain them, a situation which continues until late winter. The possession of antlers by the females ensures them a high ranking status in the constant grazing antagonism throughout the winter, and in late winter about a month before calving the yeld females and any young males still antlered cast their antlers, leaving the pregnant females as the highest ranking animals. It has been established experimentally that reindeer which have their antlers removed experience a considerable lowering in social rank (Espmark, 1964b).

In /

Table 7.2 The social rank of different sex and age classes of reindeer in winter, as observed and as predicted by antler status, body size and sex.

Sex/age class	Antlers: Point rating A	Body size: Point rating B	Sex: Point rating C	Predicted social rank (A + B + C)	Observed social rank *
$3\frac{1}{2}$-yr. antl. ♂ [a]	7	6	2	15 (1st)	1st Dominant
$2\frac{1}{2}$-yr. antl. ♂ [b]	6	5	2	13 (2nd)	2nd
$1\frac{1}{2}$-yr. antl. ♂ [b]	5	4	2	11 (3rd")	3rd
Well-antl. ♀	6	4	1	11 (3rd")	3rd
Medium-antl. ♀	5	4	1	10 (5th")	5th
Poor-antl. ♀	4	4	1	9 (7th)	6th
Unantlered ♂	1	7	2	10 (5th")	6th
Unantlered ♀	1	4	1	6 (8th)	8th
Well-spiked calf	3	1	1-2	5-6 (9th)	9th [c]
Poor-spiked calf	2	1	1-2	4-5 (10th)	9th [c]
Unantlered calf	1	1	1-2	3-4 (11th)	9th [c] Subordinate

Point rating A: where 1 = unantlered; 2 = poor spikes; progressing to 7 = large antlers of a nearly-mature male.
Point rating B: where 1 = approximately 40 kg body weight; with 10kg between successive points to 7 = 100kg.
Point rating C: where 1 = female; 2 = male.

a. Becomes an unantlered male from wid-winter.

b. Becomes an unantlered male by late winter.

c. Calf attains higher rank if closely associating with mother (see text).

* From 448 antagonistic encounters recorded in winter (Nov.-Apr.), in mixed groups and all-male groups on Hardangervidda, Snøhetta and Forelhogna. All other encounters observed fitted this pattern.

In other deer species, the female does not carry antlers and the segregation of males in winter may be seen as an adaptive mechanism whereby the females benefit from the lack of male competition (e.g. as in red deer). For reindeer in South Norway, mature males are commonly found within the female herds in winter, where they can literally pose no threat to the females. Where segregated all-male groups do form, as on Hardangervidda in the winter of 1969/70, the dominance-subordination relationships are as regular and as frequent as they are in the mixed herds of winter. One such "batchelor" group of 20 males was observed on Forelhogna range over two days in early March, 1970. All the 14 males which had cast their antlers were subordinate to all the 6 males which still retained theirs. Within the 6 antlered males the hierarchy was linear in that the relative size of the antlers was an automatic visual guide to the individual's status (Table 7.3). The rank of one male who had cast his left antler only, appeared to be what would have been expected if he had still retained both, as he was dominant to a male with two poor spiky antlers. The prolonged antler sparring bouts which occur between the antlered males in winter (re. Ch.5.3.3.) may provide them with a useful continuous assessment of the relative stature of their antlers viz-a-viz their "opponents". Within the very similar looking males of the unantlered segment it is probable that ranking relationships are less linear, as in the course of grazing and lying encounters there were more often disputes by rearing-up and boxing at each other, or kicking out with the forelegs.

The /

Table 7.3 Social rank relationships in an all-male group on 3rd & 4th March, 1970, Forelhogna range.

	Animal's Code Name	BT	M-B	M	MB-L	CT	TS	14Un
6 antlered ♂♂	Big Thick		+		+			+
	Medium-Big	-		+	+		+	
	Medium		-			+		+
	Medium Broken-Left	-	-			+		
	Curl Top (right)[1]			-	-		+	+
	Thin Spikes		-			-		+
	14 Unantlered ♂♂	-		-		-	-	±

Reading across the rows: + = Animal dominant in observed antagonistic encounters.
- = Animal subordinate in observed antagonistic encounters.

1. This male had already cast the antler on its left side.

The place of the calf in the winter hierarchy is an interesting one. Calves do dig their own feeding craters in the snow and as subordinate animals are frequently usurped by any older animal which chooses to occupy that crater or grazing spot. The calf is then only capable or taking over the grazing spot of another, even lower-ranking calf, or moving on to find a vacated spot or to dig a fresh crater. Occasionally, however, a calf will be seen feeding muzzle to muzzle from a female's feeding crater, clearly benefitting from the lack of aggression inherent in the mother-infant bond. It was observed that as long as a calf grazed in the craters dug, procured, or defended by the mother, it temporarily shared the mother's social rank. This notable but not frequent association of female and calf in winter is reported to be the normal winter situation amongst semi-domestic reindeer in Sweden (Espmark, 1964b), and in the U.S.S.R. (Baskin, 1970). Clearly the implications of a low social rank is altered if calves do not always "go it alone". Henshaw (1968b) did not observe such an association between caribou calves and their mothers in winter, and on theoretical grounds argued that it could not be adaptive since it would place an additional burden on those females who were pregnant, in that they would require to commandeer the best nutrition that their status could afford. However, although some reindeer females can and do produce calves every year, the females who are yeld in one year may make up the bulk of the productive females the next year (E. Reimers, pers. comm.), so that a prolonged mother-infant association, which may be observed, does not necessarily have negative implications for the next generation /

generation of calves. In any case, Henshaw's theory cannot negate actual observation.

Conceivably a flexible situation may apply whereby the relative frequency of calves digging and feeding from their own craters on the one hand, or sharing the mother's crater and thus her social status on the other hand, is dependent on the severity of the prevailing conditions. In overcrowded or overgrazed winter pasture, or with a loss in body condition, the calf may come to rely more on the "umbrella" of the mother's social rank. Baskin (1970) reports that for domestic reindeer it is not found expedient to remove calves from their mothers in winter, and on one enterprise up to 20% of the calves so separated subsequently died. Although the wild reindeer calves in South Norway were predominantly seen to fend for themselves in winter, the continuing association between mother and calf did allow the option of feeding alongside the mother, as well as infrequent suckling events (re.Ch.5.4.4.).

I consider that the hierarchial relationships in winter groups are such that it tends to benefit those animals who are most often dominant in the frequent encounters between grazing animals. From an early stage of observations of herds in winter it was noted that animals would seldom graze more than a few minutes in the one spot before being moved on by a dominant, or voluntarily leave to usurp the grazing site of a nearby subordinate. Animals lowest in rank appeared to have to move around more frequently in the course of a grazing period, coupled with a lesser ability to procure or defend the grazing spot acquired. To test this, the number of spots grazed /

grazed and antagonistic encounters for and against an individual in 20 minutes of grazing was recorded for four individuals of differing social rank in January and March 1971 on Hardangervidda (Table 7.4). The low-ranking animals observed, namely an unantlered female and a medium-spiked calf (not associated with its mother) were frequently threatened off their grazing spots and usually had to find a vacant crater, or dig in a fresh area, until threatened off once again. On average they were able to feed for up to 1 minute in any spot, and on being moved on there would be few animals around from which they were able to "steal" a crater. By contrast, the high-ranking animals, a well-antlered female and a $2\frac{1}{2}$-or $3\frac{1}{2}$-year antlered male, moved around much less and grazed on any one spot for 3-4 minutes on average. When the high-ranking animal did vacate a spot it would generally move towards a subordinate and usurp its crater. This small pilot study supported impressions of the advantages of high social status in winter. High ranking animals have undisputed access to the best grazing sites and readily take over craters which subordinates have first cleared by digging. Low-ranking animals for their part are at the receiving end of antagonistic encounters, and must walk more in search of a grazing spot and possibly also dig more. Dominants have first call on the limited food resource available and spend less energy in the process. Thus it is to be expected that by the end of winter this competition for a food supply which is limited in quantity and quality will result in lower ranking animals losing proportionately more in body condition.

For /

Table 7.4 Individual rank and winter grazing competition recorded in 20 minute periods; Hardangervidda, January & March, 1971.

Type of animal	Time period	No. of craters grazed	No. of antagonistic interactions	Result of antagonistic interactions			
				Craters grazed or held	Subordinate opponent	Craters lost	Dominant opponent
2-or 3-year antlered ♂	20 mins.	9	6	5	3 times a 2-year ♂. 1 time a 1-year ♂. 1 time a medium -antlered ♀.	1	1 time a 2-or 3-year ♂.
Well-antlered ♀	20 mins.	6	5	5	3 times a medium -antlered ♀. 1 time a poor-antlered ♀. 1 time a calf.	None	-
Unantlered ♀	20 mins.	23	22	3	2 times a poor-spiked calf. 1 time a well-spiked calf.	19	14 times a 1-year ♂. 2 times a 2-year ♂. 1 time a poor-antlered ♀. 1 time an unantlered ♂.
Medium-spiked calf (not close to mother)	20 mins.	21	19	5	5 times a medium -spiked calf.	14	8 times an antlered ♀. 1 time an antlered ♂. 2 times an unantlered ♂. 3 times a well-spiked calf.

For a population far in excess of range carrying capacity in winter, or in prolonged severe weather, such a differential in body condition might be expected to lead to differential mortality rates.

The social hierarchy assists the unequal distribution of food, and when food is short it eliminates only a proportion of the population by starvation. This was the conclusion reached by Lockie (1956) recording antagonism for food amongst flocks of rooks in winter, and has been propounded as a general thesis by Wynne-Edwards (1962). In reviewing the evidence for behaviour as a possible population regulation mechanism, Watson and Moss (1970) could find no conclusive hard evidence that populations in fairly natural conditions had been limited by dominance or aggression within hierarchies. A study on white-tailed deer fawns (Odocoileus virginianus) measuring body weight and femur marrow fat content as indices of body condition, found that dominance in the winter hierarchy did correlate with condition (Robinson, 1962). However, as the author points out, the experiment was conducted on a small scale under artificial conditions.

Unfortunately on Hardangervidda in the two winters of observation, 1969/70 and 1970/71, neither weather nor grazing conditions were unusually severe, and comparitive studies on body condition before and after winter have not been undertaken. Further study is planned (E. Gaare, pers. comm.). At present it can be said that the observed winter hierarchy may have survival value for the population by favouring the more productive /

ive classes. In particular, females are the favoured class in winter, irrespective of whether or not the males are segregated. In the last month of winter only the pregnant females retain their antlers, and thereby dominance. Young males have a high rank in winter, in batchelor groups or in mixed herds, until they cast their antlers. Calves have a subordinate status but can benefit from association with their mothers. The potential of dominance relationships in severe winters operating as a population regulation amongst reindeer has also been noted by Espmark (1974).

However, as well as operating to the advantage or disadvantage of certain classes, a social hierarchy might conserve energy for the group as a whole, by minimising fights or disputes in competitive situations (J.D. Lockie, pers. comm.). One animal accepts the role of subordinate by withdrawing at the approach or threat of another, the dominant, and overt aggression is avoided. Unless it can be demonstrated that subordinates suffer a damaging loss in body condition as a result, this alternative hypothesis of benefit to the group as a whole, can fit the observed winter hierarchy relationships for reindeer also.

Since the pioneer study of the pecking order in hens (Schjelderup-Ebbe, 1922), it has been frequently asserted that the establishment of the social hierarchy is dependent on animals learning their social rank through individually recognising other members of the group. However, reindeer do not live in small closed groups but in large amorphous herds which /

which change in number frequently as groups split or other animals join, so that there would appear to be no possibility of long-term recognition of all other individuals. Instead it appears that two reindeer with no previous experience of each other can instantly assess which one of them is dominant and which subordinate in any conflict situation, and encounters are predictable on the basis of the possession and relative size of their antlers, body size and sex.

Lent (1966) also considered that the hierarchial relationships he observed in caribou in late winter time could not be explained by any of the recognised formats for classification of social hierarchies. Rejecting the theory of individual recognition for caribou, he considered that the hierarchy must therefore be based primarily on the recognition of other classes of individuals, or the social releasers presented by these classes. However, I would argue that while categorising animals into classes may be a convenient way of demonstrating social rank (e.g. Table 7.2), the animals themselves appear capable of making a finer distinction based on a direct assessment of an adversory's ranking attributes, notably antler size, body size and sex, viz-a-viz its own attributes. This is a finer distinction than assessment of class alone. For example, unantlered males in winter are generally subordinate to antlered females, but if rank was entirely dependent on recognition of class alone, then they would also be subordinate to the small poorly-antlered females, which they are not. Similarly, animals of the same sex and age, such as two $2\frac{1}{2}$-year males, accept dominant and subordinate roles if one has slightly superior /

superior antlers to the other although clearly they both belong to the same class. While individual recognition *per se* cannot apply in wild reindeer and caribou herds, recognition of an individual's attributes normally determines who is dominant and who is subordinate at any encounter. Where two animals are very close in rank and neither accepts the subordinate role, then a short dispute occurs to settle the issue. As noted above, such disputes were particularly a feature of animals of similar rank, but not necessarily of the same class.

While individual recognition is clearly not a *sine qua non* for a hierarchy, there is evidence from this study that reindeer grazing near each other can learn to capitalise on their dominance over a particular neighbour. For example, the calf recorded in Table 7.4 was dominant in 5 out of 19 encounters in the grazing period, and each time this dominance was won at the expense of a particular calf, also with medium-sized spiked antlers, which it would seek out whenever it had lost its crater. Similarly, a 1½-year antlered male followed around an unantlered female and of the 19 encounters in which this female was subordinate, 14 of them were from this particular male (Table 7.4).

The opportunities for an individual associating with another, and for individual recognition as such, are obviously much greater in small "closed" groups who do not meet up with new animals frequently. For example, in the Scottish tame reindeer herd, which is kept at around 70-100 animals, dominance-subordination /

ination relationships were found to be only approximately attuned to the possession and size of hard antlers. It appeared that certain individuals could establish dominance over others by threat and attack postures regardless of their respective attributes or "social releasers". Similarly, in Espmark's (1964b) study of the dominance-subordination relationships amongst 16 reindeer kept in an enclosure for seven months in autumn and winter, it appeared that while the size of antlers obviously did influence the rank order, the age, body size and strength of the animals in disputes at the feeding cribs provided were all important. While these factors were undoubtedly the determinance of rank order under these conditions, it is difficult to see how in free-ranging semi-domestic or wild herds it would be possible for two strange animals to assess each other's age, or know each other's strength without learning through several disputes with each other. Also, Scott (1958) has pointed out that due to an unnatural concentration of food supply "dominance relationships in captivity can be strengthened or even created where none existed before". In quoting Scott, Lent (1966) adds that it is likely that "unnatural dominance relationships can be established merely by an opportunity to recognise other individuals that might never occur under natural conditions".

In wild reindeer, natural dominance relationships are primarily based on the size of hard antlers as signal attributes, or social releasers. While there is a limited food supply, competition by overt aggression is thus kept to a minimum. The winter hierarchy may also have survival value for the population /

population in ensuring a high ranking status for the females, whether they are pregnant or have a calf at heel, and then latterly favouring the pregnant females only.

7.3. WINTER WINDS AND HEAT LOSS

> "In the Abitibi country, and doubtless elsewhere the Woodland Caribou has the habit, already ascribed to the Moose, of racing in a circle during a windstorm. George Linklater has witnessed this several times also....."
>
> 'Strange Habits' noted by E.T. Seton (1910).

The winter activity and behaviour of reindeer were seen to remain remarkably constant under the wide variety of weather and snow conditions in the mountains. Grazing and lying periods alternated more regularly in winter than at any other season, irrespective of sun or cloud, fair weather or snow, cold or mild (from -30°C to above 0°C), and at a range of moderate wind speeds (Beaufort 0-4) (Thomson, 1973). A clear predictability of activity in response to changing weather and snow conditions, as reported by Henshaw (1968a) for barren-ground caribou in Northern Alaska, was not found to be the case in this study.

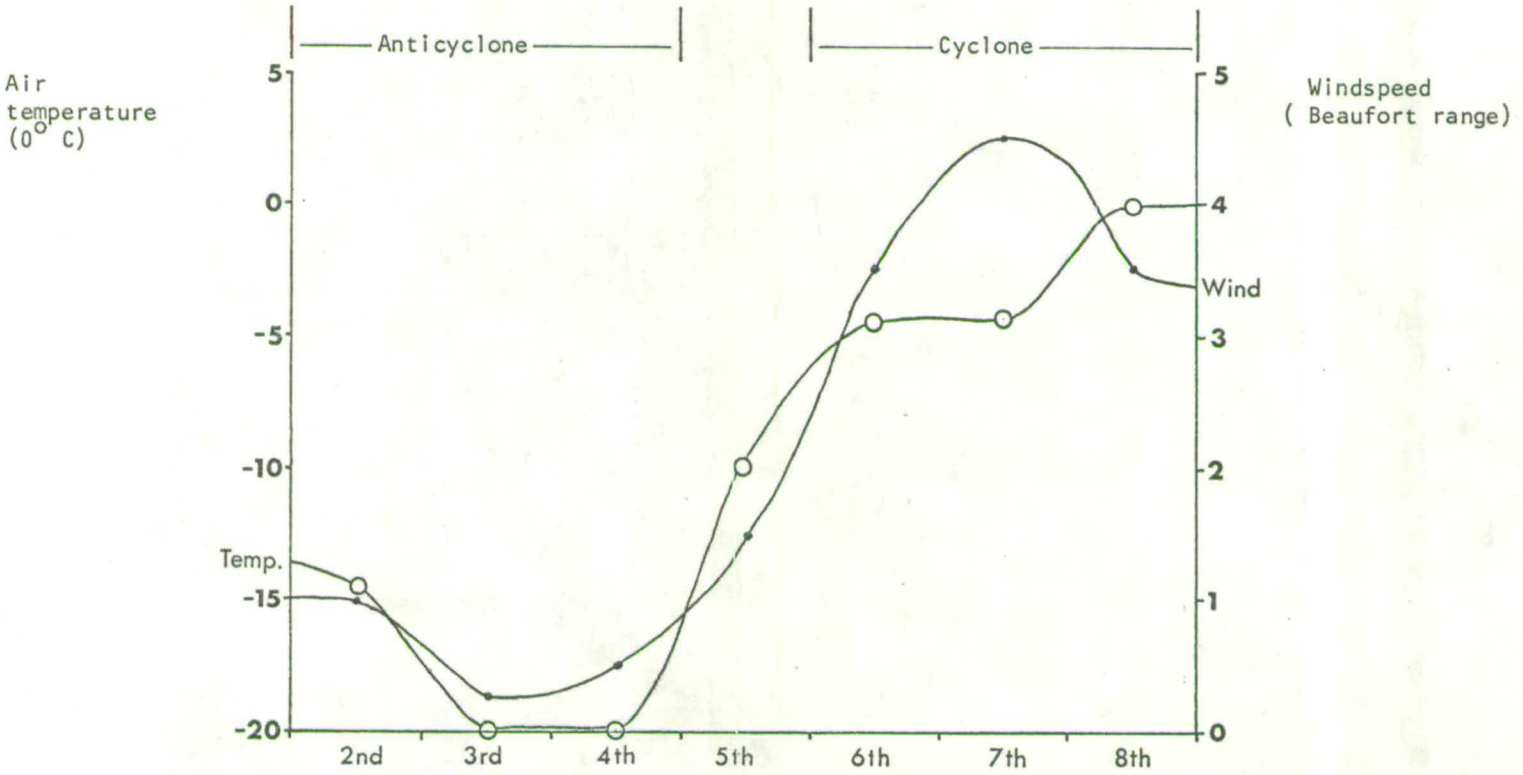
As in North Alaska, the mountain ranges of South Norway experience cyclic weather in winter. Typically a week to ten days of cold, calm and sunny weather is followed by several days of milder temperatures, snow falls, and winds. A combin-

ed increase in air temperature and wind speed is characteristic of a developing cyclone (e.g. Fig.7.4). Cyclones often result in temperatures up to and above 0°C, and strong winds which together can create ice-hard snow conditions. Such difficult conditions for grazing are frequent by late winter. For example, on Forelhogna in March, 1970, the deer were wholly restricted in their grazing possibilities to feeding on vegetation on the "bare" or thin icy patches, and from the lichens on outcropping boulders. This they did, while continuing to alternate grazing and lying periods in the normal manner.

However, activity response <u>is</u> shown to winter winds as such, independently of their effect on snow conditions. As winds build up to Beaufort 3-4 (12-28km/h) a herd grazes closer together and becomes orientated into the wind. There is also a tendency for increased movement. For example, on Hardangervidda winter groups in March, 1971, moved less than 2km daily for several days of calm anticyclonic weather (Beaufort 0-1, air -14°C to -20°C), and as winds increased to Beaufort 3-4 (air -4°C) they increased their daily movement up to 6-7km/day. Similarly on Snøhetta in November, 1969, (Beaufort 0-1, air -25°C) as winds built up to Beaufort 3 (air -10°C) two herds moved upwind in the night and changed their grazing location.

At winds of Beaufort 5 and over (30km/h+) grazing is progressively disrupted and animals clump together to stand facing into the wind (Plate 37). Some animals will then lie down with their dorsal side presented to the wind and their heads tucked /

Fig. 7.4 Example of a developing cyclone.

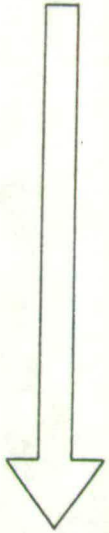


March 1971 (Hardangervidda)

tucked round into their bodies. Such groups in high winds will often be seen to start slowly trekking into the wind, then stop, and as lying builds up again individuals or the whole group might suddenly start trotting or running down wind for several hundred metres before turning to face the wind again. As a result of this behaviour groups would often split up. The combination of behaviour observed at increasing wind-speeds in winter is shown in Table 7.5. While the group is stationary standing animals are concentrated upwind while animals tend to lie behind them. The animals standing would often remain motionless for long periods and suddenly turn, walk back and lie down. Antagonism for lying spots was frequent. A group could remain lying for three hours or more under gale or blizzard conditions, during which time an occasional animal would get up to shake itself, then lie again, or stand with its head held low facing into the wind. From the responses of the twelve groups observed under strong winds on seven separate days of observation (summarised in Table 7.5), there is evidence of a direct sequence in behavioural response as wind speeds increase, and also evidence of differing behavioural strategies.

It was apparent from the observed behaviour and in particular the characteristic sudden change in activity or posture that the reindeer were experiencing some discomfort. On not every occasion were the gale-force winds whipping snow along so that the winter "wind behaviour" could not be attributed merely to physical discomfort of snow or ice particles striking the face or eyes; nor would their behaviour in standing with head low facing /

Table 7.5 Effect of increasing windspeeds on reindeer activity and behaviour at air temperatures of -10°C to 0°C.

Windspeed range	Reindeer activity	Increasing windspeed
Beaufort 3-4 12-28 km/h	Lying periods as normal. Grazing is oriented upwind. Amount of walking increases - upwind.	
Beaufort 5-7 30-60 km/h	Grazing disrupted and ceases. Group moves closer together. Short slow treks upwind. Standing with head held low facing upwind. Lying with rump or broadside to wind, head curled round into body. Bursts of running or trotting downwind, occasional leaping or bucking. Group may split up.	
Beaufort > 8 > 60 km/h	As for Beaufort 5-7 or shelter-seeking at lower elevations, woods, buildings.	

facing into the wind in any way reduce this impact. However, the range of behaviour observed was consistent with the known responses of animals subject to cold exposure. Schein and Hafez (1969) list several behavioural response types which are characteristic of domestic ungulates exposed to a cold environment - decreasing the exposed body surface, seeking warmer bodies by group clumping, minimising air movement over body surfaces, and increasing motor activities to create bodily warmth. As will be discussed, the reindeer behaviour observed under high winter winds conforms to these heat conservation and heat generation strategies.

Reindeer showed no behavioural response to cold air temperatures per se. In anticyclonic weather I observed reindeer graze and lie at still air temperatures of -25°C on Hardangervidda and -30°C on Snøhetta, without displaying any unusual behaviour. At a still air temperature of -30°C, the cooling effect on the human skin is 660 kcals/m^2/hour and this is equalled at the warmer temperature of 0°C with a light wind of only 4km/hour (Siple & Passel, 1945). At the prevailing recorded wind speeds of over 30km/hour with air temperatures from -10°C to 0°C, the cooling effect is from 1150-1450 kcals/m^2/hour (Siple & Passel, op.cit.), and the present observations suggest that it was within this human windchill range that the reindeers' insulating capacity could no longer conserve sufficient heat without a behavioural response. The thick winter pelt of reindeer apparently allows them to remain in a thermoneutral state up to this degree of windchill.

Other deer species probably have a lower threshold of tolerance to /

to windchill. The effect of wind on the insulating capacity of the winter coat of white-tailed deer has been tested: for a 60kg deer at 0°C with no wind, loss of heat from convection (air flow) is 40kcals/hour, this doubles to 80kcals/hour with a 5km/hour wind, and doubles again to 150kcals/hour with a 20km/hour wind. At wind speeds of 20km/hour and greater, heat loss from convection accounts for more than 80% of total heat loss in white-tailed deer (Moen, 1973). Similarly, a 10mph wind (16km/hour) halves the insulation capabilities of a 5cm wool fleece in hill sheep (Slee, 1967).

