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THE UNIVERSITY OF ALBERTA

ECOLOGY OF FERAL HORSES
IN WESTERN ALBERTA

by

RICHARD EDWARD SALTER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled 'Ecology of Feral Horses in Western Alberta' submitted by Richard Edward Salter in partial fulfilment of the requirements for the degree of Master of Science.

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Date 1978

ABSTRACT

A population of feral horses in the foothills of west-central Alberta was studied from June, 1975 to June, 1977 to determine their use of the environment and the degree of overlap with cattle and native ungulates. Of the 206 individuals described during 1976 53% were adults, 12% two year olds, 17% yearlings and 18% foals. The horses were organized into harem groups consisting of a dominant male and two or more adult mares and/or immature animals. Surplus stallions formed bachelor groups. Herds remained within overlapping home ranges of less than 15 km² throughout the study. Herd integrity was maintained by stereotyped behaviour during interactions between dominant males and possibly by within-group bonding.

The area was classified into 17 habitat types based primarily on the composition and structure of the vegetation. Pellet group and track counts were used in 1976 to determine the winter, spring and year-long distribution of horses within these, and to relate distribution to individual features of habitat. Use was made of the entire spectrum of habitat types but seasonal use was markedly non-random. The availability of preferred forage plants appeared to be a primary determinant of habitat utilization during all seasons. Horses spent about 75% of daylight hours foraging during winter and spring with an apparent decrease in feeding time in summer. Fecal fragments analysis showed that gramineous plants were the major dietary constituents, never falling below a level of 83% in 1976 monthly diets. Carex spp., Elymus innovatus and Festuca spp. were the most important food plants. A fecal index technique suggested strong seasonal variation in diet quality.

Distributions of cattle and native ungulates were determined concurrently with the study of horse distribution and were compared to the latter using association and coincidence indices and a coefficient of association. Horses were more ubiquitous in their distribution than any other ungulate (elk, white-tailed and mule deer, moose, cattle) and overlapped onto the range of these species to a large degree. Lack of behavioural interactions and probable dietary differences suggested ecological separation of horses and deer and horses and moose. Horses and elk both used dry grasslands during winter and spring but competition for forage was minimal due to the low number of elk present. Horses occupied in spring some areas and habitats later preferred by cattle but range use was not excessive when measured in early June, 1977. There was little contemporaneous spatial overlap of horses and cattle although their summer diets were 67% identical. Potential for competition likely was highest between horses and cattle but grazing relationships were complex.

ACKNOWLEDGEMENTS

This thesis is the culmination of a long process of field research, interviews, laboratory and data analysis, discussion, writing and finally mechanical preparation to which many people have contributed; although they are far too numerous to mention individually I express my sincere gratitude to them all.

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The Albert Forest Service permitted me to stay at the Red Deer Ranger Station throughout the field study. Special thanks go to Gary Erickson for his assistance in the field during summer 1975. Finally, I thank Cal Hayes, who freely shared his knowledge of horses with me, and whose kind hospitality made my stay at the Red Deer Ranger Station a memorable and enjoyable experience.

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Introduction

Feral or so-called 'wild' horses (Equus caballus L.) are widely distributed throughout much of western North America but only recently have become the subjects of scientific study. Due largely to their status as a non-native species feral horses have been treated primarily as problem animals, but attempts at management have been frustrated by the lack of general ecological information. No previous studies have been conducted in Alberta, even though relatively large populations are found in some parts of the Rocky Mountain foothills.

Objectives of the present study were to consolidate existing information regarding the status of feral horses in Alberta and to conduct appropriate field studies for collection of ecological data necessary for their management. Specific objectives of the field studies were 1) to examine in detail the use of habitat and forage in the foothills environment, including an assessment of social behaviour and productivity factors influencing habitat use, and 2) to assess possible competition with native ungulates and cattle. Field work was conducted primarily during June - August 1975 and January - December 1976, although intermittent visits to the study area also were made outside of these periods.