The various behavioural responses of reindeer to winds of 30km/hour to 70km/hour at air temperatures from 0°C to -10°C may therefore be analysed in regard to their thermoregulatory benefit to the animal (Table 7.6). Lying clearly minimises the area of exposed body surface and consequently minimises heat loss. By lying with its back to the wind the animal is presenting the thickest part of its pelt to the blast, while the legs are under the body, and the muzzle and head tucked round into the belly in a sleeping position. Similarly, polar bears at high windchill values adopt an equivalent compact lying position (Øritsland, 1970). The heat conservation benefit of a compact lying posture has been demonstrated for husky dogs, which can maintain a warmth of 32°C in the environment of their tightly curled bodies, while the prevailing air temperature is -25°C (Irving, 1972). Lying has an additional advantage in that wind speeds are least nearest the ground, especially over rough ground or vegetation, but also over snow at high wind speeds (Moen, 1973). Measurement of wind flow over /

Table 7.6 The themoregulatory effect of behaviour in strong winter winds.

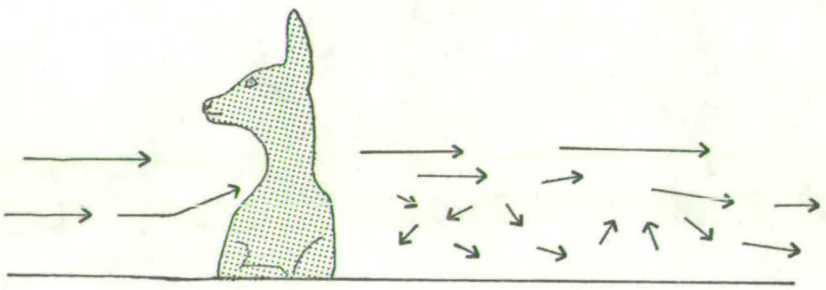
Behaviour	Thermoregulatory effect	Type of Thermoregulation
Lying, broadside to wind, head curled round.	Minimising exposed body surface by drawing extremities close to the body; presenting thickest part of coat (dorsal) to the wind; some reduction in wind velocity at ground level.	HEAT CONSERVATION
Standing, facing into wind, head held low.	Reducing conductive heat loss (to the ground); aerodynamic posture maximising air flow around body; presenting cool extremities (legs and head) to the wind.	
Shaking.	Restoring insulative properties of the coat.	
Running or trotting down-wind, leaping and bucking.	Active bursts to generate warmth; downwind running temporarily reduces windspeed.	HEAT GENERATION
Group clumping.	Wind flow broken up for animals on leeside of others; possible heat exchange between liers.	REDUCED WINDSPEED
Shelter-seeking.	Reduced windspeed in the lee of boulders, buildings, and in woods.	

over models of lying deer shows that air flows smoothly over the back of the deer then is broken up into eddies on the leeside (Fig.7.5). It is known from work on shelterbelts that the full force of the wind is not built up again on the leeside until after 30 times the height of the obstruction (Caborn, 1965). By clumping together in high winds and lying 2-3m from each other, most of the reindeer in the group are benefitting from the shelter afforded by others. Standing animals in the front of liers may further assist in breaking up the wind flow (see Fig.7.6). Where reindeer lie very close to each other, say 1m or less, there is the possibility of further reduction in heat loss through some exchange of radiant heat between animals. Baskin (1970) has similarly noted that reindeer move into a compact group in blizzard conditions of strong winds of snow, and refers to other studies in the U.S.S.R. which claim that the metabolic rate of reindeer lowers when the animals aggregate.

By standing facing into high winds reindeer appear to be adopting a rather different heat conservation strategy than when they are lying. Animals standing oriented into the wind with heads held low are receiving the full blast on their heads and legs, while the main air stream flows directly over the coat. Moen (1973) has shown that the direction in which the wind strikes the fur is important. Thus, if reindeer were to stand broadside or facing the wind, the fur's insulating capacity would be considerably reduced (Fig.7.7).

Although the legs and head are fully exposed in the standing position,/

Fig. 7.5 The disruption of airflow on the lee-side of a lying deer.



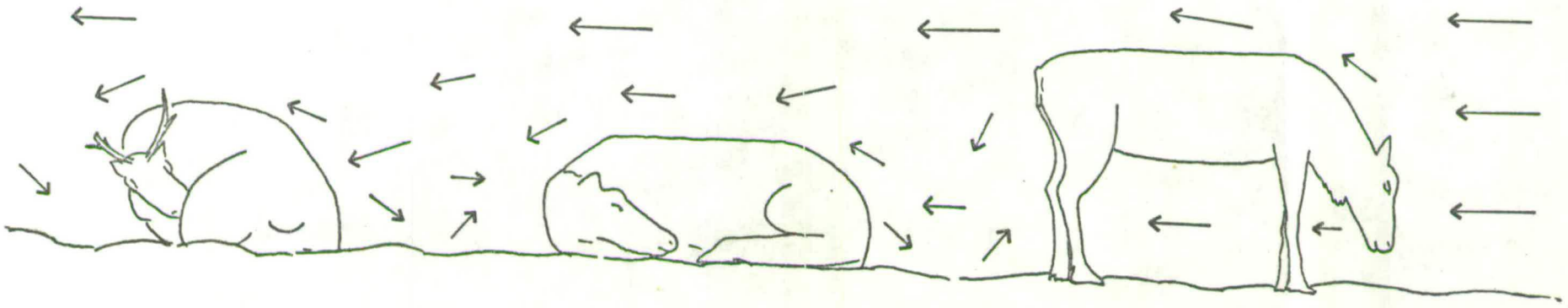
(From a photograph of airflow patterns over a model white-tailed deer; in Moen, 1973)

position, the heat loss through these organs need not be as great as deep body temperature and the relative sparseness of pelage on these extremities might suggest. Core temperature need not be maintained over all parts of the reindeer's body. Thus, it was found that at an air temperature of-31°C while reindeer maintained a rectal temperature of 38°C, the internal tissues of the feet and legs were at only 9°C, while the muzzle was 20°C, increasing up to 36°C on the forehead (Irving & Krog, 1955). The potential loss of heat from these extremities in winter is obviously less than would be the case with a uniform body temperature. This variable temperature is made physiologically possible by limiting the blood supply through constriction of the veins (vasoconstriction); also the cold venal blood is warmed by heat exchange with close arteries before it re-enters the heart (Moen, 1973). Vasoconstriction has been shown to be a main heat-saving mechanism in winter for hill sheep in Scotland (Slee, 1967).

A further possible advantage of standing as a heat conservation strategy is that, whereas liers must lose some heat directly by conduction from the underside, belly and flanks in contact with snow, standers will have minimal conductive losses by having only hoof contact with the ground. A compressed pelt loses more conductive heat than an open one, which could explain the frequency of shaking at times of high wind-chill, particularly amongst animals who have risen from lying.

An alternative to heat conservation through suitable postures, aerodynamic orientation, and group clumping at high wind speeds /

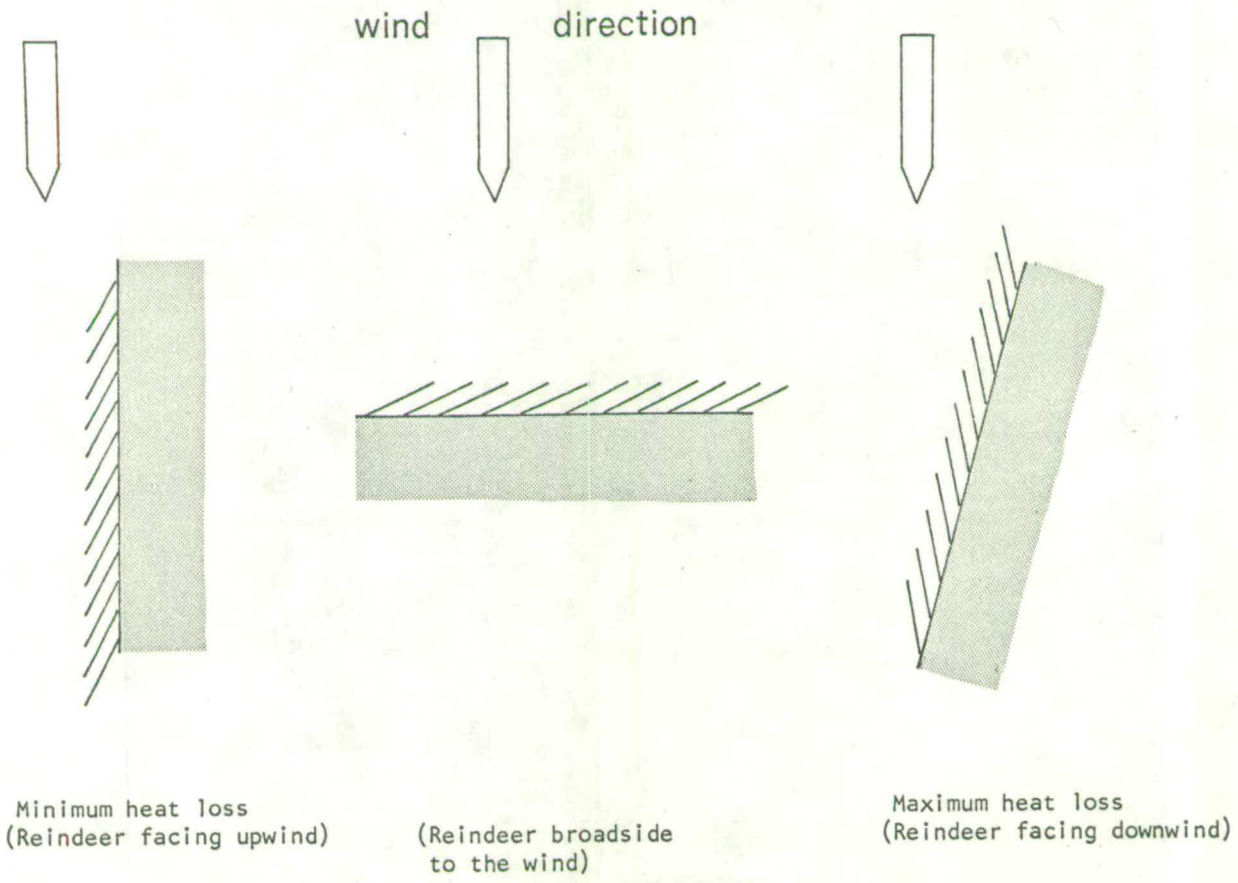
Fig. 7.6 The presumed sheltering effect obtained by standing and lying reindeer in a clumped group under strong winter winds.



speeds and low temperatures is for the animal to generate heat by muscular activity. Individual reindeer turning to run down wind, often with leaping and kicking, were apparently generating heat by indulging in activity costly in terms of energy (see Chapter 8). Irving (1972) points out that since motion diminishes the insulation of the fur, not all heat generated by muscular activity is applicable to warmth. Indeed, when they turn down-wind the reindeers' hair can be seen to be blown and ruffled by the wind. However, by running down-wind the reindeer was quite capable of matching the speed of the wind, and for these 10-20 seconds the animal might receive little or no windchill effect (Fig.7.8), as well as generating warmth which could then be conserved by turning to stand or lie. For example, one animal in a partly-standing, partly-lying herd of 275 in high winds in December was seen to get up, run quickly down-wind, then walk slowly 100 m back up wind to lie in its original bedding place, again with its head tucked round into its body.

It was not possible to determine from field study alone the extent to which these behavioural responses for maintaining heat production might allow little or no increase in the reindeers' metabolic rate. For white-tailed deer, Moen (op. cit.) postulates a sequence of energy-conserving responses with increasing cooling effect; from vasoconstriction, piloerection of the fur, both vasoconstriction and piloerection, lying, lying with the head alongside the body, and finally at -40°C with a 22km/hour wind several or all of these responses could be employed and the deer would still be losing heat at less than /

Fig. 7.7 The way in which the lie of coat hairs relative to wind direction influences the degree of insulation of a reindeer's pelt.

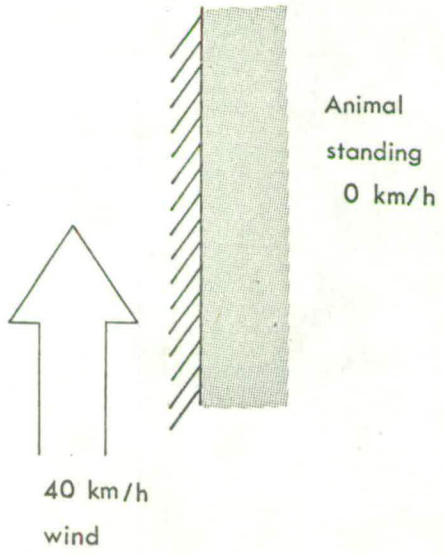


than twice their basic metabolic rate. Without these physiological and behavioural responses, the deer would lose heat at 6 x B.M.R.. Clearly, deer have a considerable potential for withstanding cold conditions if they are well-insulated, have suitable physiological and behavioural responses, and have a sufficient source of energy for heat production.

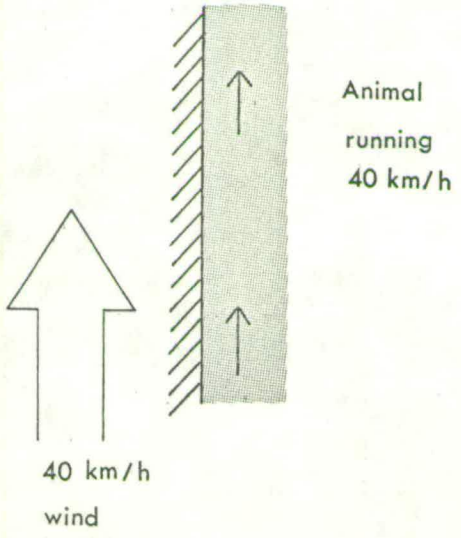
Caribou are thought to reach a critical temperature at below $-40^{\circ}C$ without a wind, and at temperatures lower than this body temperature is not maintained, and/or B.M.R. increases (R.G. White, pers. comm.). In Rangifer the possible physiological responses, such as vasoconstriction and piloerection, have not so far been studied. For hill sheep fully acclimatised to their environment the critical temperature depends on the quality of their nutrition, their sex, and if ewes, whether pregnant, lactating or yeld (Slee, 1967). Red deer stags on Scottish mountains show indications of being more sensitive to cold exposure than the female hinds. The stags tend to be located in the more sheltered winter habitats, and under blizzard conditions will lie in shrubby heather for long periods (A. Jackes, pers. comm.). It is thought that the stags spend less energy, both metabolically and in activity in resisting cold, and that this behaviour may be a factor in their concentration on lower ground in the winter, segregated from the hind groups (A. Jackes, pers. comm.). Red deer of both sexes actively seek out lee slopes, dry ground or long vegetation in harsh winter weather (Staines, 1970).

No active movement to lee slopes was seen in reindeer, nor even /

Fig. 7.8 The behaviour of reindeer in running downwind in a strong winter wind thereby reducing heat loss through the pelt.



Animal facing downwind -
poor insulation in strong wind



Animal running downwind -
effective windspeed (and heat loss) reduced to nil

even to the birchwoods when they lay nearby, which suggests that the reindeers' presumed physiological mechanisms, and their observed behavioural responses both as individuals and as a group, were adequate in preserving body heat under the prevailing windchill conditions (-10°C to 0°C at 30km/h to 60km/h). The range of recorded wind speeds and air temperatures which provoked "wind" behaviour by a group is compared with times of normal winter behaviour, and a threshold for this type of behaviour suggested in Figure 7.9. There are indications that even greater wind speeds of Beaufort 8-9 (60km/h to 90km/h) may cause reindeer to actively seek shelter. For example, in a blizzard of Beaufort 8 in December, 1970, reindeer were reported to have been seen in the birch zone around Solheimstul, Hardangervidda, and on the following day faecal pellets and lying beds in the snow were found in the shelter of farm buildings in the birch zone. On Forelhogna in March, 1970, pellets revealed that in Beaufort 7 winds reindeer had moved around and even entered a deserted cabin, through a doorway passage of 0.7m x 1.6m. The following day in Beaufort 5 winds, two males were observed lying in the lee of a large boulder, with frequent competition from other males in the group for this favoured lying site. Henshaw (1968b) noted that a lone calf in winter, separated from the herd, obtained protection during times of severe windchill by lying tightly curled in one of its own feeding craters. It has been reported from both Canada and Siberia that at a temperature of -40°C and some wind, caribou do not move out into the open areas for feeding as normal, but remain within the forest (Kelsall, 1968; Zhigunov, 1968). Without shelter, reindeer /

Fig. 7.9 The range of windspeeds and air temperatures at which reindeer were observed to react with heat conservation and heat generation behaviour in winter.

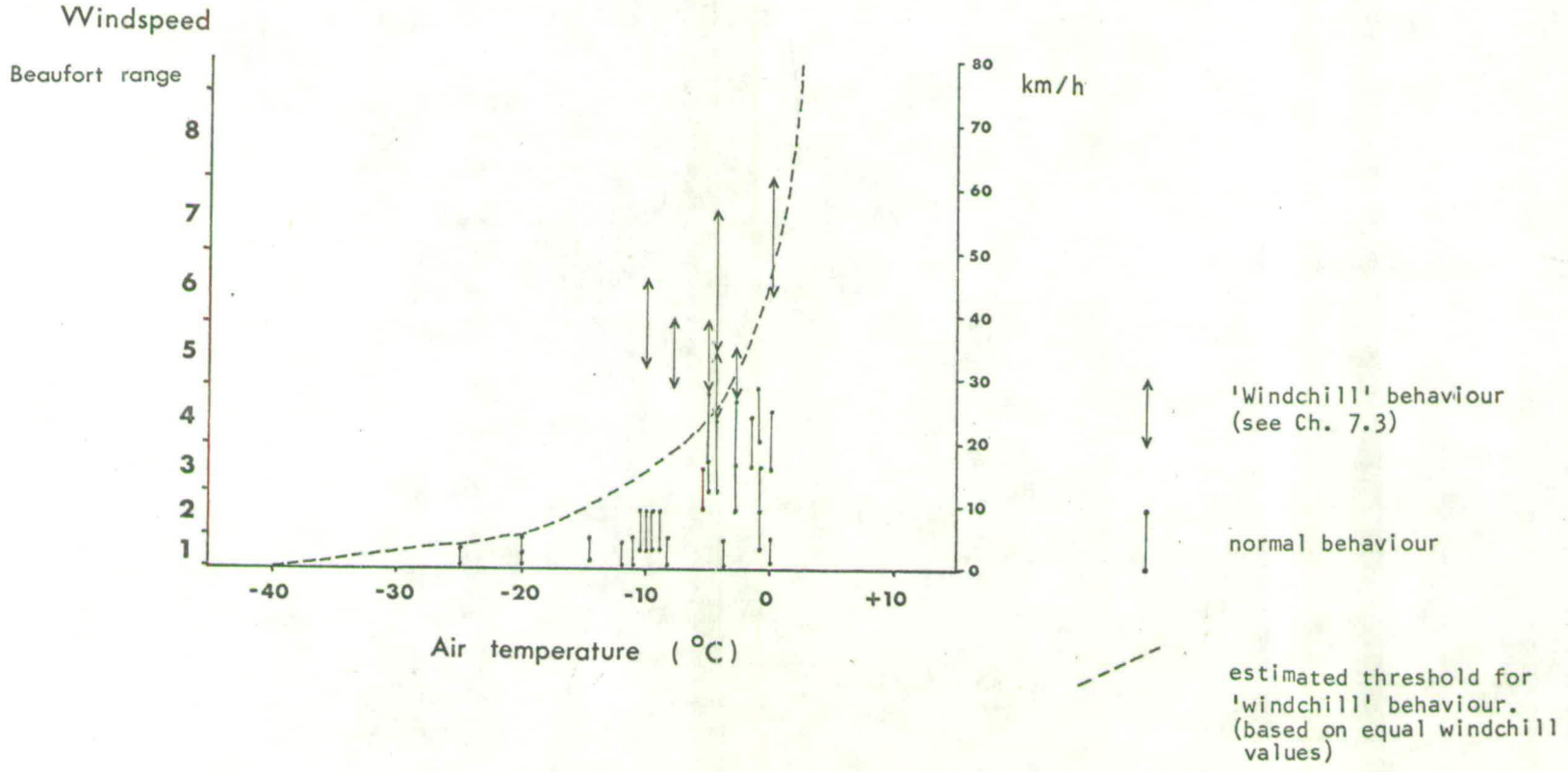
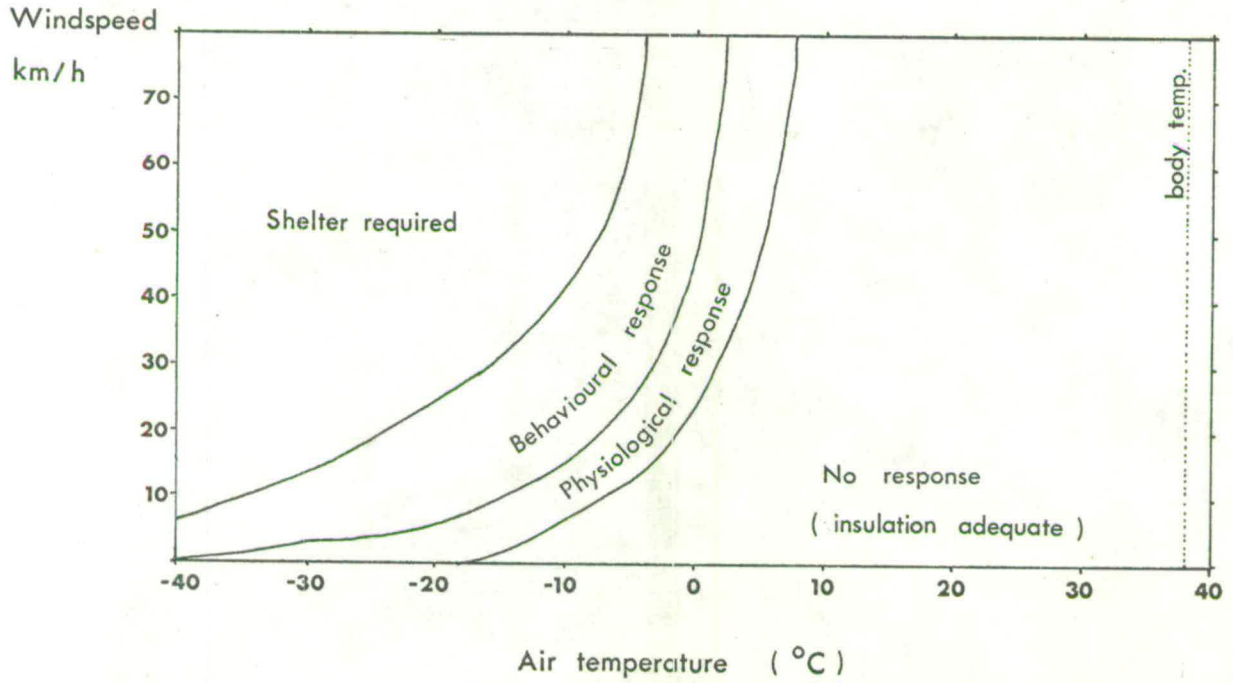


Fig. 7.10 Estimated thresholds of windspeeds and air temperatures for physiological response, behavioural response, and sheltering response of reindeer in winter.



reindeer will crowd together in severe storms and try to heat themselves by running, so that if the storm is prolonged, they run without food and can freeze to death (Zhigunov, op.cit.)

It is probable that the range of behaviour under strong winds is the same for caribou. De Vos (1960) observed that for barren-ground caribou in Canada in the calving season, winds over 25 mph (40 km/h) induced lying in the group with heads pointing downwind, with two standing animals in a group facing into the wind. In Alaska, feeding ceased as winds rose above 40 km/h ($-2^{\circ}C$ to $-15^{\circ}C$) and with continuing high winds to 64 km/h, caribou lay for long periods, usually broadside to the wind (Henshaw, 1968a).

From the observed behavioural responses of reindeer to cold exposure I would postulate that there is a threshold of combined air temperature and wind speed below which non-behavioural response is adequate (e.g. by increased metabolic rate, vasoconstriction and piloerection), and a zone beyond behavioural response where shelter is required to avoid excessive heat loss (Fig.7.10). Physiological studies and further field observations are required to determine precisely where these thresholds lie for Rangifer in their natural winter environments, and the extent to which sex, age, body condition, and nutritional regimes influence their observed tolerance to cold.

7.4. MIGRATION TO CALVING GROUNDS

> "What we have learned about orientation, the physiology of the migratory impulse and the fundamental causes of migration /

migration is still like a few guide posts planted in an almost virgin forest."

Jean Dorst, 1962.

The regular migrations of North American caribou populations from their wintering ranges to their calving grounds have been documented by Northern travellers since the 18th century, yet the factors governing their migration and orientation, and the benefits derived from use of these specific areas for calving are still unknown. In the U.S.S.R. too, wild reindeer annually migrate hundreds of miles from the taiga to selected calving sites on the Northern tundra.

On Hardangervidda in the late winter months of March and April reindeer groups and herds start to leave the easterly wintering grounds and shift their range progressively west for 60-100km so that by the start of calving at the end of May they are concentrated in a specific calving area in the western uplands (see Map, Fig.11, p.37, App.3). While this is a modest shift of range compared with the spectacular migrations of barren-ground caribou in Canada, where the distance covered may be over 1000km, and a continuously trekking herd may itself by 300km in length (Kelsall, 1968), the annual predictability of the movement and the purposeful behaviour of the reindeer at this time justifies its consideration as a migration. The return to the wintering areas in autumn on the other hand is quite indistinct, as by late summer and rut the animals are typically already on the borders of their usual wintering areas.

In /

In mid-April 1970 herds were located in the Krossvassh'd area midway between the wintering range and the calving grounds (Map, Fig.2.4). Reindeer were spread out over the available grazing on exposed summits and ridges alternating grazing and lying periods as they had done earlier in the winter. Yet over ten days it was observed that at least 1300 deer, some 11% of the Hardangervidda population at this time, filtered south and west through the Krossvassh'd area. Movement did not take up a major part of the animals' activity time, but yet was highly characteristic. Animals crossing the snow between adjacent grazing areas would walk slowly in single file in the tracks of the animals which had gone before. Where a whole group or herd was on the move, they would be strung out in long slowly trekking columns with the column leader tending to follow the tracks of animals which had preceeded them. Such movement was most often seen during the active period around midday, or following a disturbance. When alarmed by ravens, eagle, or human presence, the deer would typically trot together from their dispersed grazing sites, then irrespective of the direction from which the alarming stimulus had come, would continue to trek in long lines in a south or westerly direction for several kilometres.

It is known that pregnant females tend to be at the forefront of spring migration, yeld females and yearlings are concentrated further back, while males lag even further behind (Kelsall, 1968; Espmark, 1970). At Krossvassh'd in April 1970, sex and age counts of the groups passing through showed that yearlings (calves of ten months) were disproportionately numerous, while males /

males were scarce in the first few days but became increasingly abundant in those groups which moved into the area on later days (see Table 7.7). From the composition of the total 1320 deer observed it is likely that the mid to end section of the population's migration was being observed.

Males could often be seen to graze or lie out of synchrony with a mixed group, which occasionally resulted in them being left behind. For example, on 18th April, of the 20 animals which remained lying and grazing after a herd of 115 had moved on, 13 were males, 10 of them unantlered and 3 young antlered males. One hour later all 7 females and yearlings and one of the males walked slowly towards the herd a few kilometres off leaving behind a segregated group of 12 males.

Observations on the winter range in the following year showed that already by the first week of March some females were displaying the migratory urge (Photo 38). Females were usually the first to move between adjacent grazing areas and as others would follow in their tracks they would become the leaders of long columns. However, these migratory columns would not persist for long. For example, on 4th March, 1971, animals from a herd of 400 started to trek out from the grazing area and after 50m the leading animals stopped and stood; and as animals continued to move up from behind and crowd round many started lying. One of the females still walking in line moved around this stationary group and continued trekking, followed by only 9 other animals, before it too stopped after 200m. These 9 followers then backtracked to the stationary group, and /

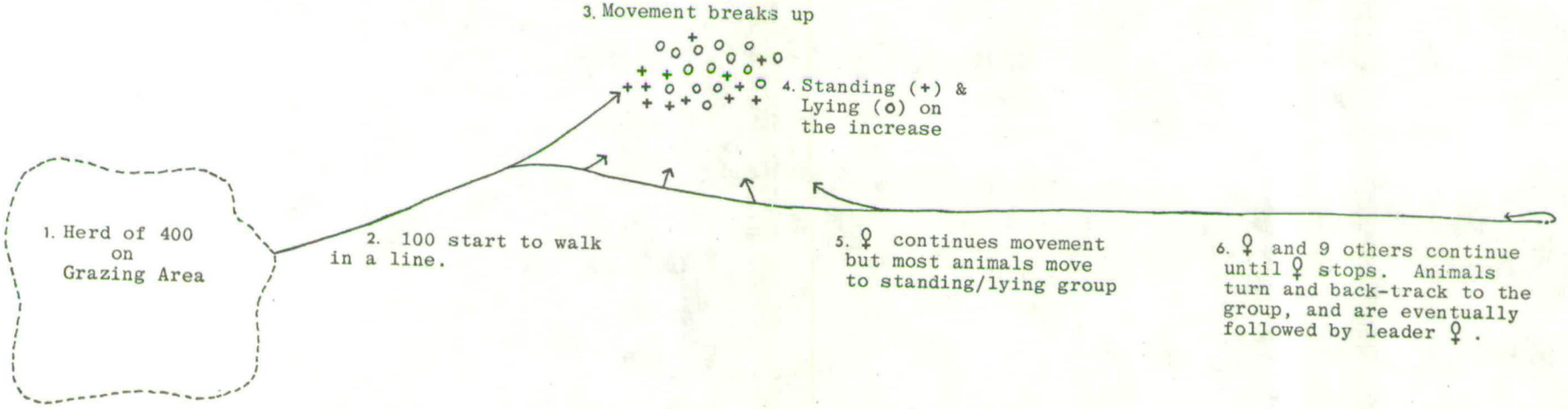
Table 7.7 The composition of groups on migration through the Krossvassh'd area of Hardangervidda, in mid-April, 1970.

April, 1970	No. of reindeer (to nearest 10)	Classified counts Calf ♀ ♂	Calf ratio Calf : ♀	Sex ratio ♂ : ♀
10th, 11th,	300			
12th, 13th, 14th,	530	131 201 8	65 : 100	4 : 100
15th, 16th, 17th,	260	92 92 22	100 : 100	24 : 100
18th, 19th.	230	38 58 26	66 : 100	45 : 100
Total deer moving through area 10th - 19th April	1320			
Approx. proportion of total population	11%			

and were eventually followed by their "leader" (Fig.7.11). From this and other examples it was clear that some of the females were displaying a definite urge to migrate west, but at this time (early March) most of the herd had not yet a sufficient disposition for this movement even to become passive followers. Kelsall (1968) has similarly noted that general drifts along migration routes may be observed as early as February amongst some wintering caribou groups.

The continued concentration on grazing and lying periods on the peak migratory period of March and April, and the lack of increase in time spent on moving compared with early winter activity (Thomson, 1973), contrasts with the situation in migratory caribou in Canada, where animals are said to be almost continuously on the move during migration. This difference, however, is not surprising considering the relatively short distance which the Hardangervidda reindeer have to travel. The period in which the migratory behaviour is most evident spans two months, from mid-March to mid-May, with calving at the end of May. To cover the 60-100km distance requires only an overall westward rate of travel of 0.07km/h. Allowing only 10% time for moving activities (the common winter average - Thomson, 1973) a modest walking speed of only 0.7km/h is required, or a distance of 1.7km/day in a westerly direction. On some days in March and April the herd did not even move this far, but on other days moved 5-7km/day without loss of grazing time. (If they were to move 5-7km/day westward, they could cover the required 100km within a two week period.) Adverse snow and weather conditions could hardly prevent the Hardangervidda /

Fig. 7.11 Migratory tendencies within a herd of 400 reindeer on eastern Hardangervidda on 4th March, 1971.



Hardangervidda reindeer from reaching their calving area as is thought to occur in caribou occasionally (Kelsall, 1968). The segregation of classes at calving time, in particular the scarcity of males, can therefore only be explained by the males lagging behind and electing not to move into the calving area.

On the other mountain ranges in South Norway, late winter behaviour has not been studied, but migration as such is hardly possible, if only because of the proximity of the winter areas to the calving area on these smaller ranges. For example, on North Ottadalen I observed calving in the uplands and valleys around Asbjørndalen in 1970 and 1971, on average 20km from where they were rutting in the previous seasons. Some caribou populations in Newfoundland are known not to undertake migration but to calf on the winter areas (Bergerud, 1974b).

The factors which stimulate Rangifer to migrate, their undoubted orientation and homing abilities to arrive at a regular calving area, or the extent to which learning or hereditary factors operate, have been the subject of no systematic investigation so far. This is also the case with the few other land mammals which display extensive seasonal movements. In migratory birds, although the physiological basis is not yet fully explained, it has been shown that the timing of the urge to migrate is as fundamentally dependent on the endocrine system, in particular the effect of changing day-length on the pituitary gland, as is the breeding and moult cycles (Dorst, 1962; Ricard, 1969). /

1969). It seems likely that Rangifer migration is also controlled by such a fundamental internal mechanism.

However, it has been argued that since the precise time of onset of Rangifer migration can vary from year to year, there must be an environmental "trigger" which sets off migration, but despite field measurements, factors such as snow characteristics or air temperature cannot be implicated (Pruitt, 1959; Kelsall, 1968; Bergerud, 1974b). It is known that pregnant females display the greatest urge to migrate and are in the van of migration (de Vos, 1960; Skoog, 1968; Bergerud, 1974b; this study). This suggests a possible physiological link between migration and hormonal changes taking place prior to parturition.

Explanations as to how the animals can orient themselves en route and move into the specific calving area from various directions have usually been sought on a minimalist basis; i.e. to find one environmental factor such as snow, topography or vegetation which might account for it (Kelsall, 1968). Since experiments on various species of migratory birds have indicated extraordinary orientation and homing capabilities in their being able to relate to the changing position of the sun, stars, prevailing wind direction, visual topography, and even the earth's magnetic field, and then home-in to a traditional nesting area, it seems dangerous to assume that reindeer and caribou migration is a much simpler affair wholly related to some variable characteristic of their habitat.

Cases /

Cases where reindeer or caribou have been transplanted indicate that uninterrupted learning of the migratory route may be necessary for successful migration, and also that young animals without experienced "leader" animals in the herd will not migrate (Espmark, 1970; Bergerud, 1974b). The study of the neuro-hormonal basis of migratory behaviour, and for pregnant females in particular, and of their innate or learned abilities to orient towards and thus lead others to a traditional calving area, is now likely to prove a more fruitful lead towards understanding the proximate causes of Rangifer migration in spring, than further measurement of habitat characteristics alone.

The ultimate cause or causes (survival valve) of migration in the species are presumably bound up with their use of a restricted and traditional calving area, considered in the following chapter.

7.5. CALVING - A TIME AND PLACE

It is well established that reindeer and caribou return each year to traditional calving grounds (Lent, 1966; Kelsall, 1968; Skoog, 1968; Skjenneberg & Slagsvold, 1968; Baskin, 1970; et. al.). Kelsall (op. cit.) notes that certain calving grounds in Canada have been used regularly for at least twenty years since observation began, while Lent (op. cit.) presents historical evidence that calving of the Arctic Herd of Alaska has been in the same area for at least a century.

Up /

Up to 1970 little was known of the timing or location of calving on Hardangervidda. In that year Skogland and I observed calving in the last week of May in a west-central area of Hardangervidda some 80km from the winter range (Gaare, Skogland & Thomson, 1970), as did Kjos-Hanssen, (1973b). The same area was used again in 1971 (Thomson, 1973; Skogland, 1974; Kjos-Hanssen, op.cit.), 1972 and 1973 (Skogland, op. cit.). Air reconnaissance flights by Direktoratet for Vilt og Ferskvannsfiske just before calving in 1971 found no concentration of female reindeer outside this area. The main calving grounds lie within the area between Viersla-Grøndalen-Hårteigen-Hadlaskard (Map, Fig.2.4), covering some 260km^2. The calving terrain is unremarkable, mainly comprising exposed undulating upland at 1300-1500m dissected by river valleys at 1100-1200m. Calving was observed at 1200-1400m on flat and gently sloping rocky knolls, which were free of snow. In both 1970 and 1971 the amount of snow-free ground increased from some 20% to over 50% in the week of calving (Plate 39).

Within these calving grounds the reindeer were dispersed widely as individuals, and in scattered small groups, often splitting and mingling with other groups and wandering in various directions. These local movements averaged 4-5km per day. In 1970, 800 adult deer were observed around Olavsdalen in an area of approximately 40km^2, equivalent to a density of 20 animals per km^2; and in 1971, 1700 deer were observed within the calving area at a density of around 13 animals per km^2, excluding calves. Because of the broken boulder-strewn nature of the terrain contrasting with bright patches of snow it was easy /

easy to overlook stationary animals such as single females and their calves. The reddish-brown of the calf's fur in particular camouflages perfectly with the autumn colours of the old dry vegetation being revealed as the snow recedes. The animals' use of such broken snow-flecked terrain and their extreme dispersion over it may have evolved to make detection by predators more difficult.

In both 1970 and 1971 I observed the first calves born on Hardangervidda on 23rd May, with a rapid progression so that by the end of the month at least 80% of all calves had been born. The progress of calving for both years from day to day was guaged by comparing the proportion of calves observed to productive females observed each day (Fig.3.4). Independent observation by Kjos-Hanssen (1973b) shows the same short sharp calving period, 22nd-28th May in both 1970 and 1971. In 1972 the calving season started approximately ten days earlier, which corresponded with an earlier rutting season in 1971 (T. Skogland, pers. comm.).

From the dates of calving and preceding rutting seasons I observed on Hardangervidda and North Ottadalen from 1969 to 1971, it can be calculated that for Norwegian wild reindeer the duration of pregnancy lies between 219 and 235 days, with a mean of 227 days (Table 7.8). This corresponds exactly with reports of the average gestation period for Rangifer in other areas. For example, Schmitt (1936) reports 227 days for Russian domestic reindeer, and calculating from the peak times for rutting and calving for six different wild and domestic populations in the U.S.S.R. (in Baskin, 1970), the mean is 228 days. /

Table 7.8 Gestation period of Norwegian wild reindeer estimated from observed peaks of rutting and calving times.

Population	Peak Rut	Peak Calving	Gestation Period (days) Range	Mean
North Ottadalen	17-24 Sept, 1969	3-10 May, 1970	221-235	228
North Ottadalen	20-27 Sept, 1970	4-11 May, 1971	219-233	226
Hardangervidda	No obs.	23-30 May, 1970	-	-
Hardangervidda	9-16 Oct, 1970	23-30 May, 1970	219-233	226
Mean			219-235	227

Comparisons			
Russian domestic reindeer	Schmitt (1936)		227
Rangifer generally	Jacobi (1931)	231-242	
Swedish semi-domestic reindeer	Steen (1968)		225
Russian domestic & wild	Baskin (1970)	192-242	
	Baskin (1970) (average of dates from 6 areas)		228
Norwegian semi-domestic reindeer	Skjenneberg & Slagsvold (1968)	192-246	
Taimyr wild reindeer	Michurin (1967)	7.5 months i.e.	227

days. For Swedish semi-domestic reindeer Steen (1968) gives 225 days, and for semi-domestic reindeer in North Norway and wild reindeer on Taimyr, 7½ months (i.e. 227 days) is taken to be the mean (Skjenneberg & Slagsvold, 1968; Michurin, 1967). The gestation period also averages 227 days for caribou (McEwan, in McEwan and Whitehead, 1972; Bergerud, 1961, in Dauphiné & McClure, 1974). Despite the apparent consistency in this figure of 227 days, pregnancy can vary in duration from a range of 192 to 242 days (Baskin, 1970), or from 192 to 246 days (Skjenneberg & Slagsvold, 1968).

There are some indications that undernutrition may produce long gestation periods (McEwan & Whitehead, 1972). However, this range of 50 days in average gestation period may allow latitude for the females in any one population, which were conceived on different dates in Autumn, to synchronise their date of calving. For example, weather conditions and snow cover can apparently influence the precise day of calving. Kelsall (1968) notes that in days of blizzards or snow storms few caribou females will calve. In the 1973 calving season on Hardangervidda single calves were being born around mid-May in valleys at 1100-1200m, until the onset of snow storms brought a return to winter conditions, and a cessation of further calving until the last week in May (T. Skogland, pers. comm.). Baskin (1970) claims that the longer that the snow lies on the calving ground, then the later are the calving dates, and conversely calving is earlier in those areas with less snow. There is suggestive evidence for this supposition from Hardangervidda in 1970, when Kjos-Hanssen (1973b) found that females /

females at 1400m altitude started calving three days later than those in the milder 1200m zone with less snow, so that by 26th May, whereas 30% of pregnant females had calved in the 1200m zone, only 4.5% of those in the 1400m zone had done so.

Despite this possible plasticity of a few days in calving date, the main synchrony of the calving period still appears tied to the synchrony of conception dates at rutting time. For domestic reindeer in Russia, Baskin (1970) detects peaks in calving corresponding to the oestrus cycles of females in the rut. Females not sired in the 24-48 hour period of oestrus come into oestrus again at 10-12 day or 24 day intervals until conception does occur (McEwan & Whitehead, 1972; Bergerud, 1975). Occasional late conceptions may then result in calves being born well into summer. One-to two-week old calves have occasionally been observed on Hardangervidda in July and August (this study; Skogland, pers. comm.; and Kjos-Hanssen, 1974), and as late as September on other ranges (Holthe, 1975). Late calves are at an obvious disadvantage in coping with the herds' long ranging post-calving movements, prolonged harrassment from flies, and above all a shorter growing season in which to develop their body size and energy reserves. As a result, it is likely that they are the first animals to succumb to predation and severe weather or grazing conditions in their first winter.

The optimum birth period is likely to have evolved as a balance between allowing the earliest possible utilisation of the new plant /

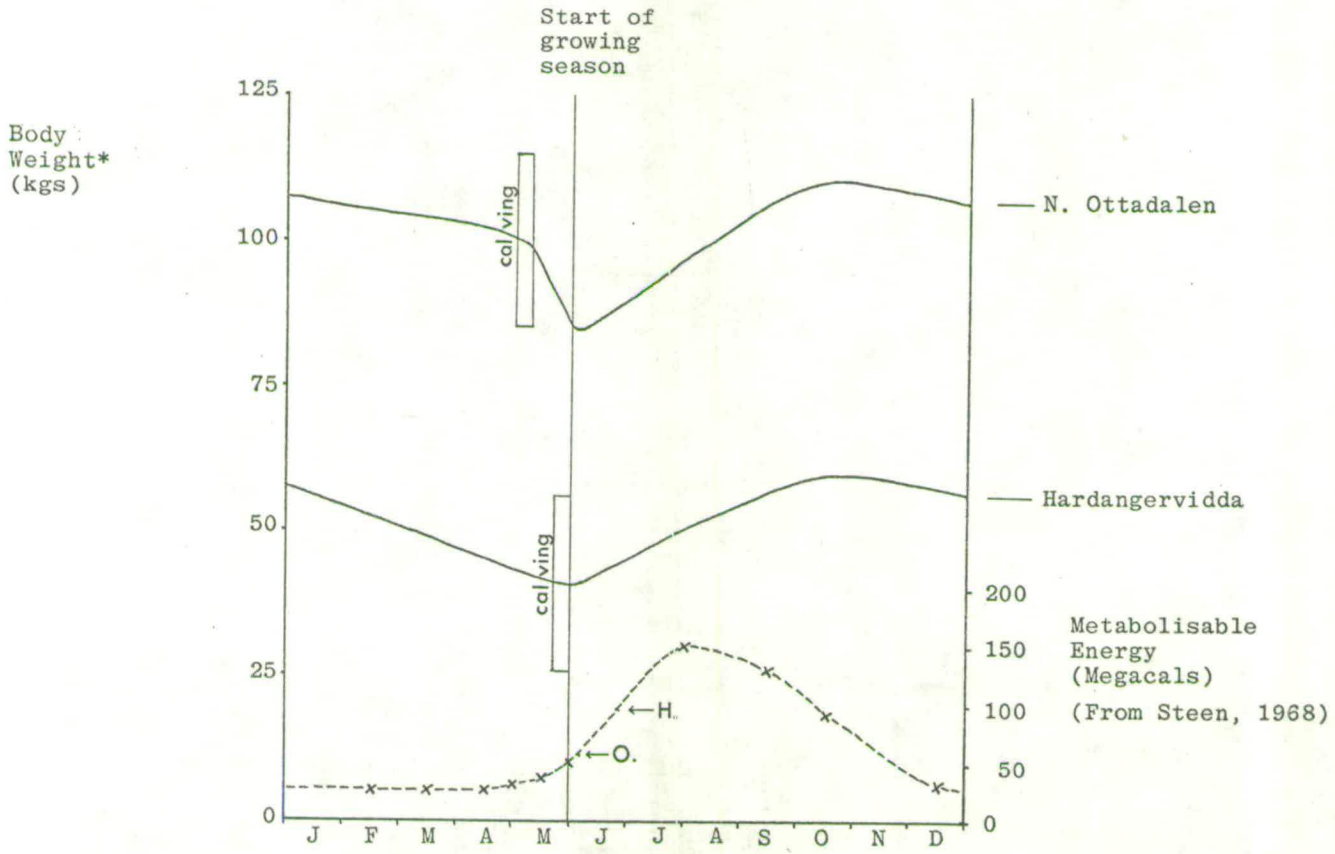
plant growth in spring but not so early that calves' survival is consistently jeopardised by poor grazing conditions and bad weather in late winter. When calving does coincide with cold and windy weather calf mortality may be considerable as young calves succumb to prolonged "human" windchill values of over 1100kcals/m^2/h, especially if the fur is wet (Kelsall, 1968). The concentration of calving for wild reindeer and caribou over a 7-10 day period may also have been influenced by predation. It is known that losses of caribou calves to wolves are less when births are highly concentrated, as wolves are confronted with a glut of vulnerable young for the shortest possible period (Dauphiné & McClure, 1974). Calves born earlier or later will tend to be selected against, as is the case with wildebeeste (Estes, 1966) where hyaena predation acts to maintain a sharp peak in calving. The wolf ceased to be a major predator on Hardangervidda 50 years ago, but since that time there has been no indication of any trend towards an extended calving period.

Considerable differences in the dates of calving between populations have been noted for caribou (Lent, 1966; Dauphiné & McClure, 1974), for domestic reindeer, and between wild and domestic populations (Baskin, 1970). These have been attributed to genetic differences dependent upon differences in latitude and in the start of the growing season (Lent, Hemming, in Holthe, 1975). However, dates of calving seasons between wild reindeer populations in south Norway also vary widely, even although latitude and times of growing season are similar. For example, the peak of calving in North Ottadalen (62°N) I observed /

observed between 4th and 11th May in 1970 and 1971, some three weeks earlier than for the Hardangervidda population (60^{o}N) in the same years (Table 7.8). Independent observations by Holthe (1975) show a similar consistently early calving season on North Ottadalen, one week later on South Ottadalen, and three weeks later on the adjacent Snøhetta and Rondane ranges. These differences he considers in relation to possible genetic differences, variation in physical condition, maturity of the males, and human disturbance from hunting, but without implicating any factor as the principal cause (Holthe, op. cit.). However, the interplay between nutritional quality of different ranges and physical condition of females may provide the key.

There is an obvious quality difference between the ranges in that North Ottadalen has a visibly rich, little-utilised pasture with a lichen biomass of not less than 800g/m^2, compared with a lichen biomass of 200-400g/m^2 on Hardangervidda (Gaare, Thomson & Kjos-Hanssen, 1975), and this is reflected in the fact that the Ottadalen animals are generally in prime condition with considerable fat reserves even at the start of calving (visual observation, & Reimers, unpubl. data). In relation to the start of the new plant growth in late May/beginning June the timing of calving appears to operate under different "strategies" in the two populations (Fig.7.12). On Hardangervidda the females are in poor condition by late winter (Reimers, unpubl. data), but within days of calving they can select the highly nutritious, newly-emerging plants to meet the energy demands of milk production, and to begin to restore body condition. On North Ottadalen, by contrast, the winter pasture maintains /

Fig. 7.12 The relationship hypothesised between the times of calving, the plant growing season, and seasonal changes in body weight for female reindeer on Hardangervidda and North Ottadalen.



*Estimated body weights and approximate trends only (E. Reimers, pers. comm.).

O. 1-month old calf on N. Ottadalen.
H. 1-month old calf on Hardangervidda.

maintains females in good condition and it is not until after giving birth to their calves in early May that they lose body weight rapidly as their fat reserves are used for milk production (Reimers, unpubl. data). Some three to four weeks after calving the growing season on North Ottadalen starts, and by this time the calves are at an age where vegetation intake is starting to play an important role in their development (R.G. White, pers. comm.). The North Ottadalen calves thus have a longer season than the Hardangervidda calves in which to grow and mature (Fig.7.12). Many female calves on North Ottadalen mature sufficiently to come into oestrus at the age of six months, be conceived, and have calves of their own the following year, which does not occur on Hardangervidda (Reimers, unpubl. data). If the earlier rut on North Ottadalen can be explained by females in good condition coming into oestrus earlier, as suggested by Baskin (1970), then the "strategy" is at least partly self-perpetuating. However, there is evidence that the later rut on Hardangervidda is at least partly influenced by the hunting season which immediately precedes it (T. Skogland, pers. comm.).

Apart from the probable adaptive significance in the concentration of calving within one area, and its precise timing, the calving area itself might be thought to have particular characteristics of survival value. However, descriptions of various calving grounds for Rangifer populations suggest few general principles. Kelsall (1968) notes that caribou calving grounds are usually on rugged poorly-vegetated windswept terrain, at relatively high elevations in areas where snow is retained for longer than in lower adjacent areas. It is suggested that there /

there may be an advantage in seeking such areas since it is known that wolves avoid areas of wet thawing snow as much as possible (Kelsall, op. cit.). Paradoxically, calving grounds tend to be in the least hospitable portions of the total range and subject to harsh climatic conditions which can result in significant calf mortality. Another feature of calving grounds, noted by Bergerud (1974b) for Canada and Newfoundland is that they tend to be centrally located and are thus ideally suited as centres from which animals can subsequently radiate out across the summer range. Such descriptions apply equally to the Hardangervidda calving area; much of it is on relatively high windswept uplands where snow cover lies longest in spring, and it is centrally located in easy reach of the summer range. Skogland (1973) has suggested that for the Hardangervidda calving area the gradient between high alpine areas with late-lying snow and low alpine valley areas lying in rain shadow represents an optimal calving area. Unless severe weather is prevalent, in which case lower ground will be used for calving, females will tend to give birth on the exposed snow-flecked terrain at high elevations, with subsequently only a short distance to move to the lower lying areas to graze on tracts of vegetation such as Eriophorum spp. and Betula nana, being revealed as the snow recedes, and the emergent new growth of Carex bigelowii, Salix herbaceae and others (Skogland, 1973; 1974).

7.6. POST-CALVING AGGREGATION AND MOVEMENT

"No man knows the ways of the wind and the caribou."

A Chipewyan Indian saying.

By /

By the end of June, one month after the calving season, large massed herds of females, calves and males have formed which move over the terrain, grazing as they go. This profound change in group size, activity and cohesion from the dispersed segregated groups of calving time, is quantified in Table 7.9. Herds tend to reach their annual maximum size in July from an annual minimum in the calving season (re. Fig.7.1). An exception to this was a herd of approximately 10,000 (at least 80% of the population) observed on Central Hardangervidda on 4th August, 1970. By late July/early August the large aggregations are dispersing, although throughout summer animals may be brought temporarily together again into large herds because of severe fly harassment. However, the long-ranging massed movements of early summer arise independently of insect harassment.

The July herds of thousands can move rapidly over mountainous terrain, grazing as they go, and as the proportion of grazing/walking/trotting changes for individuals and sub-groups, the amoebic form of the herd changes in shape, direction and speed (Fig.6, p.21, app.2). Over a day a herd may cover 15-20km and up to 30km, and in the evening for the few hours of darkness they will tend to become stationary, usually in a flatter low-lying valley where they concentrate on lying and grazing (Fig.8, p.25, App.2).

Where there is a wind this summer movement is usually directed into it so that even small changes in the direction of a breeze results in herd adjustments. Wildhagen (1948) described the movements of summer herds on Hardangervidda under a north-west wind /

Table 7.9 Changes in the parameters of social structure from calving to early summer for the Hardangervidda population.

Social Parameter	Calving (end May)	Early Summer (July)
GROUP SIZE - Median	12	704
- Maximum	195	4000
GROUP SOCIALITY - Individual Distance	2-10m	1-2m
- Cohesion	weak: groups split.	strong: groups combine.
GROUP COMPOSITION - Male Proportion	1-10%	10-20%
GROUP ACTIVITY - Time spent grazing	54%	36%
- Time spent moving	5%	30%
- Av. distance moved per 24 hours.	4-5km (1-2km for nursery groups)	15-20km (up to 30km)

wind from southern parts through Skyttarfossen, over Dimmedalsfjellene, by Nordmannslaagen to the hills north-west of there (map, Fig.2.4), which precisely describes their movement in early July, 1971 (Fig.9, p.31, App.3). If the wind blows from one direction for several days the deer may then approach the limits of their range in which case the wind-oriented movement ceases, and the herd moves laterally to cover adjacent areas for grazing. The adaptive significance of moving upwind is not known - speculative suggestions have included a reduction in insect harassment (although it also occurs on non-fly days), an increased chance of avoiding surprise attack by a ground predator, or as a direct response to plant odours carried by the wind. So while the post-calving movement is usually directed into the wind, and may be speeded up when flies are active, it is not released or caused by these external factors.

The structure and behaviour of the reindeer herds at this time appears directly equivalent to the post-calving aggregation and migration as described for barren-ground caribou (Kelsall, 1968; Lent, 1966; Bergerud, 1974b). Caribou males are said to be in the vanguard of this post-calving migration. This is parallelled on Hardangervidda where reindeer males are proportionately more numerous in the forefront of the moving herds, while females and calves are found in greater concentration at the rear (Fig., p.29, App.3). Although large numbers of adult and juvenile males are present in the early summer herds, small bands of males may still be observed outside the central summer range until nearer rutting time (Kjos-Hanssen, 1974). /

1974). Calves in early July are 4-5 weeks old, and still exhibit a greater need for rest than adults, and may often be seen lying when a herd becomes stationary, and are invariably the last to get up at the end of the short summer lying periods (Thomson, 1971). After rising, calves often require to suckle, and this stationary activity combined with individual mothers and calves occasionally losing contact and having to back-track in search of each other can account for their concentration at the tail of the herd.

As a general principle, large herds of herbivores require to move unless the forage is to be severely eaten away or trampled out. This in itself does not explain the proximate causes of the extensive movements of these massed herds, although the availability of fresh nutritious vegetation in early summer may be a key factor. Baskin (1970) notes that "the beginning of summer is marked by the appearance in reindeer of an irrepressible drive to migrate (move) from one area to another" and that animals try to out-run one another in competition for the rarest and most attractive feed plants. Reindeer in a large herd can thus spend more time in running onto new places than on the activity of feeding itself. This was frequently seen to be the case on Hardangervidda, and for July 1970 and 1971 (including days of insect harassment) the impatient onward movement of the reindeer resulted in 33% and 28% respectively of their time being spent on walking, trotting and running, and 36% on actual grazing (Thomson, 1971; 1973). Domestic reindeer herders try to block this "running competition" between the animals so that more time is spent building up body reserves for /

for the fly season (Baskin, op.cit.).

While herds can be seen to move and graze over all types of snow-free terrain, they will slow down and concentrate grazing in some areas and hurry on through others. Skogland (1974) has established a close relationship between the time spent by Hardangervidda reindeer on the available plant communities, and the seasonal phenology of these communities in relation to duration of snow cover and aspect. In June, after calving, the animals concentrate their grazing on the emerging vegetation on south aspects of low-alpine areas, and gradually move into the mid-alpine zone as its vegetation develops. By July the animals continue to feed on the youngest vegetation by concentrating grazing on north-aspect slopes, and on the emerging snow-bed communities (Skogland, op.cit.). This strategy parallels the tendencies of domestic tundra reindeer, and their herders, which move north at this time following the receeding snow line and so take advantage of the continuously emerging new leaves and shoots (Baskin, 1970). By the end of July most spring growth succession has been completed, and two possibilities are now open to the reindeer on Hardangervidda: either to disperse east towards the winter range to feed on August-fruiting mushrooms, particularly Boletus species, or to keep following spring succession in the western mountains up towards the base of glaciers (Skogland, op.cit.). The observed break-up of large herds towards the end of July and their dispersal in August over the range seems more likely to be connected with the animals' feeding strategy, than with insect harassment, which may or may not be prevalent at this time /

time depending upon weather conditions.

The phenology of the vegetation would seem to go a long way towards explaining the herd's geographical location and the grazing pattern at different times on the snow-free range. Phenology does not fully account however for the characteristic extensive movements of the massed herds in early summer. This urge to move appears to be characteristic of cohesive groups of reindeer in snow-free terrain. Even before the start of the calving season and the emergence of new vegetation, groups of up to 100 showed some signs of the grazing/walking/trotting pattern over the largest bare areas of winter-type grazings in both Hardangervidda and North Ottadalen. It seems as if the existence of tracts of snow-free ground in spring and early summer acts as a releaser for this type of movement.

7.7. INSECT HARASSMENT

> "Every higher animal is pursued with a frenzy from which they must flee. The unprotected ears of the dogs are bit bloody by mosquito stings. The reindeer seek refuge in the rough wind of the sea shore or on the snow patches of the cold mountain tops."
>
> Ludvig Dr. Daae, 1870. (In Skisser fra Lapland, Karelstranden og Finland.)

This extract from the report of a nineteenth century traveller vividly illustrates the plague proportions which mosquitoes can reach on warm summer days on the northern tundra. The traditional, /

itional efforts of reindeer herdsmen to protect their herds by lighting smoky fires in well known and documented in Scandinavia and the U.S.S.R. In the mountains of South Norway the mosquito swarm is less intense but the reaction of reindeer is hardly less on account of harassment also by other bothersome flies, notably the parasitic warble and nostril flies, and biting clegs and blackflies. Kelsall's (1975) study of warble fly larvae infestation on caribou hides indicates that warble fly activity is greater and the season of activity is longer on southern caribou ranges such as mountainous British Columbia and Alberta (56°N) and Southern Yukon (62°N), than on northern Arctic terrain (above 66°, 35' N). Also in the Far North there are fewer species of biting flies to harass the animals.

On Hardangervidda (60°N) I observed reindeer reacting to insect harassment on any warm day from June through to September, but they were especially prone to severe harassment in the peak summer period from late June to the end of August. From observation of the response of reindeer to the attacks of these insects, and the effect that these had on their activity and range use patterns, it became progressively clear that insect harassment was a major influence on the social structure and activity patterns of the reindeer in summer. The activity study (Thomson, 1971; 1973; Apps.2 & 3) has quantified the effects of harassment, and how the time spent on walking, trotting and running increases at the expense of grazing in proportion to the intensity of insect attack. Lying becomes an increasingly uncomfortable activity under insect harassment and /

and is replaced by standing. The herds' trotting movement under severe harassment is directed into the wind and towards suitable insect-relief areas (Plate 41). On warm sunny days in July vast herds will assemble on the remaining snowfields of the steep and north-facing slopes of the mountains in the west of Hardangervidda to seek relief from the flies. By August, however, the snowfields have gone and harassed herds will then move to the tops of hills to catch the maximum prevailing wind, or move down to a lake shore and wade into the water, or attempt to create their own insect-relief area by milling together in a tight mass. From the study of activity it became clear that insect harassment was the most significant environmental factor influencing the reindeer's energy expenditure throughout the year. My supplementary studies on the summer behaviour of caribou on Arctic coastal tundra at Prudhoe Bay, Alaska, (70^{o}N) confirmed the importance of insect harassment on these animals and allowed quantification of the effects of insects, not only on the activity of caribou but also on their group size, composition, movement, and range use patterns (White, Thomson, Skogland, et.al., 1975 (App.4); Thomson, in prep.). The evident importance of insects in the summer ecology of Rangifer is all the more interesting since, apart from Banfield (1954) and Kelsall (1968), it has seldom been given other than a perfunctory mention in caribou studies. Recent translations of Russian papers make it clear from descriptions of the effect of insect activity on reindeer herds that it is considered a serious problem for domestic and wild populations alike, in tundra and in taiga (Egorov, 1967; Zhigunov, 1968).

The /

The dependence of insect activity on suitable weather in summer was found to be as predictable a relationship as the effect of their activity on the reindeer. The first signs of insect harassment, viz. tail-wagging and head-shaking by the deer, was observed on calm days at an ambient temperature around 7°C. With increasing temperature the level of insect activity increases so that beyond 12-13°C the reindeer increasingly stamp their legs, switch, and move quicker with outbursts of running. Up to and beyond 20°C the deer are typically spending much energy in trotting and running outbursts, unless they have found a relatively insect-free habitat. Wind reduces the intensity of harassment in proportion to its velocity. The way in which field measurements of air temperature and wind speed together correlated with insect activity and harassment on reindeer was illustrated for Hardangervidda (Fig.7, p.21, App.2) and Prudhoe Bay, (Fig.4, App.7), with very similar results. This relationship was then used to predict how many days each summer would be days of severe harassment, mild harassment, or be without harassment to reindeer. Records of air temperature and wind speeds from local meteorogical stations on Hardangervidda were tested for their validity against the observations made in the field. Within the 77 days between mid-June and the end of August an estimated 47 were "insect days" in 1970, and 46 in 1971 on Hardangervidda (Thomson, 1971). Similar analysis in subsequent years have shown that yearly variation is considerable, with 1972 and 1973 being particularly hot, insect-plagued summers (Fagerhaug, 1976). Differences in the weight of culled calves and the amount of fat reserves of animals on Hardangervidda between /

between years have been attributed to differences in the severity of insect harassment between years (Fagerhaug, op. cit.).

However, not all reindeer are affected similarly, even in a particularly hot summer. Those male reindeer which remain in batchelor groups on the far west of Hardangervidda for most of the summer (Kjos-Hanssen, 1974) may not be affected to the same extent, as they can ascend to high permanent glaciers in this area which must effectively minimise the extent to which they must endure harassment. Similarly, the reindeer population on rugged alpine ranges such as North Ottadalen will probably move to the high alpine tops and snow-fields on warm summer days. The occurrence of suitable insect relief areas throughout summer is likely to prove an important factor in comparing and contrasting the energy expenditure of reindeer populations on different ranges. Following the 1972 field research on caribou-insect relationships at Prudhoe Bay, Alaska, an activities model is being synthesised to simulate by computer the observed relationships on the Alaskan tundra, and to test its application to Rangifer ranges elsewhere (Bunnell, Russell, White & Thomson, in prep.).

So far there has been no systematic study of the species of flies responsible for harassment of reindeer in Norway. In common with other northern tundra or mountain habitats, Hardangervidda supports populations of mosquitoes (Culicidae) which particularly cause shaking, tail-wagging, and twitching in the deer. Swarms of small biting blackflies (Simuliidae) occur /

occur which probably affect the deer in a similar manner. Larger biting flies such as the clegs, horseflies, and gad flies, (Tabanidae),occur singly and their bite is thought to cause such observed individual reactions as turning round to bite at the affected spot, bursting into a run, etc. (hence "gadding" in cattle). The two parasitic Oestridae flies specific to Rangifer, the warble fly (Oedemagena tarandi) and the nostril fly (Cephenomyia trompe) cause a similar individual fright or avoidance reaction such as a sudden burst of running, kicking or stamping the legs, and a vigorous shaking. As a specific defence against the nostril fly, individual reindeer have been seen to thrust their muzzle hard down against the ground or vegetation, as described by Espmark (1968). That the deer should react so intensely and specifically to the sight and sound of these Oestrid flies is interesting since the rapid ejection of viviparous larvae into the nostrils of the deer, or the laying of eggs on the deers' coat hairs by the warble fly, can at the most cause only a momentary mild irritation or itch. The warble larvae hatch and migrate under the skin where they grow in size over winter and bore out in summer when they fall to the ground to pupate into adult flies. The nostril fly larvae similarly develop over winter in the nasal and throat passages and are coughed or sneezed out in late spring (see Ch.5.1.3d). From reindeer culled on Hardangervidda in April, 1970, seven adult females were found to have an average of 80 Oedemagena larvae on each of their hides, and four calves an average of 100 larvae each, while Cephenomyia larvae were abundant in the nose and throat passages.

From /

From insects collected on Hardangervidda and other mountain ranges in South Norway the genera and species of insects thought to be responsible for harassment on the reindeer are listed in Table 7.10. Further progress on the important link between insect harassment and reindeer energy expenditure (Chapter 8) now requires systematic verification of the insect species concerned and applied research on their ecology; in particular the precise activity thresholds of adult flies to combinations of ambient air temperature, wind speed, radiant heat from sunshine, and air humidity over the summer season.

7.8. THE RUT

Sex-related behaviour of the reindeer male during the autumn rut depends partly on his maturity, which is directly related to his age, and partly on his ranking status viz-a-viz other males. In a population with many mature males it can be expected that prolonged contests and rivalry will occur with only the most dominant males having consistent access to the females as they come into oestrous. By contrast, in a population with few males present, males that would normally play a subordinate role, including young males, will behave as dominants and then have access to the females. These contrasting situations were observed in the rutting seasons on North Ottadalen in 1969 and 1970, with a full complement of adult males at 1 : 1.2 male to female ratio, and in the rut on Hardangervidda in 1970, where hunting had severly culled males leaving a sex ratio of around 1 : 15 for animals over two years. The rut was also observed on Snøhetta, 1969, where there was a sex /

Table 7.10 The insects responsible for harassment of reindeer on Hardangervidda (provisional list).

ORDER DIPTERA (Flies)		
Oestridae	Oedemagena tarandi, reindeer warble fly Cephenomyia trompe, reindeer nostril fly	collected on Hardangervidda (Gaare, Skogland & Thomson, 1970)
Culicidae	Aedes spp mosquitoes probably includes A. punctor A. communis A. impiger A. excrucians	collected from various South Norway mountain ranges (Natvig, 1948).
Simuliidae	blackflies possibly includes Helodon ferrugineus Prosimulium nigripes Eusimulium bicorne Cnephia fuscipes	collected from Jotunheimen, 1250-1700 m (Carlsson, 1962).
	(Prosimulium ursinum)	collected on Hardangervidda (Østbye & Haagvar, 1972) but this sp. has non-biting mouthparts.
Tabanidae	deerflies, clegs includes Hybomitra aterrima H. montana flavicens H. lundbecki H. lapponica Haematopota pluvialis Chrysops nigripes	collected on Hardangervidda (H. Kauri, 1971, pers. comm.).
(Ceratopogonidae midges, Culicoides spp)		suggested by Skogland (1974), but requires verification as Arctic/mountain forms usually have non-biting mouthparts (Downes, 1965).

sex ratio of 1 : 7 in favour of females. The difference in the timing of the rut between these three populations allowed observation of four rutting seasons over the two years.

Despite these differences in the proportion of males the group structure and social organisation were similar in all three areas. Groups at rutting time were typically inconstant as individuals or small sub-groups wandered off or joined with other nearby groups. Only males were likely to be seen moving alone. Rutting herds of several hundred animals (up to 400) were observed in all three populations, with a mean size of herd of 50-90 animals. The spread and drift of animals over the terrain was such that temporary sub-groups would often form within a herd.

Dominant males would display, threaten and clash with each other, rush charge at subordinate males, and court the females by the head-swinging and head-stretch "driving" approach (re. Ch.5.3.1.). In the early part of the rut the male would tend to drive first at one female and then another indiscriminately, but as the rut progresses courtship by a dominant male tends to be concentrated on one female. These consort pairs form the basis of group structure at the peak of rutting time. There was less tendency for rival males to clash if they were both "tending" a different female, while subordinate males who showed interest in the females would be kept at a distance, generally around 10m. Male calves were an exception in that they would be tolerated by the tending males, even when the calf would exhibit a sexual interest in the female by attempting mounting.

Observation /

Observation showed that these tending bonds are themselves temporary associations. A male might be seen to switch his tending to a different female in the course of a day, while on other occasions it was certain that a particular consort pair were still associating together on the following day. The onset of a particular female's oestrous and thus receptivity to mounting is undoubtedly the attraction for a dominant male to consort with a female.

The open nature of rutting groups and the typical inclusion of several mature males in one group is a similar organisation to that described for wild reindeer in Taimyr (Michurin, 1967), and for barren-ground caribou in Canada (Lawrie, 1948; Lent, 1965). Woodland-type Rangifer, on the other hand, are inclined to form one-male groups, where the male actively herds the females into a discreet harem. This tendency appears to be universal amongst woodland-type reindeer males (R.t. fennicus) in a forest habitat (Espmark, 1964a), whilst other woodland-type populations in more open or partly-wooded situations apparently produce both one-male and multi-male groups (e.g. R.t. fennicus on Kola Peninsula, Semenov-Tyan-Shanski, 1948; R.t. caribou in Newfoundland, Dugmore, 1913; Bergerud, 1974a).

It would appear then that the typical composition of rutting groups and the behaviour of rutting males might depend on the sub-species of Rangifer. Mountain or tundra types (R.t. tarandus, R.t. granti, R.t. groenlandicus) are characterised by multi-male groups and tending bonds between the consort pairs, while woodland-types (R.t. fennicus, R.t. caribou) have

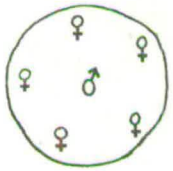
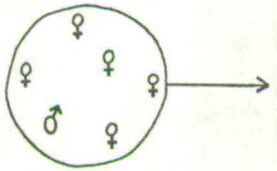
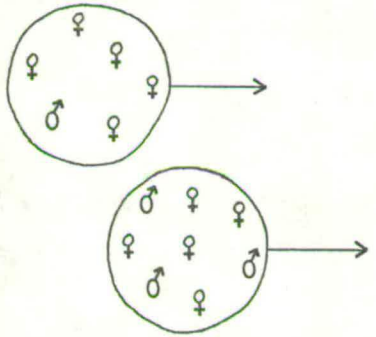
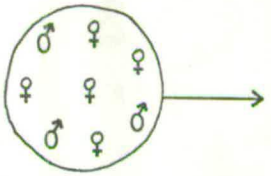
a /

a tendency towards groups with a single dominant male seeking to associate himself with several females by herding them together. For woodland-type Rangifer there may also be a direct response to the nature of the habitat at rutting time, in that the tendency for discreet harem formation appears to be strongest in the most forested habitat, while multi-male groups also occur in populations living in more open or partly-wooded habitat (Table 7.11).

From the evidence now available it would appear that these observed differences in social organisations are not due to differences in the degree to which different populations show migratory behaviour during the rut, as was suggested by Lent (1965a), and discussed by Henshaw (1970). The wild reindeer of South Norway show a parallel social organisation to barren-ground caribou at rutting time, yet show no significant signs of a migratory drive in autumn, even on the largest range Hardangervidda, when by the rut they are typically already within or adjacent to their normal winter range. Reindeer groups may be stationary for long periods then move aimlessly over the terrain, the females and young alternating grazing and lying periods, which the males more or less follow. Groups drifted an average of 4km per day while remaining in the same general area over a two-week rutting period in the North Ottadalen range. The groups appeared just as likely to split up or intermingle to form different sized units as were the caribou reported by Lent where "almost all the groups observed were travelling" as a result of their autumn migration corresponding with the time of the rut.

The /

Table 7.11 The social organisation of Rangifer rutting groups as related to racial type and habitat.

Rutting social organisation	Territorial one-male group	Shifting one-male group	Shifting groups both one-male and multi-male	Shifting multi-male group
Rutting group				
Rangifer-type	-	⊢ Woodland-type Rangifer ⊣		Mountain/tundra-type Rangifer
	-	R. tarandus fennicus (Espmark, 1964a)	R.t. fennicus (Semenov-Tyan Shanski, 1948) R.t. caribou (Dugmore, 1913) (Bergerud, 1974a)	R.t. tarandus (This study) (Michurin, 1967) R.t. groenlandicus (Lawrie, 1948) R.t. granti (Lent, 1965a)
Main habitat	-	Forest	Partly wooded	Mainly open

The extreme differences in sex and age compositions between the populations in this study afforded a unique opportunity to observe its effect on the social organisation of the rut. On Hardangervidda in October 1970 adult males were not observed in the rut following a severe reduction hunt in the previous month (sex ratio around 1 male to 15 females two years and older), and as a result the onus of breeding fell to the surviving $2\frac{1}{2}$-year males and occasional $3\frac{1}{2}$- or $4\frac{1}{2}$-year males. Sub-groups were occasionally observed where one-male groups temporarily formed in default of other males being present. (However, there was no clear evidence of any such single male attempting to gather the females around him into an established harem.) On Hardangervidda the oldest of the young males present would attempt to take on a dominant role by challenging rivals, chasing off yearling and male calves, and occasionally while standing showing the hunching posture, but not the full display and rutting repertoire typical of adult males. In particular, there was no ritualised antler clashing, muzzling and pawing, nor frequent hunching posture with urination and self-marking, nor persistent close tending of a female. The young males would often trot or run directly at the females, not always in the characteristic head stretch driving position, and as the females reacted with fright, long chases would result with frequent splitting of groups and a high level of excitement and energy expenditure.

As a result of these observations it was considered questionable how successful the Hardangervidda rut would prove that year, because of the shortage of males generally and in particular the lack /

the lack of control normally afforded by the adult mature males and their stereotyped rutting behaviour patterns and sequences. However, observations 7½ months later showed no difference in the timing of calving from the previous year. Counts at this time estimated that 50% of adult females gave birth compared with 65% the previous year (Table 3.5), and this difference may have been attributable to not all females being successfully covered in the rut. The success or partial success of the Hardangervidda rut may in fact have been attributable in part to an interesting change in female behaviour at rutting time. Despite many hours of observation during the rut on North Ottadalen and Snøhetta, it appeared to be mature males which made all the active courtship approaches with the females merely becoming increasingly receptive but remaining passive. However, on Hardangervidda on 16/10/70 a female was seen to persistently follow around the most dominant male in the vicinity (estimated age 3½ years), who would stand for long periods and only sporadically swing his head round to her, without her backing off. The female rubbed her head and antlers in the vegetation around him and nosed his stomach and flanks both before and in the interval between two unsuccessful mounting attempts of 15 sec and 20 sec. At the third attempt lasting 14 sec the male achieved intromission, following which the female walked away.

Such active behaviour of the oestrous female in encouraging the male to mount has been observed by Bergerud (1974a) for caribou females on five occasions, in particular the female rubbing her head on the male's neck several times before the male /

male mounted, otherwise passive behaviour by the females is typical of caribou also. Lent (1965a) who also observed caribou copulations detected no active behaviour by females in heat. This variability in the behaviour of the female may be a flexible mechanism whereby the female can take an active part in encouraging her own conception by provoking the male where circumstances require it. An insufficient interest or capability by the male could arise where there is a shortage of males and those present become exhausted, or where young males are inexperienced and need "encouragement". Bergerud (op.cit.) found that two captive caribou females exhibited an early desire to stand for the male and the female would frequently poke her antlers against his side or rear in between this inexperienced male's attempts at mounting over the head of the female. Captive female reindeer in oestrous are recorded as passively seeking male company (Barden, 1969). In the normal free rut with a full complement of mature experienced males (as on North Ottadalen) it may well be that active behaviour by the oestrous female is unnecessary, and is therefore not normally evident. The only significant female active behaviour on North Ottadalen was the female chases (re.Ch.5.3.1d) which may operate as an initial attractant to males, and thereafter the dominant male takes the leading role.

Thus, although courtship and display patterns in reindeer appear to be relatively fixed and often ritualised, there appears to be an important element of flexibility in group structure and behavioural performance during the rut in that where necessary young males can more or less successfully take on /

on the role of dominant male, while the adult female can adopt an active role by encouraging the male to greater efforts.

7.9. DISTURBANCE FROM PREDATORS & HUNTING

> "The behaviour of wild ungulates towards human beings is largely a consequence of our behaviour towards them; they are as wild as we teach them to be."
>
> V. Geist, 1970.

The significance of Geist's statement is not that all ungulates are equally suitable subjects for domestication, but that their response to man largely depends on their previous experience, whether of man as hunter-predator, or as a more neutral factor in their environment. Where animals are protected from hunting, as in wildlife parks and reserves, all but the shyest species have become habituated to the constant but innocuous flow of human visitors and their traffic. Similarly, but at the other extreme, there are many examples of animal populations in areas traditionally remote from man, which have appeared "tame" on encountering man, often ultimately to their detriment if man emerges as the hunter. Ungulate populations which are most consistently or severely hunted tend to exhibit the greatest wariness, and in extreme cases may alter their entire activity pattern to become active at night only. A change from a diurnal to a nocturnal activity pattern has been recorded for hunted populations of white-tailed deer (Severinghaus & Cheatum, 1956), black-tailed deer (Cowan, 1956), and American buffalo (Cloudsley-Thompson, 1961).

The /

The wild reindeer populations of South Norway are hunted annually in autumn, and are predictably wary of man's presence. However, reindeer with a recent history of domestication, such as on North Ottadalen, are noticeably less wary of man than populations which have been hunted for many decades, such as on Hardangervidda, or on Snøhetta. Even within the one population of wild reindeer the flight distance of a group is not a constant statistic as it varies considerably, dependent upon a number of factors (Table 7.12). In particular, there are marked seasonal differences in response to potentially alarming stimuli. For example, in winter the deer detect and become alert to movement against the snow, or the scent of a man up-wind, at several kms; and at a distance of approximately 1km such an alarming stimulus causes a group to clump together in alarm and move off, typically moving forward first to investigate fully the source of alarm. At the other extreme, large herds in summer often display a minimal response, particularly towards the presence of man, and occasionally grazed up to 10m of the stationary observer. Their response to human scent in summer can often be better considered as passive avoidance rather than active alarm. Such a lack of response was particularly evident on days when the deer were already harassed by insects. Similarly, males in the rut are very unwary in regard to possible external danger, absorbed as they are in their sexual behaviour.

Apart from seasonal distinctions in alarm response, reindeer clearly discriminated between different types of predator or potential predator. The sight of a golden eagle flying, or person /

Table 7.12 Factors influencing the flight distance of a reindeer group.

Factor	reduced ⟸ FLIGHT DISTANCE ⟹ increased		
History of domestication	Recent history. (e.g. North Ottadalen)	Past history. (e.g. Hardangervidda)	No history. (e.g. Snøhetta)
Season	Summer; Rutting ♂.	Spring ; Autumn (except rutting ♂).	Winter; Hunt period.
Type of Alarm	Fox, gull, raven (on ground).	raven (flying).	eagle, man.
Mode of perception	auditory.	sight.	scent (of man).

person moving, would cause a greater immediate alarm and flight response than for a raven flying, while there was usually no retreat from animals on the ground, whether ravens, common gulls, or foxes. If an eagle flew over low there was immediate alertness and clumping, followed by running if the eagle "attacked" by swooping down on the herd, with any stragglers being the subject of close attention from the eagle. Such attacks were seen in winter and summer, and successful eagle predation was encountered in this study, and in subsequent observations (Skogland, 1974; and Plate 42). Ravens flying over herds normally also caused flight, and frequently in winter when even the call of a raven could evince alertness. It may seem surprising that the deer should react with fright to ravens, usually considered as successful scavengers. However, ravens are more than just ubiquitous scavengers on reindeer carcasses or opportunist predators on new-born calves. An adult female reindeer, apparently in good health, was pecked to death by several ravens, while on Hardangervidda a flock of ravens frightened a calf over an escarpment (Østbye, 1969).

Reindeer did not take flight at the presence of foxes, and would at the most be only mildly alarmed or alerted. On several occasions in winter a group moved out towards a fox, often followed up by a female rush charging at the fox to ensure that it proceeded on past the herd (records in Table 4, App.6). Mother females with young calves often showed a similar active form of defence by charging at gulls and ravens on the ground attempting to move closer to the placenta. On one occasion filmed in spring a common gull on the ground was forced to retire /

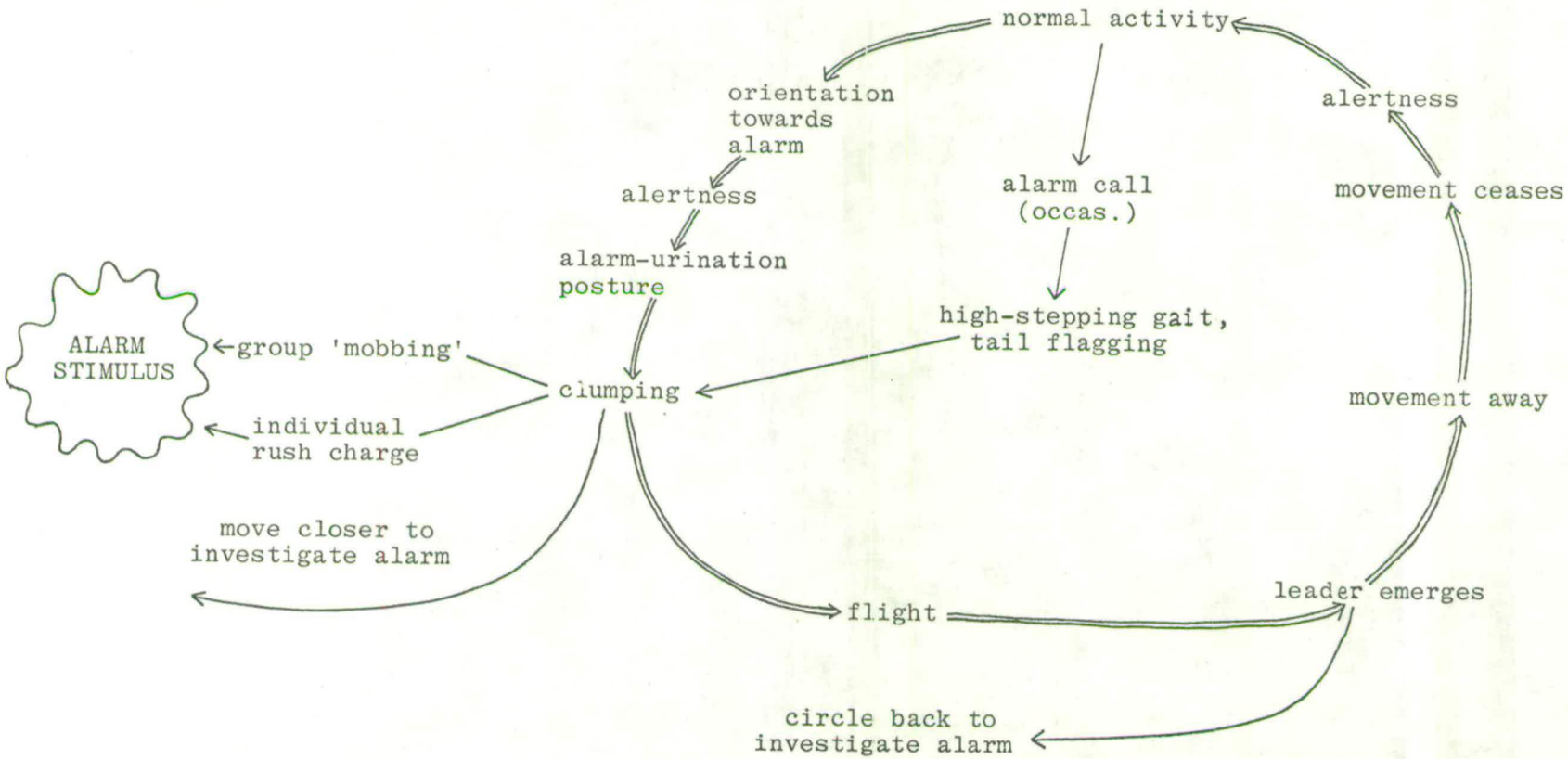
retire as the nearest animals in a group of 30 reindeer moved towards it. As the bird took off, however, one of the leading reindeer became badly startled on seeing at close range the silhouette of the bird against the sky, and this sudden startle disturbed the others in the group which then moved off.

Reindeer may occasionally stand their ground against potentially dangerous predators. Caribou mother females have been known to charge at humans (Lent, 1966). In this study a lone mother moved to stand protectively over its calf as an eagle flew over low, while a female in an alarmed nursery group was seen to rear up and wave its forelegs at an eagle swooping down. With these exceptions the normal response of reindeer to a sufficiently alarming stimulus is to group together for flight.

Prior to flight, the behaviour of a group develops from initial sensing and orientation towards the alarming stimulus, the urination-alarm posture which signals alertness to neighbouring animals, clumping of the group, then further assessment of the danger before breaking into a trot or run for anything from 20m to several kms. The distance run depends on the type and intensity of alarm and the reindeers' sensitivity to disturbance at different times of the year. The main sequence of these alarm responses is shown diagramatically in Figure 7.13. This basic pattern shows considerable variations.

Thus, if a group or individual is suddenly surprised at close range animals will tend to move off at a deliberate springy high-stepping /

Fig. 7.13 Typical sequence of responses of an alarmed group of reindeer.



high-stepping trot with tail flagged, before breaking into a run. Reindeer appear particularly suspicious of alarm sources which are partially concealed or which move out of sight, and then a group will often circle back for a better view, or down-wind to scent the air to better define the danger, before finally withdrawing from the area. Where a leader emerges from a disturbed group the direction and pace of travel away is particularly unpredictable, and along with the actions of other leader-type animals in looking out from the edges or rear of an alarmed herd, has survival value for a group in out-manoeuvering a potential predator (Thomson, 1975, App.6).

Over 850 hours of reindeer observation, mostly on Hardangervidda, demonstrated that their activity was temporarily disrupted by alarm or flight reactions once every 4 hours on average. This varied seasonally at one disturbance every 7-8 hours at winter and rutting time; one every 3 hours in summer on average; to a disturbance every 18 minutes during observations of the Hardangervidda hunt in 1970. Seasonal differences in the frequency and causes of disturbance is shown in Table 7.13. Human influence was the dominant factor in summer and autumn, on account of summer tourist hikers, reindeer-hunters, and ptarmigan-hunters during the rut on North Ottadalen. Disturbance from vacation skiers at Easter can be expected on some ranges. In winter and calving time, disturbance from human sources was found to be rare, except in regard to the research programme itself, which disturbance has been classified separately as a temporary feature (Table 7.13). The Statens viltforskningen research programme also added substantially to the /

Table 7.13 The seasonal frequency and causes of disturbances provoking alarm or flight responses amongst wild reindeer groups in south Norway.

	Raven	Eagle	Fox	Gull	Small birds	Other reindeer	Un-known	Hiker/ Skier	Dog	Hunter	Vehicle[2]	Heli-copter	Air-plane	Total No.	No. hours obser-vation	Mean no. disturb-ances in 10 hours
WINTER																
No.of disturbances	17	4	6	0	2	5	10	0	0	0	2	0	2	48	336	1.4
% Proportion	45%	11%	16%		5%	13%	-				5%		5%	100%		
(Research activity only)[1]								(28)		(5)	(12)	(1)	(1)	(47)	336	(1.4)
CALVING																
No. of disturbances	26	3	1	10	1	4	4	0	0	0	0	0	1	50	222	2.3
% Proportion	57%	7%	2%	22%	2%	9%	-						2%	100%		
(Research activity only)[1]								(36)	(1)			(2)		(39)	222	(1.8)
SUMMER																
No. of disturbances	10	1	0	2	1	7	4	27	2	0	3	0	2	59	161	3.7
% Proportion	18%	2%		4%	2%	13%	-	49%	4%		5%		4%	100%		
(Research activity only)[1]								(23)					(5)	(28)	161	(1.7)
HUNT																
No. of disturbances	4	0	0	0	0	0	0	2	0	25	0	0	2	33	10	33.0
% Proportion	12%						-	6%		76%			6%	100%		
(Research activity only)[1]								(3)						(3)	10	(3.0)
RUT																
No. of disturbances	3	0	1	0	1	2	1	0	0	6[A]	0	1	0	15	126	1.2
% Proportion	21%		7%		7%	14%	-			43%		7%		100%		
(Research activity only)[1]								(17)	(1)					(18)	126	(1.4)
ALL SEASONS																
No. of disturbances	60	8	8	12	5	18	19	29	2	31	5	1	7	205	855	2.4
% Proportion	32%	4%	4%	6%	3%	10%	-			40%				100%		
(Research activity only)[1]								(107)	(2)	(5)	(12)	(3)	(6)	(135)	855	(1.6)

1. Disturbance as a result of air census, cull sampling, and observational work by Statens viltforskningen in 1970 and 1971.
2. Vehicles include snow-scooters, cars and tractors.

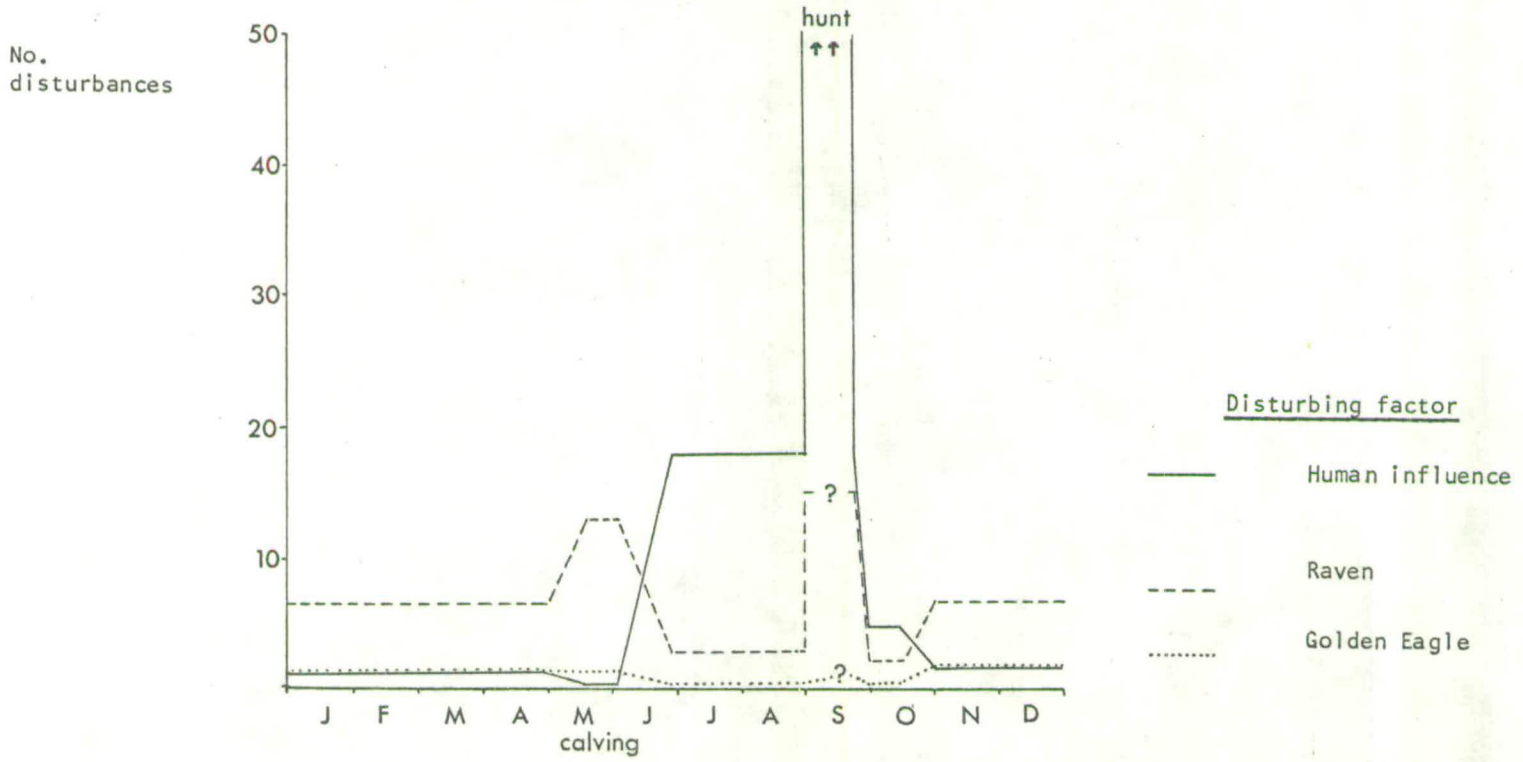
the amount of disturbance from snow-scooters, helicopters and low-flying aircraft, as described in Thomson, 1972 (App.5). Recent tests on caribou show that aircraft below 200 feet (61m) generally evoke a fast running or panic response (Klein, 1974).

More natural disturbances also occurred from startle reactions to innocuous features of the environment such as the sudden flight of a ptarmigan from the ground, or a flock of snow buntings, or even any sudden movement or unusual behaviour by a reindeer within the herd. Those instances where foxes or common gulls caused any form of active response are also listed in Table 7.13. However, ravens were by far the greatest source of disturbance to the reindeer in winter and at calving time. Seasonal variation of the impact of three important influences on reindeer, namely human influence, raven, and golden eagle, is illustrated in Figure 7.14.

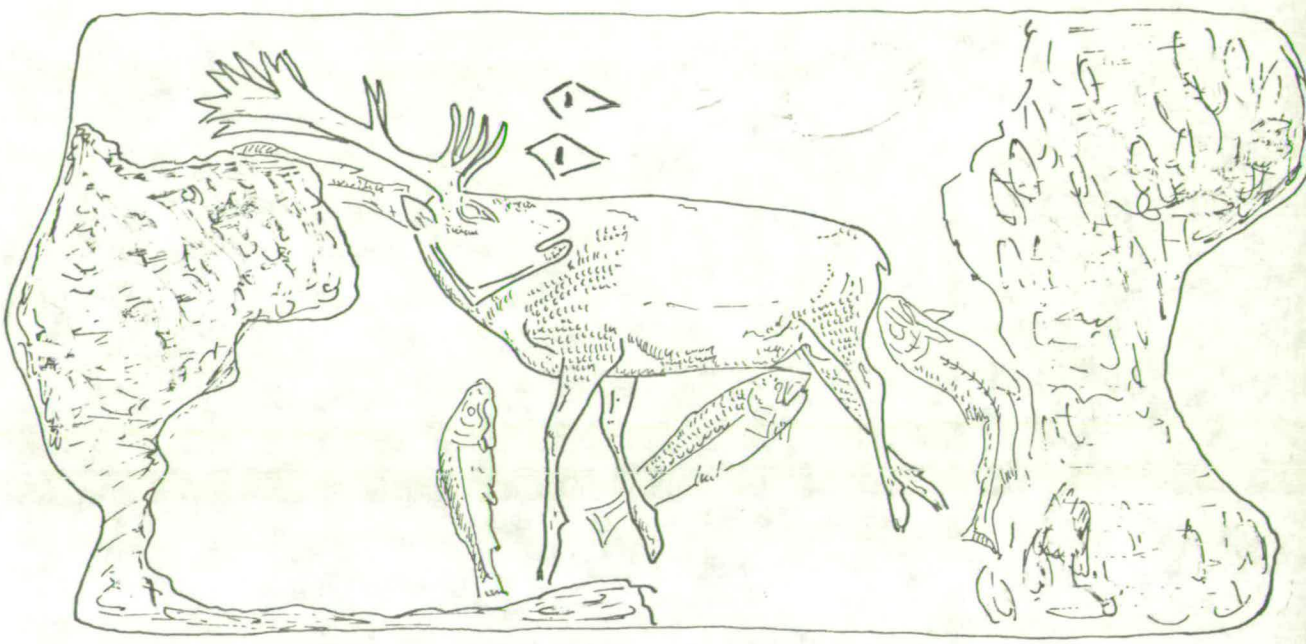
While the observed frequency of disturbance may at present seem low for most of the year, continued monitoring of disturbance would be advisable. This is particularly important in summer and autumn when any energy spent in response to a disturbing factor is in addition to that lost through insect harassment. The current proposals for protecting the central part of Hardangervidda in the form of a National Park must not be allowed to become a two-edged sword by encouraging additional foot traffic in summer to a level which jeopardises the reindeers' energy balance in a hot insect-plagued summer. The implications of disturbance on energy expenditure are discussed further in the following chapter.

Fig. 7.14 Comparison of the frequency of disturbance of reindeer groups by raven, golden eagle, and human influence at different seasons, 1970 and 1971.

(Expressed as the number of disturbances* per 100 hours of observation)



* Disturbance defined here as factor provoking alarm or flight responses; and excluding disturbances from research activity.



Sketch adapted from unrolled engraving on reindeer antler found at Lorthet, High Pyrénées, France. Fish and triangles may represent fertility symbols.(adapted from Graziosi, 1960).

CHAPTER EIGHT ACTIVITY & ENERGY EXPENDITURE

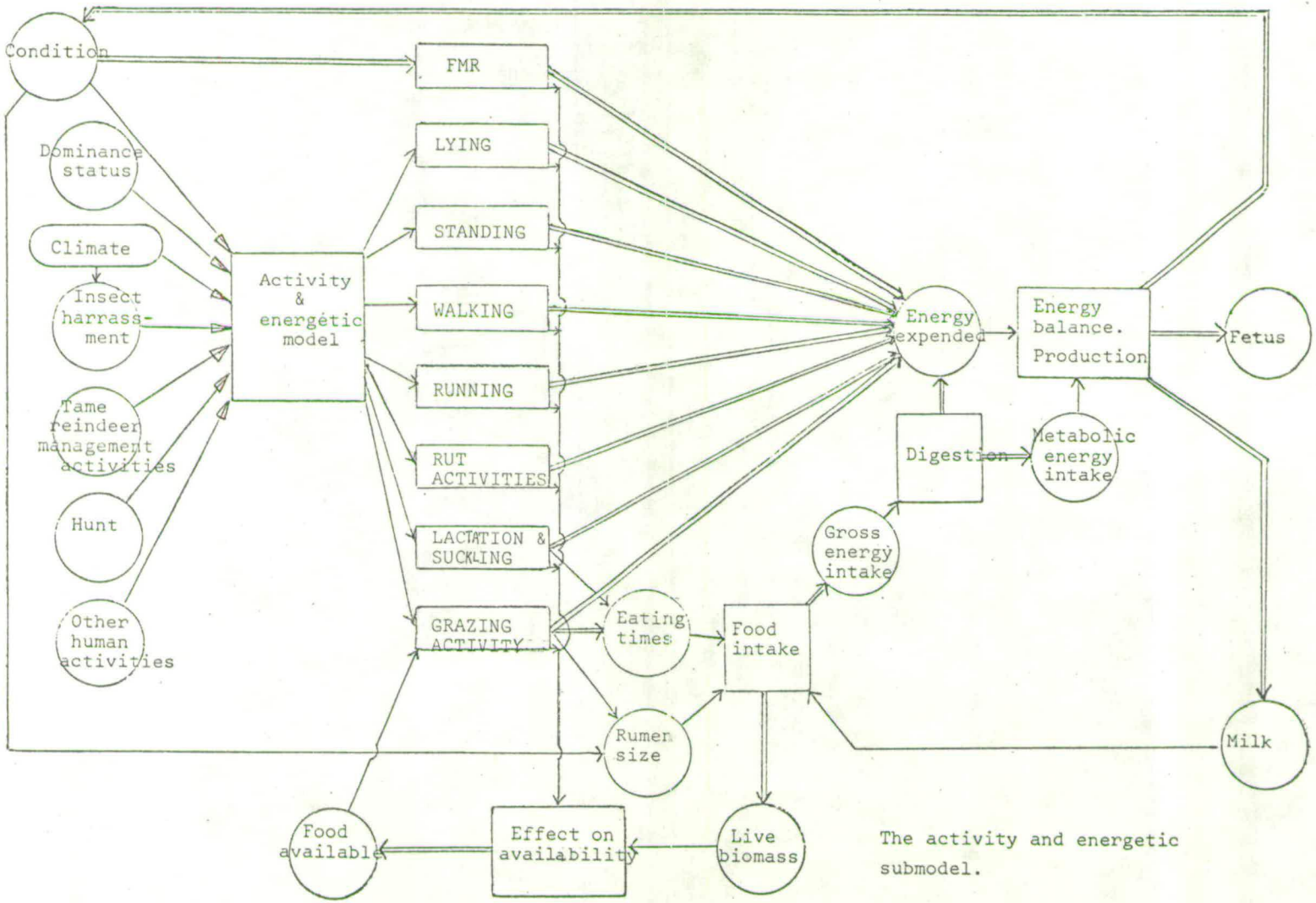
"Biologists have recognised differences in the energy and protein requirements of animals for years, but little effort has been made to analyse the importance of these requirements for free-ranging animals."

A.N. Moen, 1973.

The systematic recording of the time spent by reindeer on their major activities allowed construction of a time budget for different months and seasons of the year (Gaare, Skogland & Thomson, 1970; Thomson, 1971; 1973; Gaare, Thomson & Kjos-Hanssen, 1975). The time spent on grazing was considered to be of particular importance insofar as it could relate to the feed intake studies being investigated from using experimental tame reindeer fitted with oesophageal fistula, from wild reindeer rumen contents, and from range vegetational analysis (Gaare et. al. 1970; Gaare & Skogland, 1971; Skogland, 1974; Gaare & Skogland, 1975). Subsequently, following research comparisons between Norwegian and North American work, including co-operative field work at Prudhoe Bay, Alaska, in 1972 (White, Thomson, Skogland, et.al., 1975), an international workshop was held at Trondheim in 1973 to consider ways of modelling Rangifer systems, in particular to relate energy intake to energy expenditure (Fig.8.1).

When energy balance is positive an improvement in body condition and productivity can be expected, and conversely when energy expenditure exceeds intake a loss in condition and ultimately /

Fig. 8.1 Flow diagram of the main factors influencing the energy balance of reindeer.



The activity and energetic submodel.

(From unpubl. manuscript of International Rangifer Modelling Workshop, Trondheim, 1973)

imately population productivity will occur. It was recognised that a good estimate of carrying capacity of a range could not be made only by considering the prevailing food quality, availability, and standard feed consumption, since a population's energy requirement will vary as the activity pattern and its associated energy expenditure varies in different habitats and at different seasons.

From the best estimates available for the energy "cost" of each activity, a provisional energy budget can be calculated from the known time budget for the free-ranging reindeer on Hardangervidda.

The basic metabolic rate (B.M.R.) of a mammal requiring energy only for its bodily maintenance at rest relates to its body weight (kg) according to the equation:
$BMR = 70 \text{ kcals/kg}^{0.75}\text{/day}$
(Benedict, 1938; Blaxter, 1962; Moen, 1973).
Individual species vary around this mean. Thus, while the BMR of a sheep is 15% lower, cattle are 15% higher. For red deer (Cervus elaphus) the BMR averages 90 $\text{kcals/kg}^{0.75}$/day (Brockway & Maloiy, 1967). For barren-ground caribou the BMR of fasting animals was found to average 97 $\text{kcals/kg}^{0.75}$/day (McEwan, 1970).

Thus a 100kg caribou or reindeer wholly at rest for 24 hours in its thermoneutral range would be expected to expend 3068 kcals of energy per day in maintaining its bodily functions. Over and above this a free-ranging animal must spend energy on standing, eating, ruminating, and moving. A technique for measuring /

Table 8.1 Estimated energy costs of activities for ruminants.

Activity	Energy expenditure	Reference
Basal Metabolism (Lying)	97 kcals/$kg^{0.75}$/day	Caribou - McEwan, 1970.
Additional activity costs:		
Standing	0.117 kcals/kg/hr	Blaxter, 1962.
Lying to Standing and return	0.025 kcals/kg	Blaxter, 1962.
Eating	0.36 kcals/kg/hr	Bunnell et.al., in prep.
Ruminating	0.18 kcals/kg/hr	Graham, 1964. (half of eating energy expend.)
Movement	(0.53+0.0033 velocity in m/min) cals/kg/m.	Blaxter, 1962; Bunnell et.al., in prep.
Walking:	At mean of 2mph (53.64 m/min)	0.000707 kcals/kg/m.
Trotting:	" " 4.5 " (120.69 m/min)	0.000928 kcals/kg/m.
Running:	" " 10 " (268.22 m/min)	0.001415 kcals/kg/m.
Trotting & Running	" " 6 " (160.93 m/min)	0.001061 kcals/kg/m.

(Mean speeds of movement activities of reindeer from Figure 5.2)

For calculating energy expenditure of different activities:

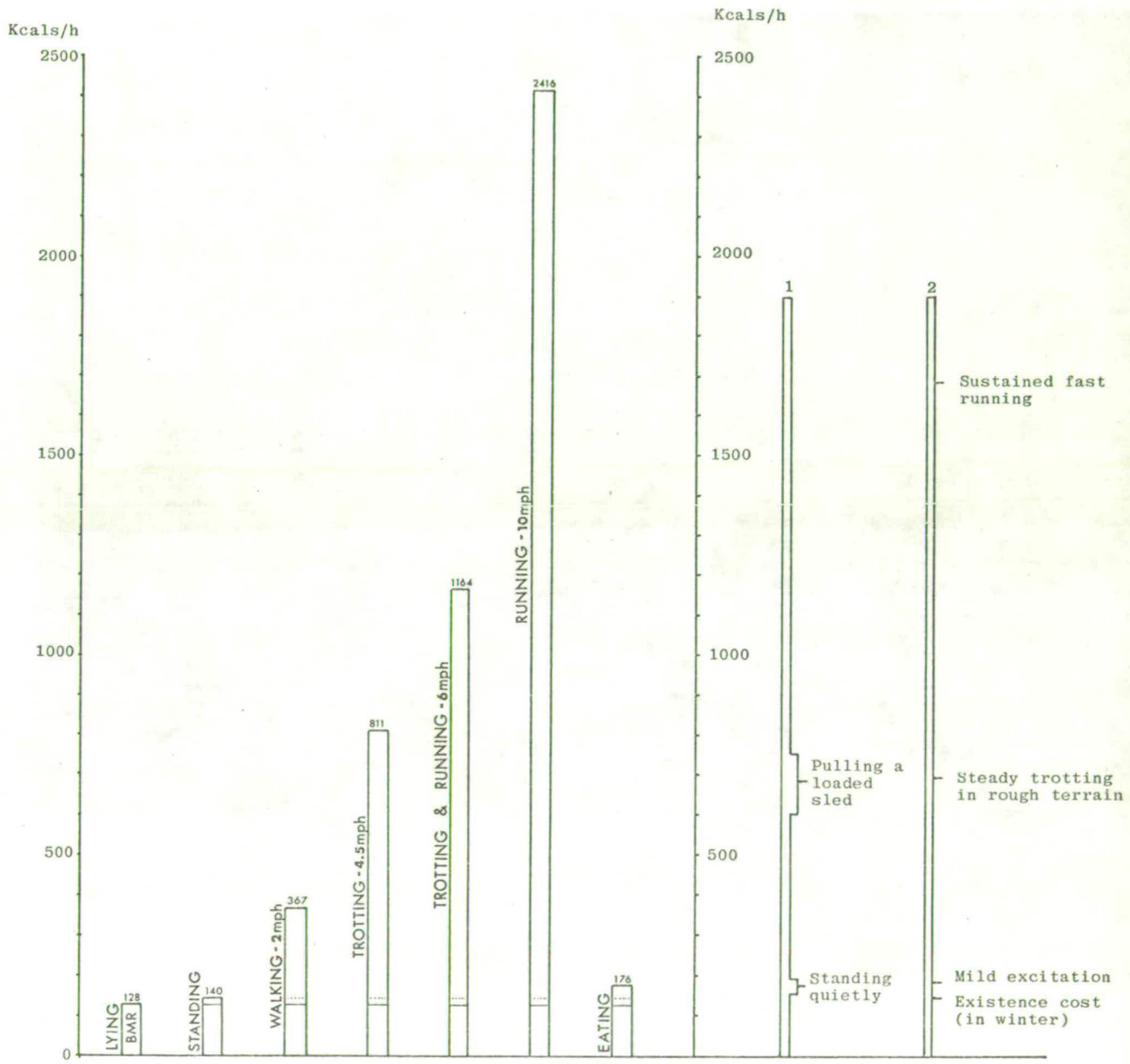
Lying = BMR
Standing = BMR + standing costs.
Grazing = BMR + standing costs + eating costs.
Walking = BMR + standing costs + walking costs.

measuring the costs of different activities has been developed - viz. the CO_2 entry rate technique (Young & McEwan, 1975) - and has been tested on experimental reindeer at Prudhoe Bay, Alaska (R.G. White, unpubl. results). In the meantime, the best estimates for activity energy costs are mostly those derived from domestic ruminants. These are displayed in Table 8.1.

The energy which an adult reindeer of 100kg live weight would spend in one hour on each of its main activities is calculated and shown in Figure 8.2. The high energy cost of movement is notable. Trotting and running were not recorded as separate activities on Hardangervidda and have been considered together at an estimated average speed of 6 mph (from field trials, see Fig.5.2, and Ch.5.1.2a.). At this speed of movement an energy expenditure of 1164 kcals/h or 9 x Basic Metabolic Rate can be expected. Hammell et. al.(1962) actually measured the metabolism of a 100kg male reindeer and found that it spent 688 kcals/h (605-752) while pulling a loaded sled, which was 4 times its metabolic rate while standing quietly (157-192 kcals/h), or 5 x BMR as measured by McEwan (1970) (Fig.8.2). Some estimates by Geist (1971b) of the energy expenditure of active caribou have been converted to hourly expenditures for a 100kg animal, and appear to conform reasonably well to the calculated pattern for reindeer (Fig.8.2).

Using the actual time budget I recorded for wild reindeer on Hardangervidda, a seasonal energy budget may be constructed (Table 8.2). The weight of animal chosen is of little significance /

Fig. 8.2 Estimated energy costs of different activities for an 100kg reindeer.



1. Metabolism of an 100kg reindeer as measured by Hammel et. al., 1962.
2. Converted from estimates for caribou by Geist, 1971b.

nificance to the results. In this case an 80kg deer is taken to be representative of the average adult weight on Hardangervidda. The active energy expenditure of reindeer in winter is thus estimated to be around 1.5 times their Basic Metabolic Rate, but with the increased movement characteristic of summer this increases to an average of 2.5 times their BMR (Table 8.2). Maximum energy conservation is apparently achieved at calving time with the minimal movement characteristic of this season reducing active energy expenditure to 1.3 times their BMR, whereas on days of severe fly harassment or in the hunt, the daily maintenance energy requirement increases to 2.9 and 3.8 times the BMR respectively. This considerable seasonal variation in energy expenditure is illustrated for a Hardangervidda animal in Figure 8.3.

Over the whole year an 80kg reindeer on Hardangervidda may therefore be spending 1.8 million kcals on its basic metabolism and activity. This represents an average of 1.9 times its BMR, or 1.8 times if the effect of the hunt is excluded. 6.6% of the maintenance energy requirement can be attributed to the increase of activity associated with hunt disturbance. A previous estimate of the effect of the hunt was 8-9% of the annual maintenance requirement (by Gaare; in Gaare, Thomson & Kjos-Hanssen, 1975).

As well as the energy expended on activity, estimates of the energy required for body growth, gestation, and lactation in females is being considered in the energy model (Bunnell, White, Russell & Thomson, in prep.). Further refinements in calcul-

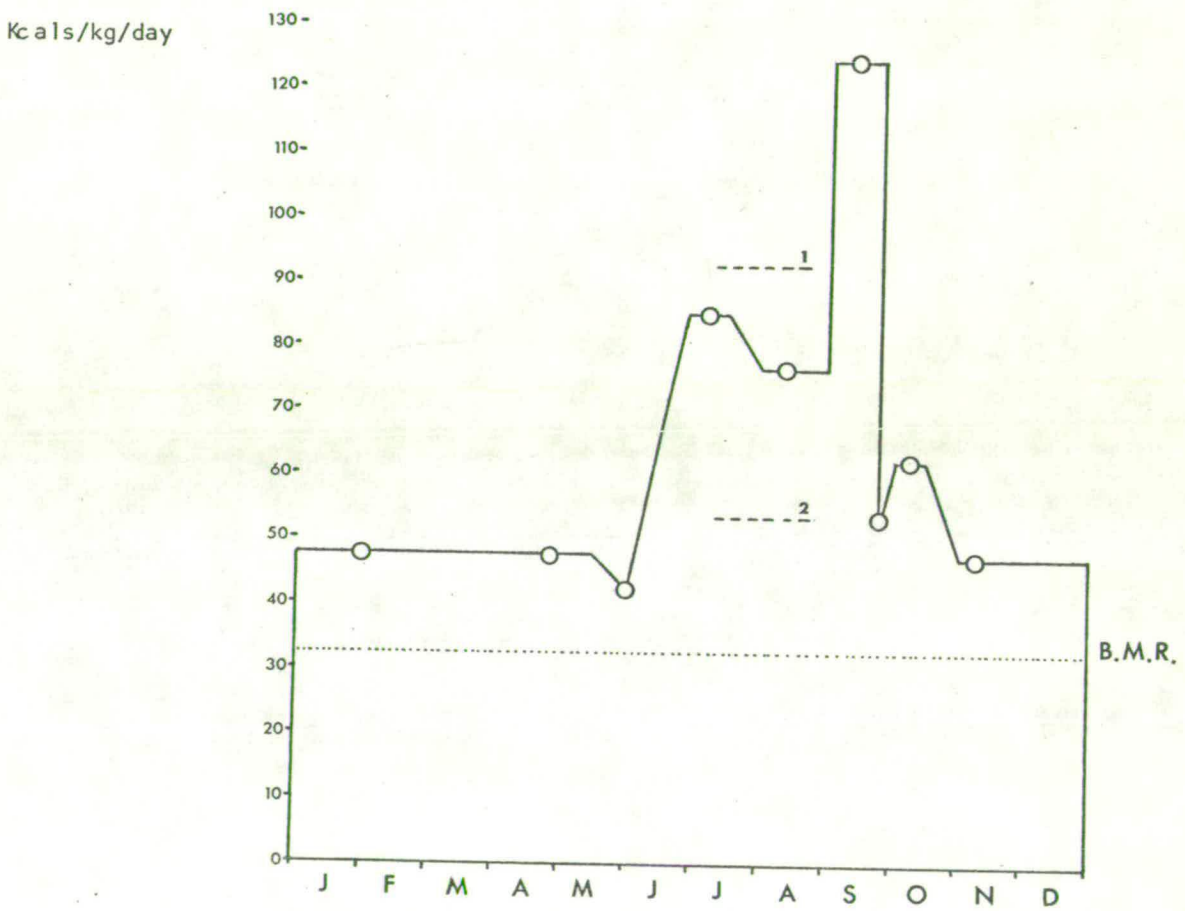
Table 8.2 The daily energy expenditure of an 80kg reindeer over different seasons.

Activity	WINTER			CALVING			EARLY SUMMER			SUMMER (average)			with severe fly harassment			days of no fly harassment			HUNT			RUT		
	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe	% Time	Qe	%Qe
Basal metabolism	100	2595	-	100	2595	-	100	2595	-	100	2595	-	100	2595	-	100	2595	-	100	2595	-	100	2595	-
Lying	37	960	25	37	960	28	28	727	11	21	545	9	10	260	4	30	780	18	17	441	4	25	649	13
Standing	8	226	6	4	113	3	3	85	1	8	226	4	15	423	6	4	113	3	3	85	1	10	282	6
Lying down & getting up	(10 events)	20	1	(16 events)	32	1	(16 events)	32	1	(14 events)	28	1	(14 events)	28	1	(14 events)	28	1	(12 events)	24	1	(12 events)	24	1
Grazing	43	1510	40	54	1898	56	36	1264	19	42	1473	24	37	1297	17	49	1722	40	30	1053	11	43	1511	30
Ruminating	(18.5)	64	2	(18.5)	64	2	(14)	48	1	(21)	91	1	(5)	18	1	(15)	52	1	(8.5)	30	1	(12.5)	43	1
Walking	11	791	21	4	287	8	18	1293	19	18	1293	21	22	1578	21	13	937	22	19	1366	14	16	1150	23
Trotting & Running	1	225	6	0.1	23	1	15	3373	49	11	2474	40	17	3823	51	3	675	16	31	6973	70	6	1349	27
Totals	100	3796		99.1	3377		100	6822		100	6130		101	7427		99	4307		100	9972		100	5003	
Multiple of BMR		1.46			1.30			2.63			2.36			2.86			1.66			3.84			1.93	

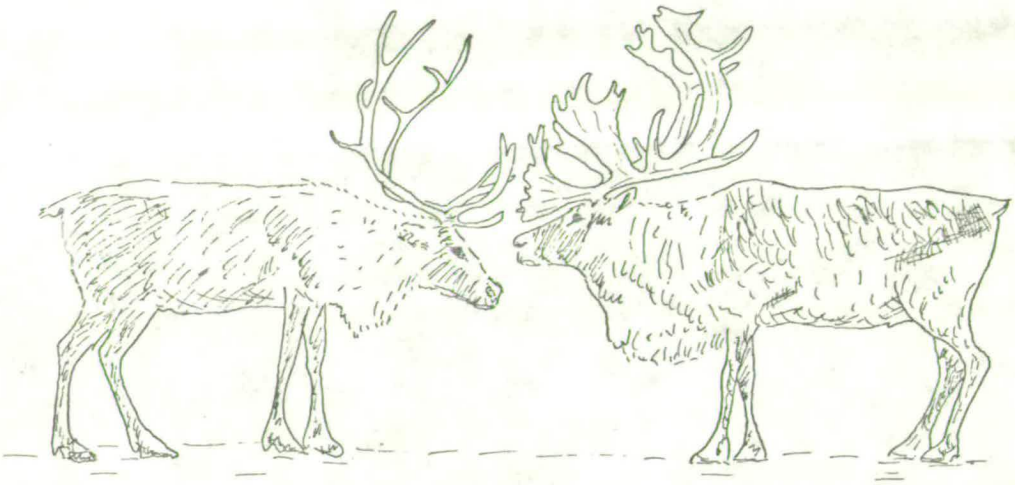
Qe = kcals/day

ation will be achieved when the energy costs of activities are satisfactorily measured for reindeer, including the cost of digging through snow in winter; and when sex and age differences in activity are more closely monitored - for example amongst different ages of males at rutting time, and amongst dominant and subordinate ranking animals in winter. In addition, although the increase in activity due to disturbance from insects, natural predators, and hunters is included in the activity budget, this may not fully evaluate their effect on the individual. Physiological stress may operate in addition to the simple expenditure of heat calories. For example, disturbances are said to increase the susceptibility of reindeer to diseases, such as pulmonary emphysema in cold weather, and can cause pregnant females to abort in domestic reindeer populations in the U.S.S.R. (Zhigunov, 1968). There is evidence to suggest that as a direct consequence of the stress and social confusion of close herding, domestic reindeer can lose physical condition (Reimers, 1972a). The obvious irritation experienced from insects in summer may conceivably have a stress effect, additional to the direct energy cost of avoidance behaviour.

Fig. 8.3 Active energy expenditure throughout the year for an 80 kg reindeer. (Based on activity data).



1. Energy expenditure on days with severe insect harassment.
2. Energy expenditure on days without insect harassment.



Reindeer and Caribou

(from sketch by A.R. Dugmore, 1913)

Or is it Caribou and Reindeer?

CHAPTER NINE COMPARISON WITH OTHER RANGIFER POPULATIONS

> "From the time of McDougall's 'Psychology of Animals' up to now, it has been generally recognised that the pace-maker of evolutional processes is the evolution of behaviour."
>
> A.B. Bubenik, 1975.

Every behavioural investigation of an animal population in its natural habitat is sooner or later confronted with the question of which aspects of behaviour are relatively fixed and can be considered characteristic of the species, and which aspects are flexible in that their manifestations depend directly on the prevailing social or physical environment. This relates directly to the traditional ethological dichotomy as to which behaviour is "instinctive" or innate, and which is learned, and whether the learned behaviour is flexible in response to a slowly or suddenly altered environment. To attempt to answer this question fully would require a long programme of comparitive experimental studies in controlled environments, and in no higher mammal are there definitive answers covering the range of a species' behaviour patterns and social organisation.

Systematic comparison of different Rangifer tarandus populations was not the object of this study, but the opportunity was taken to observe and record the behaviour of reindeer on ranges other than the main study area, Hardangervidda, notably on Snøhetta, North Ottadalen, and Forelhogna (Table 1.1). The observed /

observed differences, or more correctly the observed similarities in behaviour and social structure between these different populations, prompted me to consider the behaviour of wild reindeer in Norway (i.e. on the mountain ranges of South Norway) as a whole. Also, the opportunity arose to make behaviour comparisons with the sedentary tame reindeer herd in the Cairngorms, Scotland, and with migratory herds of barren-ground caribou on the Alaskan coastal tundra. By relating this experience to other behavioural studies of Rangifer populations; particularly by Pruitt (1960), Kelsall (1968), and Miller et.al.(1975) on barren-ground caribou in Canada, and in Alaska by Lent (1965a, 1966); by Bergerud (1971; 1974a, b) on woodland caribou in Newfoundland; by Espmark (1964a, b; 1971a) on semi-domestic reindeer in Sweden, and in Norway by Skjenneberg and Slagsvold (1968); and by Baskin (1970) on wild and domestic reindeer in the U.S.S.R.; it becomes possible to draw some tentative conclusions on the nature of the differences observed. In particular, whether such differences have arisen in direct response to population characteristics or range quality parameters, to human influence through herding or domestication, to differences between the mountain, tundra and woodland habitats, or to racial differences between mountain/tundra type and woodland type Rangifer, or between Palaearctic Rangifer (reindeer) and Nearctic Rangifer (caribou). Differences in the behaviour of animals belonging to different racial types cannot be assumed to be of genetic origin until all the possible responses to environmental factors have been eliminated as possibilities.

Comparing /

Comparing the various studies on Rangifer, one is immediately struck by the similarity in the behaviour patterns recorded, both in their performance and their timing in respect to seasonal changes. Not only acts of individual behaviour but social behaviour patterns and relationships are seen to be identical or closely parallel in different populations, and this is obvious from my own comparitive observations as well as comparison with the literature. Nevertheless, perhaps as a consequence of Pruitt's (1960) warning that "extreme care should be used in any attempt to interpret caribou behaviour within the same frame of reference as wild or domestic reindeer", it was with some surprise that Skogland and I experienced such a strong sense of deja vue within the first few minutes of observing caribou on the Alaskan tundra. Subsequent observation and analysis of caribou-range and caribou-insect relationships confirmed the close parallel with wild reindeer on the Hardangervidda mountain plateau, some 6000km distant (White, Thomson, Skogland, et.al., 1975).

However, unity of behaviour between Rangifer populations cannot be taken prima facie as characteristic of the species as such when the Northern environments in which they live are so similar in regard to habitat, climate, food supply, snow regime, etc. Indeed, there are many ungulate populations living in similar open habitat, not necessarily in Arctic/Alpine zones, whose recorded social structure and behaviour bears some interesting similarities to that of reindeer herds; e.g. mountain goats in British Columbia (Geist, 1965), Pronghorn antelopes on Alberta prairies (Bruns, 1969), Saiga on the steppes /

steppes in the U.S.S.R. (Bannikov et. al., 1961), Marco Polo sheep in the Pamir Mountains of Afghanistan (Skogland, in press), and even wildebeest herds on the African savanna (Estes, 1966). The behaviour and social structure of reindeer in their tundra or mountain habitat bears a closer relation to any of these ungulate populations, to which they are only distantly related taxonomically, than it does to, say, other Cervidae living in forest habitat, such as roe deer or moose populations. While an inter-species comparison is outwith the scope of this study, the influence of habitat on the social organisation of different ungulate populations living in temperate environments, could be integrated into a worthwhile analysis, as has been attempted for tropical antelopes by Jarman (1974).

Having stressed the similarity between populations in parallel environments and in particular between the Rangifer populations in Northern habitats, it is nevertheless desirable to attempt to analyse the origin of such behavioural differences as can be detected between wild reindeer populations on different ranges, between wild and domestic reindeer, between mountain, tundra and woodland living Rangifer, and between caribou and reindeer.

9.1. WILD REINDEER POPULATIONS IN SOUTH NORWAY

No differences in behaviour were observed between reindeer on Hardangervidda, Snøhetta, North Ottadalen, and Forelhogna which could not be attributed directly to differences in their prevailing /

prevailing population structures, body conditions, or respective quality of the ranges. For example, the observed differences in rutting behaviour between ranges (Ch.7.8) was concluded to be a direct consequence of widely divergent sex ratios and age of rutting males. The difference in activity times and nursing behaviour of females on North Ottadalen compared with Hardangervidda (Ch.5.4.4.) was seen as a difference in behaviour between females in good body condition and females in poor condition, respectively, at calving time. Differences in range quality as regard food supply undoubtedly influences factors such as the amount of time spent grazing, the extent of movement, etc. For example, following the overgrazing of the Snøhetta range animals adopted a new seasonal pattern of moving in early winter to the ungrazed pastures of the Knutshø area and returning in spring (Ch.3.1.). On Hardangervidda this late winter/early spring movement from wintering areas to calving grounds is distinct and prolonged enough to consider it a definite migration (Ch.7.4), whereas most other ranges are too small to allow extensive lateral movement, although altitudinal movements may compensate for this.

Apart from this particular constraint put on a population by the physical size of the range they inhabit, variation between ranges in population structure, body condition or pasture quality at any one time can equally apply to any one population over a period of time. The difference in behaviour observed between ranges were the same as those which would be expected from within one population experiencing progressive changes /

changes in these dynamic variables. Geist (1970) considers that in the near future we may be able to construct "behavioural performance criteria" from which it would be possible to compare relative body condition and pasture quality between ranges, or to monitor a single population over a period of time. For wild reindeer I would suggest that to develop such performance criteria, attention should be paid to comparison of activity times, nursing behaviour, and the extent of play within a population.

9.2. WILD AND DOMESTIC REINDEER

The differences which might be observed between the behaviour of a wild and a domestic or semi-domestic population might include all of the differences outlined above, and these should be considered before assuming that man's husbandry has had any influence on behaviour. From the behavioural reports for domestic and semi-domestic reindeer in Norway, Sweden and the U.S.S.R. (references as previously), it would appear that there are few essential differences with the wild reindeer of South Norway. Unlike most other domestic animals, reindeer have been subject to minimal genetic manipulation by man. Domestic populations can and do revert to the wild state if permitted. For example, the present free-living population of North Ottadalen is for the most part descended from domestic reindeer released in 1964, and some 5-6 years later showed no discernible differences with truly wild populations such as on nearby Snøhetta, apart from them still having a slightly lesser flight distance, and with a higher percentage of white calves /

calves born. (25-30% of young calves on North Ottadalen were white or greyish-white, and only 1-2% on Hardangervidda. Domestic reindeer herders favour white animals for breeding purposes.)

Apart from their reaction to man, and flight distance, the main behavioural differences in a domesticated population appear to be in the realm of social relationships. Domestic reindeer are rounded up into corrals at least twice a year for ear-tagging of calves, castration of selected males, and for slaughtering. These mass round-ups must at least temporarily obscure and confuse normal social relationships such as dominance-subordination, leader-follower, and encourage separations of mothers and calves. Reimers (1972a) suggests further that the poor body condition of particular domestic populations may be directly linked to the stressful conditions which animals experience when they are herded together.

Social relationships are also altered where deer are provided with artificial feed or salt licks. Frequent aggressive acts may occur in competition for the limited resource which would not have occurred in the wild situation. Where particular reindeer are kept together over a long period they have the opportunity to learn to individually recognise each other which can lead to an entirely untypical social organisation. For example, in the sedentary herd of tame reindeer in the Cairngorms, deliberately kept at less than 100 head, familial associations of three or four generations of deer are apparent, while hierarchial relationships in winter appear to be as much based /

based on individual recognition as such as on signal releasers such as antler size (Ch.7.2.). Even for semi-domestic reindeer in the mountains around Røros, Norway, the dominance-subordination relationships were apparently less predictable than in the wild populations (T. Skogland, pers. comm.).

At the lower level of individual or social behaviour patterns however, there would appear to be no significant differences between reindeer populations directly on account of human influence; e.g. the incidence of "thief-suckling" or multiple suckling by semi-domestic reindeer calves is definitely not, as Espmark (1971a) speculated, the result of human influence since it is equally common amongst wild reindeer (Ch.5.4.4.), whereas it does not occur in caribou (see Ch.9.4.).

9.3. MOUNTAIN, TUNDRA AND WOODLAND REINDEER

The effect of habitat type on the behaviour and social organisation of reindeer cannot yet be fully evaluated, confounded as it is by type differences in the animals themselves; viz. in Eurasia, Rangifer tarandus tarandus, the tundra- or mountain-type reindeer, and R.t. fennicus, the forest-or woodland-type reindeer. The mass of evidence points to the fact that the basic individual and social behaviour patterns are common to reindeer, whether they live on open habitat or in woodland, and whether they are R.t. tarandus or R.t. fennicus. Espmark's studies on rutting behaviour patterns (1964a), dominance-subordination relationships (1964b), and the mother-young relationship (1971a) were conducted on R.t. fennicus, but they

do /

do not conflict with the equivalent descriptions for R.t. tarandus in this study. However, at the level of social structure and organisation some differences are apparent.

In the view of Bubenik (1975a), woodland reindeer are less sociable, of "higher social temperature", and less migratory than tundra reindeer, but he considers that these behavioural differences may be reversed completely as soon as the herds leave the taiga forests. (My underlining.) Recent evidence from Finland suggests that while a population's adaptation to a new habitat may indeed by considerable, it may still not be as suited to the new environment as the type which has evolved in it. Domestic reindeer in Finland are mountain-type, which 200-300 years ago were brought to live year-round in the Northern forests (Sulkava and Helle, 1975). There they have abandoned their migratory behaviour, and in winter regularly dig for food in greater hardnesses of snow than is normal for tundra Rangifer (Sulkava and Helle, op.cit.). However, the original woodland-type reindeer, represented in Finland by a small wild population on the eastern border, have additionally evolved morphological adaptations to suit forest life. In particular, R.t. fennicus are larger and stronger and thus more suited to coping with the abundant forest snow in winter (Siivonen, 1975), while their typically narrow upright antlers must facilitate their passage between the trees in dense forest. The domestic forest-living reindeer, on the other hand, have retained their spread mountain-type antlers (illustrated in Siivonen, op. cit.).

Other /

Other differences in social structure or organisation between reindeer populations in different types of habitat are now considered briefly:

a) In common with other ungulates, reindeer living in forested terrain consort in smaller groups than when in open habitat (re.Ch.6.2.).

b) The activity pattern of Rangifer is particularly sensitive to environmental influences (Thomson, 1973). When activity studies of woodland populations are conducted they may well exhibit differences, for example, active peaks at dawn and dusk as is common for forest-living ungulates, and not a regular alternation of active periods during the day, typical of populations living in open habitats (Thomson, op. cit.).

c) As an example of the direct influence of habitat on reindeer movement and aggregation patterns, it may be observed that the nature of the habitat, whether forest, mountain or tundra, determines both the type and abundance of harassing insects, and the availability of insect-relief areas such as mountain tops, snow patches, or lake and sea coasts.

d) There is evidence for harem formation at rutting time being restricted to woodland-living or woodland-type Rangifer, while larger multi-male rutting groups are characteristic of mountain-type Rangifer (re.Ch.7.8.).

e) An apparent difference between the behaviour of woodland-type and mountain-type reindeer at calving time is that pregnant females of the former type seek seclusion or avoid other deer until the calf is dropped (Espmark, 1971a), /

1971a), while the latter will not normally seek seclusion and may calve in the company of other animals (Espmark, op. cit.; and this study, Ch.5.4.2.).

Unless there is firm evidence to the contrary, it should be assumed that these differences arise as a direct response to the habitat and are not genetically fixed as part of a racial type. However, prolonged differences in behaviour between populations can ultimately lead to genetic differences in behaviour, and this more rapidly in small, isolated populations and where the behaviour in question is of immediate consequence to survival. For example, Bergerud (1971) studying a woodland-type caribou (R.t. caribou) population in Newfoundland found that the calves experienced heavy mortality from lynx attacks while in the forest in summer. The defensive behaviour of caribou has evolved to match the predatory behaviour of the wolf, but not the lynx. Bergerud hypothesises that heavy lynx predation in the absence of wolves may have started evolutionary selection of these caribou in a new direction. One would then expect greater concealment of calves, a more spread calving season, and a rapid dispersal after calving. These tendencies are, in fact, evident amongst caribou in another population in Newfoundland which might explain why there is less predation on this population (Bergerud, op. cit.).

9.4. REINDEER AND CARIBOU

Justification for considering reindeer and caribou behaviour within the same framework has been questioned. Pruitt (1960) contended /

contended that reindeer are more sedentary, phlegmatic and gregarious than caribou. When comparing caribou with domestic reindeer this might certainly hold true as a generalisation. However, wild reindeer are only more sedentary than caribou when they are restricted by the size of their ranges, as in South Norway, whereas in the U.S.S.R. their migrations are hardly less prolonged and extensive than those of barren-ground caribou in North America. As to whether wild reindeer are more phlegmatic, it would seem that their flight distance is as great in winter and as short in summer as that reported for caribou. Nor do the vast herds of caribou in spring and summer support the supposition that they are less gregarious than their reindeer counterparts (although a greater degree of sexual segregation may occur in caribou - considered later).

The way in which aspects of the social structure and organisation of populations are influenced by particular factors of the environment is evidently parallel whether it occurs on Rangifer in the Palaearctic or Nearctic zones. This is evident from comparing the results of this study with other recorded studies on caribou, as well as from direct comparison with barren-ground caribou on the Arctic tundra in summer 1972. As a documented example, the influence of insect activity on caribou activity and group structure was largely predictable on the basis of previous summer observations of wild reindeer on Hardangervidda (Thomson, 1971; 1973; White, Thomson, Skogland, et. al., 1975; Apps. 2, 3 & 7).

However, while a vast repertoire of behaviour acts and responses are /

are common to both reindeer and caribou, there are particular differences evident from direct observation and literature comparison (references in Table 9.1), in particular four interesting differences in acts of behaviour at the individual level. The excitation jump, head bobbing, ritualised alarm pose, and head-high threat of caribou are not performed by reindeer or very rarely or imperfectly (Table 9.1). These acts were particularly looked for in reindeer when it became clear that they are relatively common patterns for caribou in the appropriate situations. In general it would appear that caribou behaviour has attained a greater degree of ritualisation, at least in regard to these acts. A functional pattern when used as a communicative signal can become a progressively more effective signal through ritualisation. Thus the urination stance in reindeer functions as an alarm posture but only in caribou has it developed as a more effective signal in that one back leg is held particularly far out. Similarly, a single reindeer suddenly frightened at close range may occasionally bound off from its back legs, but without exhibiting the conspicuous exaggerated vertical leap and twist characteristic of caribou, and termed the excitation jump. The head-high threat is a common threat pattern of active caribou but not of reindeer, except uncommonly from a lying reindeer. In the rut the basically similar "driving" position of the male with the head stretched out towards the female is, however, common to both reindeer and caribou. Also head-bobbing by the female towards its young calf is used as an attraction pose only by caribou; only reindeer calves bob their heads indiscriminately or while playing. Such differences in individual /

Table 9.1 Differences in the behaviour patterns of reindeer and caribou.

Type of Behaviour		Occurrence in Caribou		Occurrence in Reindeer
INDIVIDUAL BEHAVIOUR				
Excitation Jump	+	common fright reaction. (Dugmore, 1913; Murie, 1935; Pruitt, 1960; de Vos, 1960; Lent, 1966; Bergerud, 1974b).	—	very rare; occasionally an incomplete fright bound seen.
Head Bobbing	+	common ♀ to calf attraction pose. (Pruitt, 1960; Bergerud, 1964; Lent, 1966; Miller & Broughton, 1973).	—	rarely by ♀ ; occasionally by calves in play. (Not recorded by Baskin, 1969; "very infrequently" by Espmark, 1971a).
Alarm Pose	+	ritualised urination posture - one hindleg held well out. (Pruitt, 1960; Lent, 1966; Alaska 1972*).	—	normal urination posture used in alarm - both hindlegs equidistant.
Head-high Threat	+	common threat type. (Pruitt, 1960; Lent, 1966; Kelsall, 1968).	—	not recorded in active reindee infrequently by lying animals.
Multiple Suckling (of a ♀ by two or more calves)	—	very rare. (Not recorded by de Vos, 1960; Lent, 1966; Alaska 1972*; 1 record by Bergerud, 1964).	+	common in summer calves. (also Espmark, 1971a; Skjenneberg & Slagsvold, 1968 ; Luick et. al., 1971).
♂ RUTTING BEHAVIOUR				
Hunching & Urinating	+	frequent (Lent, 1965a; Bubenik, 1975b); uncommon (Bergerud, 1974a).	+	common. (also Espmark, 1964a; Skogland 1974).
Muzzling & Pawing own Urine Patch, (then body contacts)	—	not recorded.	+	frequent. (also muzzling own urine patch recorded by Espmark, 1964a).
Muzzling & Pawing ♀ Urine Patch	+	frequent (Bergerud, 1974a).	—	not recorded (sniffing then flehmen only).
Pawing ground, near rival	—	very rare (1 record by Bubenik, 1975b).	+	occasional. (also Espmark, 1964a).
Female Chase	—	not recorded.	+	occasional.
♀ CALVING BEHAVIOUR				
Time for ♀ to pass placenta		Short. (few minutes after birth in Pruitt, 1960; few mins. to over 2 hours, Lent, 1966).		Long. 2 to over 5 hours after birth. (1.5-7 hours, Espmark, 1971a).
Time for ♀ and calf to leave birth site		Short. (1 hour after birth in Pruitt, 1960; 3.6 hours in de Vos, 1960; 1-3 hours & up to 4 hours, Lent, 1966).		Long. 8 to 40 hours after birth. (3-30 hours, Espmark, 1971a).
SOCIAL STRUCTURE				
Segregation of Sexes	+	Mixed summer herds constantly de-segregate after periods of insect harassment - Alaska, 1972*.	—	Mixed summer herds remain integrated - Hardangervidda.
Calf Groups	+	Groups of resting calves form. (de Vos, 1960; Alaska, 1972*).	(+)	Not observed. (but recorded by Espmark, 1971

* Unpubl. observations of barrenground caribou at Prudhoe Bay, Alaska, in summer 1972.

idual behaviour cannot be readily explained in terms of differing environments between populations, as the physical and social conditions preceeding the event appear to be parallel, suggesting that real and possibly genetic differences exist for these specific acts of individual behaviour.

Calving behaviour of the female is a further aspect which appears to differ between reindeer and caribou. Caribou females pass the placenta within a few minutes or up to two hours after birth of the calf, whereas reindeer take at least 1½-2 hours and up to 7 hours (Table 9.1). Reindeer females normally take a day or two to leave the birth site with their calf whereas caribou females will leave within 1-4 hours. This latter difference may however be related to the on-going migratory urge in barren-ground caribou females during the calving season. In summer, multiple suckling of one female by several calves is a common occurrence in both domestic (Espmark, 1971a) and wild reindeer (Thomson, 1973), but is not performed by caribou (Lent, 1966; Thomson, in prep.: Prudhoe Bay). Since it is the calf which initiates or attempts to initiate suckling on a strange female it is a behavioural difference which arises at an early stage in the ontogeny of behaviour patterns.

While the above differences are clear and unarguable, there are other aspects of behaviour which appear to differ between reindeer and caribou but may yet prove to be the result of incomplete observations of caribou behaviour to date. For example, the rutting behaviour of the mature reindeer includes frequent hunching and urinating, occasionally followed up by a muzzling /

muzzling, pawing, and a rubbing sequence which distributes urine and possibly also glandular scent over its body (Ch.5.3.1.) While hunching and urinating is recorded as a caribou pattern, the rubbing sequence is not. The rare individual pawing action when a reindeer male in rut is confronted by a rival is also not recorded for caribou, nor is the "rutting chase" of the female by a string of males (Ch.5.3.1g.). Further observation on caribou will be required to determine whether these are real differences or due to lack of sufficient observation, probably the latter. For example, violent pawing at the ground with soil thrown up is described for a barren-ground caribou bull in the rut when approached by the dummy antlers of Bubenik (1975b). This is also true of other aspects of social behaviour recorded in this study for wild reindeer, such as play by adults, leadership, the winter hierarchy, behaviour under winter winds, and residual sex behaviour in winter, all of which have either had only a passing mention for caribou, or none at all. Indeed, at one time it was even claimed that caribou have no social organisation (de Vos, Brokx & Geist, 1967). However, recent studies are confirming the importance of such factors as the mother-infant relationship (Miller & Broughton, 1973), group cohesion (Parker, 1972; Miller et.al., 1975), and leadership (Child, 1973; Miller, et.al., 1972) for caribou populations.

Even at the level of social organisation differences between reindeer and caribou as such may apply and require further investigation. For example, at Prudhoe Bay, Alaska, it was clear that without insect harassment caribou groups readily segregated into male groups and female-young groups, which would /

would only come together again and form massed herds during insect harassment; then segregate again on dispersal. On Hardangervidda there was no tendency for mixed herds to segregate when insect attacks subsided. Similarly on Hardangervidda I did not observe that calves in summer associated together in small temporary sub-groups for grazing and lying, whereas this was occasionally seen for caribou calves on non-insect days at Prudhoe. However, occasional resting groupings of calves older than one month have been observed in domestic reindeer (Espmark, 1971a).

Misleading conclusions can often be drawn from insufficient or lack of concentrated observation. For example, in support of the contention that caribou wean much earlier than reindeer, Kelsall (1968) noted that "many field men have observed large herds of (barren-ground) caribou for long periods from mid-July onward without seeing suckling". This is surprising since with 127 hours of concentrated caribou observation at Prudhoe Bay in summer 1972 I observed 55 successful suckling events, with 19 of them from "mid-July onward" to the beginning of August, at a frequency which would be expected from observation of reindeer calves at the same age.(The real difference apparent was that reindeer events were often multiple sucklings, whereas all the caribou sucklings observed were single mother-calf events).

It has been said that milling round in a massed circle is characteristic of reindeer herds and does not occur in caribou. However, it is not such a common pattern in wild reindeer even under insect harassment, and conversely I have observed thousands /

ands of caribou massed together under insect harassment behaving no different from wild reindeer under the same conditions.

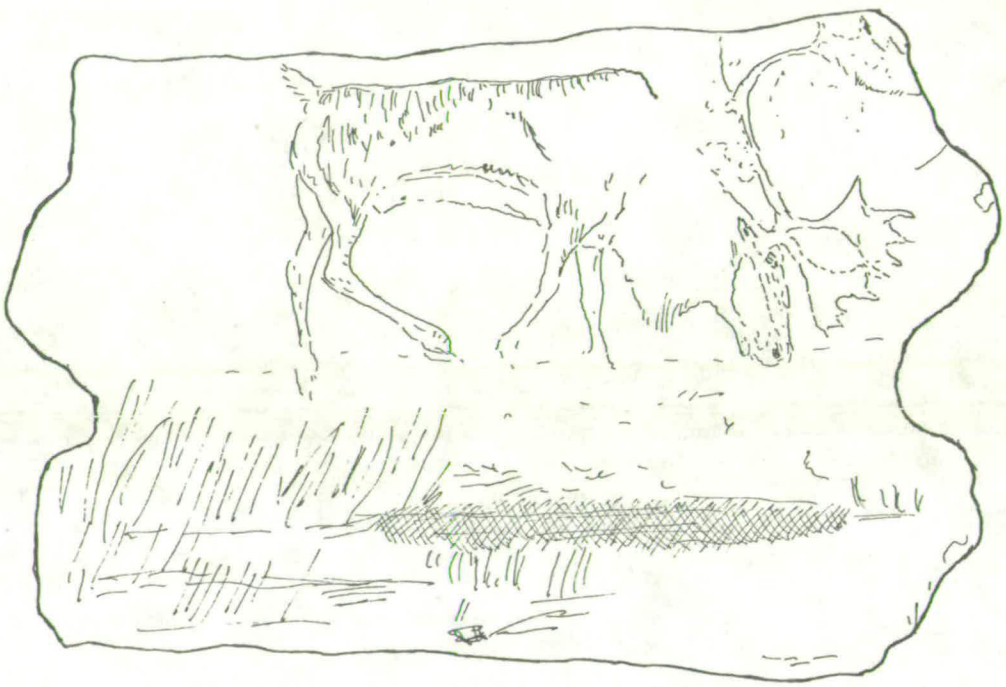
The evidence for well-defined differences in the social structure and organisation of caribou as distinct from reindeer herds is at the best weak, whereas the impact of a particular environment or environmental influence on the behaviour of a Rangifer population can be identified with more certainty. This is presumably why the behaviour of wild mountain reindeer in Norway bears a firm resemblance to that of barren-ground caribou on Alaskan tundra, although the populations are geographically and genetically remote from each other, whereas the Scottish tame reindeer herd in the Cairngorms, although it has recently descended from Scandinavian mountain reindeer stock mostly (Reindeer Council, 1955), shows an entirely different social structure and individual relationships.

The evidence for the importance of the physical and social environment in moulding the behaviour of all Rangifer populations is outstanding. However, it should be recognised that the potential does exist for geographically distinct populations of Rangifer to evolve behavioural or morphological features peculiar to that area. For example, in the small Altai-Sayan population of wild reindeer in the U.S.S.R., up to 25% of the females possess no antlers (Shaposhnikoff, 1955). This he claims to be a "primitive feature", but it may equally well be a developing characteristic within this small population. As Bergerud (1971) argues for Newfoundland caribou, natural selection can occur relatively rapidly in small isolated populations. /

populations. So far, most of the evidence for evolved differences in behaviour seems to come from comparisons of reindeer and caribou. To re-cap, caribou have developed or developed further the excitation jump, head bobbing, one-legged alarm stance, and head-high threat. Interesting differences also exist in the time taken to pass the placenta, and to leave the birth site. Unless subsequent observations of caribou prove otherwise, the rutting behaviour pattern of reindeer males appears to have developed to a greater extent, while the behaviour of older reindeer calves in moving to join an existing suckling event has not so far been taken up by their caribou counterparts.

Nevertheless, the massive uniformity in behaviour between reindeer and caribou is more than sufficient justification for considering the behaviour of the species within a unified frame of reference, and for analysing differences in the social and physical environment of different Rangifer tarandus populations to explain most observed differences in behaviour.

REFERENCES



Late Palaeolithic engraving on perforated bone staff, Kesserloch, Thayngen, Switzerland (from Seton, 1910).

REFERENCES

ALTMANN, M., 1952. Social behavior of elk, Cervus canadensis nelsoni in the Jackson Hole area of Wyoming. Behav. 4 (2): 116-143.

ALTMANN, M., 1956. Patterns of social behavior in big game. Trans. 21st N. Amer. Wildl. Conf.: 538-545.

AUNE, O.A., 1971. Produksjonen av villrein i Forelhogna området 1971. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 4pp.

BANFIELD, A.W.F., 1954. Preliminary investigation of the barren-ground caribou, Part 2 : Life history, ecology and utilisation. Wildl. Mgmt. Bull. I (IOB): 1-112. Canada Dept. of Northern Affairs.

BANFIELD, A.W.F., 1961. A revision of the reindeer and caribou, genus Rangifer. Nat. Mus. Canada Bull. 177: 1-137.

BANNIKOV, A.G.; ZHIRNOV, L.V.; LEBEDEVA, L.S.; & A.A. FANDEEV, 1961. Biology of the saiga. Eng. Transl., Springfield, Va., USA.

BARDEN, P., 1969. Oestrous behaviour in reindeer (Rangifer tarandus). Brit. Vet. Jour. 125: 48-50.

BASKIN, L.M., 1968. "Change in the behaviour of reindeer in relation to environmental conditions and the physiological state of the animal." Byull. Mosk. Obshch. Ispyt. Prirod. Otd. Biol. 3: 135-136.

BASKIN, L.M., 1969. "Maternal instinct in reindeer." Priroda (Moscow) 5: 73-75.

BASKIN, L.M., 1970. "Reindeer: Ecology and behaviour." 'Nauka', AS USSR, Inst. Evol. Morph. and Ecol. Animals, Moscow. (Eng. Transl. by Canadian Wildl. Serv.).

BENEDICT, F.G., 1938. Vital energetics; a study in comparitive basal metabolism. Carnegie Inst. Publ. 503: 1-215. Washington, D.C..

BERGERUD, A.T., 1960. Fall breeding behaviour of Newfoundland caribou. Canadian Wildl. Serv. Unpubl. Manuscript. 46pp.

BERGERUD, A.T., 1964 (?). Doe-calf relationship (caribou). Unpubl. Manuscript. (mimeo) 32pp.

BERGERUD, A.T., 1971. The population dynamics of Newfoundland caribou. Wildl. Monog. 25: 1-55.

BERGERUD, A.T., 1974a. Rutting behaviour of Newfoundland caribou. In: Symp. on Behav. of Ungulates and its Relation to Mgmt.; Univ. of Calgary, 1971. I.U.C.N. 24(1): 395-435.

BERGERUD, A.T., 1974b. The role of the environment in the aggregation, movement and disturbance behaviour of caribou. In: Symp. on Behav. of Ungulates and its Relation to Mgmt.; Univ. of Calgary, 1971. I.U.C.N. 24(1): 552-584.

BERGERUD, A.T., 1975. The reproductive season of Newfoundland caribou. Can. Jour. Zool. 53: 1213-1221.

BERGERUD, A.T. & M.J. NOLAN, 1970. Food habits of hand-reared caribou. Canadian Wildl. Serv. Unpubl. Manuscript. 46pp.

BLAXTER, K.L., 1962. The energy metabolism of ruminants. Hutchinson & Co., London.

BOLWIG, N., 1963. Facial expression in primates. Behav. 22: 167-192.

BROCKWAY, J.M. & G.M.O. MALOIY, 1967. Energy metabolism of the red deer. Jour. Physiol. 194: 22-24.

BROWNLEE, A., 1954. Play in domestic cattle in Britain: an analysis of its nature. Brit. Vet. Jour. 110: 48-68.

BRUNS, E.H., 1969. A preliminary study of behavioral adaptations of wintering pronghorn antelopes. M.Sc. Thesis, Univ. of Calgary, Alberta. 60pp.

BUBENIK, A.B., 1975a. Taxonomic value of antlers in genus Rangifer. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 41-63.

BUBENIK, A.B., 1975b. Significance of antlers in the social life of barren ground caribou. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 436-461.

BUNNELL, F.L.; WHITE, R.G.; RUSSELL, D.E.; & B.R. THOMSON, (in prep.). Active: A simulation model of the activity patterns and associated energy expenditure of Rangifer near Prudhoe Bay, Alaska.

BURLAND, C., 1973. Eskimo art. Hamlyn, England.

CABORN, J.M., 1965. Shelterbelts and windbreaks. Faber & Faber, London.

CALEF, G.W. & G.M. LORTIE, 1975. A mineral lick of the barren-ground caribou. Jour. Mamm. 56: 240-242.

CARLSSON, G., 1962. Studies on Scandinavian black flies. Opuscula Entomol. Suppl. 21: 1-280.

CHILD, K.N., 1973. The reactions of barren-ground caribou (Rangifer tarandus granti) to simulated pipeline and pipeline crossing structures at Prudhoe Bay, Alaska. Rep. of Alaska Coop. Wildl. Res. Unit. 49pp.

CLOUDSLEY-THOMPSON, J.L., 1961. Rhythmic activity in animal physiology and behaviour. Academic Press, London.

COWAN, I.McT., 1956. Life and times of the coast black-tailed deer. In: The deer of North America. W.P. Taylor (ed.). Stackpole Co., Pa..

CROOK, J.H.; ELLIS, J.E.; & J.D. GOSS-CUSTARD, 1976. Mammalian social systems: structure and function. Anim. Behav. 24: 261-274.

DARLING, F.F., 1937. A herd of red deer. Oxford Univ. Press, London.

DAUPHINÉ, T.C. & R.L. McCLURE, 1974. Synchronous mating in Canadian barren-ground caribou. Jour. Wildl. Mgmt. 38: 54-66.

DE VOS, A., 1960. Behavior of barren ground caribou on their calving grounds. Jour. Wildl. Mgmt. 24: 250-258.

DE VOS, A.; BROKX, P.; & V. GEIST, 1967. A review of social behavior of the North American cervids during the reproductive period. Amer. Midl. Nat. 77: 390-417.

DORST, J., 1962. The migration of birds. W. Heinemann, London.

DOWNES, J.A., 1965. Adaptations of insects in the Arctic. Ann. Rev. Entomol. 10: 257-274.

DUGMORE, A.R., 1913. The romance of the Newfoundland caribou. J.B. Lippincott Co., Philadelphia.

EDWARDS, R.Y. & R.W. RITCEY, 1960. Food of caribou in Wells Gray Park, British Columbia. Can. Field Nat. 74: 3-7.

EGOROV, O.V., 1965. "Wild ungulates of Yakutia." 'Nauka', Moscow. Israel Programme for Scientific Transl., Jerusalem, 1967.

ERICSON, C.A., 1975. Some preliminary observations on intra-specific acoustic communications of semi-domestic reindeer, with emphasis on the mother-calf relationship. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 387-397.

ESPMARK, Y., 1964a. Rutting behaviour in reindeer (Rangifer tarandus L.). Anim. Behav. 12: 159-163.

ESPMARK, Y., 1964b. Studies in dominance-subordination relationship in a group of semi-domestic reindeer (Rangifer tarandus). Anim. Behav. 12: 420-426.

ESPMARK, Y., 1968. Observations of defence reactions to oestrid flies by semi-domestic reindeer (Rangifer tarandus L.) in Swedish Lapland. Zool. Beiträge 14: 155-167.

ESPMARK, Y., 1970. Abnormal migratory behaviour in Swedish reindeer. Arctic 23: 199-200.

ESPMARK, Y., 1971a. Mother-young relationship and ontogeny of behaviour in reindeer (Rangifer tarandus L.) Z. Tierpsychol. 29: 42-81.

ESPMARK, Y., 1971b. Antler shedding in relation to parturition in female reindeer. Jour. Wildl. Mgmt. 35: 175-177.

ESPMARK, Y., 1971c. Individual recognition by voice in reindeer mother-young relationship. Field observations and playback experiments. Behav. 40: 295-301.

ESPMARK, Y., 1974. Dominance relationships as a possible regulating factor in roe deer and reindeer populations. In: Symp. on Behav. of Ungulates and its Relation to Mgmt., Univ. of Calgary, 1971. I.U.C.N. 24(1): 787-796.

ESPMARK, Y., 1975. Mother-young relationships in reindeer at birth of the new calf. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 409-413.

ESTES, R.D., 1966. Behaviour and life history of the wildebeest (Connochaetes taurinus B.). Nature 212: 999-1000.

ETKIN, W. (ed.), 1964. Social behaviour and organization among vetebrates. Univ. Chicago Press, Chicago.

EWER, R.F., 1968. Ethology of mammals. Logos Press, London.

FAGERHAUG, A., 1976. Vekst- og kondisjonsendringar hos villrein (Rangifer tarandus tarandus L.) pa Hardangervidda, 1969-1974. Hovedfagsopp. Thesis, Univ. of Trondheim, Norway. 70pp.

FRASER, A.F., 1968. Reproductive behaviour in ungulates. Academic Press, London.

FREEMAN, M.M.R., 1968. Ethnozoological interpretation of the brow tine in Arctic caribou. Arctic Circular 18: 45-46.

GAARE, E., 1968. A preliminary report on nutrition of wild reindeer in the Southern Scandes, Norway. Symp. Zool. Soc. London 21: 109-115.

GAARE, E., 1971. Vinterbeiter i Setesdalsheine villreinområde. Intern. Rep. of Direktoratet for jakt og ferskvannsfiske, Trondheim. (mimeo) 11pp.

GAARE, E.; SKOGLAND, T.; & B.R. THOMSON, 1970. Villreinens naeringsvaner og adferd. Hardangervidda, januar-juni 1970. Rep. of Norwegian IBP - Statens viltundersøkelser, Trondheim. (mimeo) 97pp.

GAARE, E. & T. SKOGLAND, 1971. Villreinens naeringsvaner. Hardangervidda, juli-desember 1970. Rep. of Norwegian IBP - Statens viltundersøkelser, Trondheim. (mimeo) 40pp.

GAARE, E. & T. SKOGLAND, 1975. Wild reindeer food habits and range use at Hardangervidda. In: Fennoscandian Tundra Ecosystems, Part 2: 195-205. Springer-Verlag, Berlin.

GAARE, E.; THOMSON, B.R.; & O. KJOS-HANSSEN, 1975. Reindeer activity on Hardangervidda. In: Fennoscandian Tundra Ecosystems, Part 2: 206-215. Springer-Verlag, Berlin.

GAARE, E. & G. HANSSON, 1975. Noen beite- og beitevaneundersøkelser i Forelhogna villreinområde. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 15pp.

GEIST, V., 1965. On the rutting behaviour of the mountain goat. Jour. Mamm. 45: 551-568.

GEIST, V., 1966. The evolution of horn-like organs. Behav. 27: 175-214.

GEIST, V., 1970. A behavioural approach to the management of wild ungulates. In: E. Duffey & A.S. Watt (eds.), The Scientific management of animal and plant communities for conservation. Blackwell Scientific Publics., Oxford.

GEIST, V., 1971a. Mountain sheep: a study in behavior and evolution. Univ. Chicago Press, Chicago.

GEIST, V., 1971b. Is big game harassment harmful? Oilweek 22(17): 12-13.

GJAEREVOLL, O. & R. JØRGENSEN, 1967. Mountain flowers of Scandinavia. F. Bruns Bok. Forlag, Trondheim.

GORBUNOV, E.I., 1939. "Sexual cycle and methods of diagnosis of rut in reindeer females." The Reindeer Industry 5: 101-134.

GOSSOW, H., 1974. Natural mortality pattern in the Spitsbergen reindeer. In: 11th Int. Congr. Game Biol., Stockholm, 1973. Nat. Swed. Environ. Protect. Board Public.: 103-106.

GRAF, W., 1956. Territorialism in deer. Jour. Mamm. 37: 165-170.

GRAHAM, N.McC., 1964. Energy costs of feeding activities and energy expenditure of grazing sheep. Austr. Jour. Agr. Res. 15: 969-973.

GRAZIOSI, P., 1960. Palaeolithic art. Faber & Faber, London.

HAFEZ, E.S.E. (ed.), 1969. The behaviour of domestic animals. Baillière, Tindall & Cassell, London.

HAGEN, A., 1965. Rock carvings in Norway. J.G. Tanum Forlag, Oslo.

HAMMEL, T.H.; HOUPT, T.R.; ANDERSEN, K.L.; & S. SKJENNEBERG, 1962. Thermal and metabolic measurements of a reindeer at rest and in exercise. Tech. Rep. of Arctic Aeromedic. Lab., Fort Wainwright, Alaska. 34pp.

HARANGVIDDENS FJELDBEITEKOMITEEN, 1911. Indstilling fra Fjeldbeitekomiteen om Hardangerviddens utnyttelse. Landbruks Depart. Rep., Kristiania (Oslo).

HAWKINS, R.E. & W.D. KLIMSTRA, 1970. A preliminary study of the social organisation of white-tailed deer. Jour. Wildl. Mgmt. 34: 407-419.

HEMMING, J.E. & R.E. PEGAU, 1972. Caribou report 12, Projects W-17-2 & 3. Alaska Dept. Fish & Game. Juneau, Alaska.

HENSHAW, J., 1968a. The activities of wintering caribou in north-western Alaska in relation to weather and snow conditions. Int. Jour. Biomet. 12: 21-27.

HENSHAW, J., 1968b. A theory for the occurrence of antlers in females of the genus Rangifer. 'Deer', Jour. Brit. Deer Soc. I: 222-226.

HENSHAW, J., 1970. Consequences of travel in the rutting of reindeer and caribou (Rangifer tarandus). Anim. Behav. 18: 256-258.

HOLTHE, V., 1975. Calving seasons in different populations of wild reindeer in south Norway. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 194-198.

HOLTHE, V., 1976. Villreinkvoter 1976. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 9pp.

I.B.P., 1971. International Biological Programme: Scandinavian Countries Progress Report 1969-70. 70pp.

IRVING, L., 1972. Arctic life of birds and mammals, Vol. 2: Zoophysiology and ecology. Springer-Verlag, Berlin.

IRVING, L. & J. KROG, 1955. Temperature of skin in the Arctic as a regulator of heat. Jour. Appl. Physiol. 7: 355-364.

JACOBI, A., 1931. Das rentier. Eine zoologische monographie der gattung Rangifer. Zool. Anzeiger 96. Leipzig.

JARMAN, P.J., 1968. The effect of the creation of Lake Kariba upon the terrestrial ecology of the Middle Zambezi valley, with particular reference to the large mammals. Ph.D. Thesis, Univ. of Manchester.

JARMAN, P.J., 1974. The social organisation of antelope in relation to their ecology. Behav. 48: 215-267.

JOHANSEN, A., 1973. The Hardangervidda Project for Interdisciplinary Cultural Research (HTK) : A presentation. Norweg. Archael. Rev. 6: 60-73.

KELSALL, J.P., 1968. The migratory barren-ground of Canada. Canad. Wildl. Serv.; Queen's Printer, Ottawa. 1-339.

KELSALL, J.P., 1975. Warble fly distribution among some Canadian caribou. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 509-517.

KJOS-HANSSEN, O., 1973a. Reindeer antlers and what they can tell us about the reindeer population. Norweg. Archaeol. Rev. 6: 74-78.

KJOS-HANSSEN, O., 1973b. Utbredelse og reproduksjon hos reinen på Hardangervidda. Hovedfagsopp. Thesis, Univ. of Bergen, Norway. 218pp.

KJOS-HANSSEN, O., 1974 (?). Wild reindeer buck-areas on Hardangervidda, southern Norway. Intern. Rep. of Hardangervidda Project for Interdisciplinary Cultural Research (HTK), Univ. of Bergen. (mimeo) 5pp.

KLEIN, D.R., 1974. The reaction of some northern mammals to aircraft disturbance. In: 11th Congr. Game Biol., Stockholm, 1973: 377-383. Nat. Swed. Environ. Protect. Board Public.

KRAFFT, A., 1972a. Villreinbestanden i Snøhetta og Knutshøfeltet. Jakt-fiske-friluftsliv 101: 412-413.

KRAFFT, A., 1972b. Prosjektnummer C 16. In: Forskningsprosjekter ved Statens viltundersøkelser. As, Norway. Intern. Rep.. 96pp.

KRAFFT, A., 1974. Villreintelling på Hardangervidda, sommeren 1974. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 4pp.

KRAFFT, A.; GAARE, E.; & E. REIMERS, 1970. Villreinen på Hardangervidda. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 10pp.

KROPOTKIN, P., 1902. Mutual aid, a factor of evolution. W. Heinemann, London.

LAWRIE, A.H., 1948. Barren ground caribou survey 1948. Canad. Wildl. Serv. Unpubl. Manuscript.

LENT, P.C., 1965a. Rutting behaviour in a barren-ground caribou population. Anim. Behav. 13: 259-264.

LENT, P.C., 1965b. Observations on antler shedding by female barren-ground caribou. Canad. Jour. Zool. 43: 553-558.

LENT, P.C., 1966. Calving and related social behaviour in the barren-ground caribou. Z. Tierpsychol. 6: 701-756.

LENT, P.C., 1975. A review of acoustic communication in Rangifer tarandus. In: Proc. Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 398-408.

LEWIN, V. & J.G. STELFOX, 1967. Functional anatomy of the tail and associated behaviour in woodland caribou. Canad. Field Nat. 81: 63-66.

LINCOLN, G.A.; YOUNGSON, R.W.; & R.W. SHORT, 1970. The social and sexual behaviour of the red deer stag. Jour. Reprod. Fert. Suppl. II: 71-103.

LINSDALE, J.M. & P.Q. TOMICH, 1953. A herd of mule deer. Univ. California Press, Berkeley, Calif.

LIVINGSTONE, L., 1973. Shieling transhumance and changes in land-use in the Scottish Highlands. M. Phil. Thesis, Univ. Edinburgh.

LOCKIE, J.D., 1956. Winter fighting in feeding flocks of rooks, jackdaws and carrion crows. Bird Study 3: 180-190.

LOIZOS, C., 1966. Play in mammals. In: Play, exploration and territory in mammals. P.A. Jewell & C. Loizos (eds.). Symp. Zool. Soc. London 18.

LORENZ, K., 1966. On aggression. Univ. Paperbacks, Methuen & Co., London.

LUICK, J.R.; HOLLEMAN, D.F. & R.G. WHITE, 1971. Studies on the nutrition and metabolism of reindeer-caribou in Alaska with special interest in nutritional and environmental adaptation. 1970/71 Tech. Prog. Rep. of Inst. Arctic Biol., Alaska.

McEWAN, E.H., 1970. Energy metabolism of barren ground caribou (Rangifer tarandus). Canad. Jour. Zool. 48: 391-392.

McEWAN, E.H. & P.E. WHITEHEAD, 1972. Reproduction in the female reindeer and caribou. Canad. Jour. Zool. 50: 43-46.

McEWAN, E.H. & A.J. WOOD, 1966. Growth and development of the barren ground caribou; Part I: Heart girth, hind foot length, and body weight relationships. Canad. Jour. Zool. 44: 401-411.

MARINGER, J. & H.-G. BANDI, 1953. Art in the Ice Age. Holbein Co., Basel.

MELI, J.J., 1975. Rapport fra flytelling av reinstammen i Forelhognaområdet i Mars 1975. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim.

MERLEN, R.H.A., 1953. Some notes on the reindeer. Brit. Vet. Jour. 109: 74-76.

MESCHAKS, P. & M. NORDKVIST, 1962. On the sexual cycle in the reindeer male. Acta. Vet. Scand. 3: 151-162.

MICHURIN, L.N., 1967. "Reproduction of wild reindeer on the Taimyr peninsula". Zool. Zh. 46: 1837-1841.

MILLER, D.R., 1975. Observations of wolf predation on barren ground caribou in winter. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 209-220.

MILLER, F.L., 1971. Mutual grooming by black-tailed deer in Northwestern Oregon. Canad. Field Nat. 85: 295-301.

MILLER, F.L.; ANDERKA, F.W.; VITHAYASAI, C.; & R.L. McCLURE, 1975. Distribution, movements and socialisation of barren ground caribou radio-tracked on their calving and post-calving areas. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 423-435.

MILLER, F.L. & E. BROUGHTON, 1973. Behaviour associated with mortality and stress in maternal-filial pairs of barren-ground caribou. Canad. Field Nat. 87: 21-25.

MILLER, F.L.; JONKEL, C.J.; & G.D. TESSIER, 1972. Group cohesion and leadership response by barren-ground caribou to man-made barriers. Arctic 25: 193-202.

MILLER, F.L. & G.R. PARKER, 1968. Placental remains in the rumens of maternal caribou. Jour. Mamm. 49: 778.

MOEN, A.N., 1973. Wildlife ecology. W.H. Freeman & Co., San Francisco.

MUNSTERHJELM, E., 1953. The wind and the caribou; hunting and trapping in northern Canada. Allen & Unwin, London.

MURIE, O.J., 1935. Alaska - Yukon caribou. N. Americ. Fauna 54.

MÜLLER, D. & E. LEMPERLE, 1964. Objektivierung und analyse olfactorischer signale der saügetiere mit hilfe der gaschromatographie. Naturwiss. 51: 346-347.

MÜLLER-SCHWARZE, D., 1967. Social odors in young mule deer. Amer. Zool. 7: 807.

MYKTOWYCZ, R., 1970. The role of skin glands in mammalian communication. In: Advances in chemoreception, Vol. I: J. Johnston, D. Moulton, A. Turk (eds.). Meredith Corp. N.Y..

MYRBERGET, S., 1971. Game management in Norway. Norweg. State Game Res. Inst. Pap. 2nd ser. 35: 1-22.

NATVIG, L.R., 1948. Contributions to the knowledge of the Danish and Fennoscandian mosquitoes. Norsk Entom. Tidsskrift Suppl. I: 1-567.

NAUMOV, N.P., 1933. "The wild reindeer". Dik. sever. olen'., USSR.

NAUMOV, N.P. & L.M. BASKIN, 1969. "Leadership in herds of reindeer as a group adaptation". Zhurnal obshchei biologii 30: 147-156.

ØRITSLAND, N.A., 1970. Temperature regulation of the polar bear (Thalarctos maritimus). Com. Biochem. Physiol. 37: 225-233.

ØSTBYE, E., 1969. Ravn som angriper rein. Fauna 22: 265-266.

ØSTBYE, E. & S. HAGVAR, 1972. List of terrestrial invertebrates of Finse area, Hardangervidda, south Norway. Rep. of High Mt. Ecology Res. Stat., Finse 1972:2. 1-21pp. Univ. Oslo.

ØSTBYE, E. et.al. (18), 1975. Hardangervidda, Norway. In: Structure and function of tundra ecosystems. Ecol. Bull. (Stockholm) 20: 225-264.

PALMER, R.S., 1951. The white-tailed deer of Tomhegan Camps, Maine, with added notes on fecundity. Jour. Mamm. 32: 267-280.

PARKER, G.R., 1972. Distribution of barren-ground caribou harvest in northcentral Canada. Canad. Wildl. Serv. Occas. Pap. 15: 1-20.

PRUITT, W.O., 1959. Snow as a factor in the winter ecology of the barren-ground caribou (Rangifer arcticus).

PRUITT, W.O., 1960. Behavior of the barren-ground caribou. Biol. Pap. Univ. Alaska 3: 1-44.

PRUITT, W.O., 1960b. Locomotor speeds of some large northern animals. Jour. Mamm. 41: 112.

PRUITT, W.O., 1966. The function of the brow-tine in caribou antlers. Arctic 19: 111-113.

QUAY, W.B., 1955. Histology and cytochemistry of skin gland areas in the caribou, Rangifer. Jour. Mamm. 36: 187-201.

REIMERS, E., 1972a. Growth in domestic and wild reindeer in Norway. Jour. Wildl. Mgmt. 36: 612-619.

REIMERS, E., 1972b. Prosjektnummer C17 - C25. In: Forsknings-prosjekter ved Statens viltundersøkelser. Ås, Norway. Intern. Rep. 96pp.

REIMERS, E., 1975. Age and sex structure in a hunted population of reindeer in Norway. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 181-188.

REIMERS, E. & E. GAARE, 1970. Villreinstammen på Hardangervidda må reduseres kraftig. Jakt-fiske-friluftsliv 99: 11-12.

REINDEER COUNCIL, 1955. Annual reports of the Reindeer Council of the United Kingdom, 1949-55 (1-6), Cambridge.

RICARD, M., 1969. The mystery of animal migration. Transl. by P.J. Whitehead. Constable & Co., UK.

ROBINSON, W.L., 1962. Social dominance and physical condition among penned white-tailed deer fawns. Jour. Mamm. 43: 462-469.

RYDER, M.L., 1977. Seasonal coat changes in grazing red deer (Cervus elaphus). Jour. Zool. Lond. 181; 137-143.

SCHEIN, M.W., & E.S.E. HAFEZ, 1969. The physical environment and behaviour. In: The behaviour of domestic animals E.S.E. Hafez (ed.). Baillière, Tindall & Cassel, London.: 65-84.

SCHJELDERUP-EBBE, T., 1922. Beiträge zur sozialpsychologie des haushuhns. Z. Psychol. 88: 225-252.

SCHMITT, E.V., 1936. "A determination of the period of gestation of domestic reindeer." Sov. Reindeer Ind. Arct. Inst., Leningrad, 8: 35-43.

SCHNEIDER, K.M., 1930. Das flehmen. Zool. Garten 3: 183-198; 4: 349-364; 5: 200-226, 287-297.

SCOTT, J.P., 1956. The analysis of social organization in animals. Ecology 37: 213-221.

SCOTT, J.P., 1958. Animal behaviour. Univ. Chicago Press, Chicago.

SEMENOV-TYAN-SHANSKII, O.I., 1948. "The wild reindeer of the Kol'sk peninsula." Trud. Lapland gos. zapov. 2.

SETON, E.T., 1910. Life histories of northern animals; An account of the mammals of Manitoba. C. Scribners Sons, N.Y..

SEVERINGHAUS, C.W. & E.L. CHEATUM., 1956. Life and times of the white tailed deer. In: The deer of North America. W.P. Taylor (ed.). Stackpole Co., Pa..

SHAPOSHNIKOFF, F.D., 1955. "The ecology and morphology of the northern Altai reindeer." Zool. Zh. 94: 191-207.

SIIVONEN, L., 1975. New results on the history and taxonomy of the mountain, forest and domestic reindeer in northern Europe. In: Proc. First Int. Reindeer/ Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 33-40.

SIPLE, P.A. & C.F. PASSEL, 1945. Dry atmospheric cooling in subfreezing temperatures. Proc. Amer. Philos. Soc. 89: 177-199.

SKJENNEBERG, S. & L. SLAGSVOLD, 1968. Reindriften og dens naturgrunnlag. Universitetsforlaget, Norway.

SKOGLAND, T., 1972. Villreinen pa Hardangervidda, produksjon og kalvedødelighet 1970/71. Intern. Rep. of Norwegian IBP - Statens viltundersøkelser. (mimeo) 10pp.

SKOGLAND, T., 1973. Hardangervidda: Veigdalsutbyggingen og villreinens biotopvalg. Rep. of High Mt. Ecology Res. Stat., Finse, 1973: I. Univ. Oslo: 1-15.

SKOGLAND, T., 1974. Villreinens habitatatferd, økologiske og sosiale faktorer, Hardangervidda 1970-73. Rep. of Norwegian IBP - Viltforskningen, Trondheim. (mimeo) 133pp.

SKOGLAND, T., 1975. Range use and food selectivity by wild reindeer in southern Norway. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 342-354.

SKOGLAND, T., (in press). Studies on Marco Polo sheep (Ovis ammon poli) in the Pamir mountains of Afghanistan. F.A.O. manuscript. 41pp.

SKOOG, R.O., 1959. Movements, distribution and numbers of the Nelchina Herd. U.S. Fish & Wildl. Serv., Alaska, Job Completion Rep. 13 (3): 1-49.

SKOOG, R.O., 1968. Ecology of the caribou (Rangifer tarandus granti) in Alaska. Ph.D. Thesis, Univ. California, Berkeley, Calif.. 699pp.

SLEE, J., 1967. Genetic aspects of climate physiology in sheep. In: Proc. 9th Int. Congr. of Anim. Prod., Edinburgh, 1966.

SLIJPER, E.J., 1960. Der geburt der saügetiere. Handb. d. Zool. 8 (25): 1-108.

SMITH, F.V., 1971. Purpose in animal behaviour. Hutchinson & Co., London.

SMITH, J.A., 1869. Notice of remains of the rein-deer (Cervus tarandus) found in Ross-shire, Sutherland and Caithness, with notes of its occurrence throughout Scotland. The Proc. Soc. Antiq. Scotland 8: 1-39.

STAINES, B.W., 1970. The management and dispersion of a red deer population in Glen Dye, Kincardineshire. Ph.D. Thesis, Univ. Aberdeen, Scotland.

STEEN, E., 1968. Some aspects of the nutrition of semi-domestic reindeer. In: The comparative nutrition of wild animals. Symp. Zool. Soc. Lond. 21: 117-128.

STRUHSAKER, T.T., 1967. Behaviour of elk (Cervus canadensis) during the rut. Z. Tierpsychol. 24: 80-114.

SULKAVA, S. & T. HELLE, 1975. Range ecology of the domestic reindeer in the Finnish coniferous forest area. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 308-315.

TEMBROCK, G., 1968. Land mammals (Communication), 338-404. In: Animal communication. T.A. Seboek (ed.). Indiana Univ. Press, London.

THOMSON, B.R., 1966. A roe deer browsing and fraying assessment at Glentress Forest. B.Sc. Hons. Thesis, Univ. of Edinburgh.

THOMSON, B.R., 1969. Proposed research programme on activity patterns of wild reindeer in Norway. Intern. Rep. of Direktoratet for vilt og ferskvannsfiske, Trondheim. (mimeo) 21pp.

THOMSON, B.R., 1971. Wild reindeer activity; Hardangervidda July-December 1970. Rep. of Norwegian IBP - Statens viltundersøkelser, Trondheim. (mimeo) 83 pp.

THOMSON, B.R., 1972. Reindeer disturbance. 'Deer', Jour. Brit. Deer Soc. 2: 882-883.

THOMSON, B.R., 1973. Wild reindeer activity; Hardangervidda 1971. Rep. of Norwegian IBP - Statens viltundersøkelser, Trondheim. (mimeo) 76pp.

THOMSON, B.R., 1975. Leadership in wild reindeer in Norway. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 462-473.

U.S. TUNDRA BIOME, 1971. The structure and function of the tundra ecosystem, Vol I. U.S. Tundra Biome Program, U.S. IBP Rep.: 1-282.

VAN DEN BRINK, F.H., 1967. A field guide to the mammals of Britain and Europe. Collins, London.

WATSON, A. & R. MOSS, 1970. Dominance, spacing behaviour and aggression in relation to population limitation in vertebrates. In: Animal populations in relation to their food resources. Brit. Ecol. Soc. Symp. 10: 167-220.

WHITE, R.G.; THOMSON, B.R.; SKOGLAND, T.; PERSON, S.J.; RUSSELL, D.E.; HOLLEMAN, D.F.; & J.R. LUICK, 1975. Ecology of caribou at Prudhoe Bay, Alaska. In: Ecological investigations of the tundra biome in the Prudhoe Bay region, Alaska. Biol. Pap. Univ. Alaska Spec. Rep. 2: 151-201.

WILDHAGEN, A., 1948. Reinen på Hardangervidda. Jakt-fiske-friluftsliv 19: 3-6.

WILDHAGEN, A., 1952. Aktuelt om villreinen. Riistat. Julk. (Finland) 8: 50-57.

WYNNE-EDWARDS, V.C., 1962. Animal dispersion in relation to social behaviour. Oliver & Boyd, Edinburgh.

YOUNG, B.A. & E.H. McEWAN, 1975. A method for measurement of energy expenditure in unrestrained reindeer and caribou. In: Proc. First Int. Reindeer/Caribou Symp., Fairbanks, 1972. Biol. Pap. Univ. Alaska Spec. Rep. I: 355-359.

ZHIGUNOV, P.S. (ed.), 1968. Reindeer husbandry. Israel Programme for Scientific Translations, Jerusalem: U.S. Dept. of Interior, Washington, D.C..

.....and yet there was something more; besides the
logical thought, which was often a hindrance,
a troublesome though inseparable accident;
besides the sensation, always a pleasure and a delight;
besides these there were the indefinable inexpressible
images.....a world beyond all expression or analysis,
neither of the intellect nor of the senses.....

from Arthur Machen's "Hill of Dreams".