The report is organized into seven chapters. In the first chapter the origin, distribution and management of feral horses are reviewed, with an emphasis on the situation in Alberta. Next is an account of pertinent features of the region in which field studies were conducted, followed by a description of the feral horses themselves, as they existed in 1976, in terms of general and individual physical features. How the horses were organized into social groupings, how these groups were maintained, and how social organization influenced the use of space and the productivity of ~~the~~ population as a whole are then considered. Feeding behaviour, food habits and diet quality are discussed in a chapter on feeding ecology, and these are then related to factors affecting habitat utilization. The final chapter consists of an examination of spatial and foraging relationships between feral horses and other ungulates and the effects of combined habitat use.

Chapter 1: Historical and Management Background

1.1 Origin and Historical Distribution of Feral Horse Populations

Although truly wild horses existed in North America up until about 3000 years ago (Groves 1974), it is generally agreed that all horses present in North America today are descendants of animals imported by man, beginning with re-introductions by the Spanish early in the 16th Century (McKnight 1959). Some of these earliest imports escaped to an exo-domestic or feral existence, and with more or less continuous additions from natural reproduction, newly escaped animals and animals turned loose deliberately, the North American feral horse population is estimated to have numbered between two and six million by the end of the 18th Century (McKnight 1964). Their range at this time is believed to have covered much of the continent west of the Mississippi, from the Rio Grande in the south to the Athabasca River in the north (Groves 1974).

The acquisition of horses by the Plains Indians appears to have been a major factor in the dispersal of feral populations - primarily northward along both sides of the Rockies - from an original locus in the Southwest (Wyman 1945). The first domestic horses in what is now western Canada were seen in the possession of Snake Indians along the Bow River about 1730 (McEwan 1964), and although some feral horses also may have reached the area by this time the vast numbers encountered on the Great Plains to the south apparently never reached this far north (McKnight 1964). Once introduced, horses spread quickly from tribe to tribe (Jenness 1933), lax husbandry practices probably giving rise to the first feral herds on the Canadian Prairies.

Settlers coming to western Canada at the turn of the last Century found herds of 'wild' horses from Saskatchewan to British Columbia (McEwan 1964). These were displaced and pushed into inaccessible areas as settlement continued but were supplemented, until very recently in some areas, by strays or escapes from ranching, mining and forestry operations.

1.2 Management

Government policy regarding these animals has been directed toward reduction or extirpation on both sides of the Canada-U.S. border. The rationale for control has varied from region to region, but the primary aim has been the reduction of competition with domestic stock and/or wildlife (McKnight 1964). Specific problems cited for Alberta include range and watershed damage due to overgrazing, and damage to regenerating conifers in logged areas (Petersen 1972).

Concerted attempts at management of feral horses in Alberta did not really begin until the mid-1950s. Early in the century horses were periodically captured and used as work animals or sold for profit (McEwan 1964, Scott n.d.), but it is unlikely that such sporadic activities had much effect on the population. Cattle grazing permittees played a role in more recent years, and it is documented that numbers of horses south of the Bow River were effectively reduced by roundups during the mid-forties (Wallace 1972).

In 1956 the Eastern Rockies Forest Conservation Board, then responsible for the Rocky-Clearwater and Bow-Crow Forests, instituted a policy of removing feral horses, with the stated intent of complete extermination. This followed a period of population increase during which peak numbers were probably reached (McKnight 1964). Sources of feral animals included Indian and Metis encampments, mining and logging operations in the foothills, guides' and outfitters' strings turned loose to graze during winter, and ranches on the edge of the Forest Reserve (Petersen 1972). 'Letters of Authority' for the capture of feral horses were issued by Forest Superintendents to experienced local residents and professional American 'horse chasers' were engaged to conduct aerial roundups, but the latter (1958-59) were largely unsuccessful. Attempts by one individual to use a tranquilizer gun also were unsuccessful as the horses could not be approached within range. Letters of authority continued to be issued, most recently under Ministerial Order No. 66/67 (pursuant to Section 59, Public Lands Act 1966) until 1972. Each permittee was provided exclusive rights to a large area on deposit of $100, and the permit was renewable after two years subsequent to review by the

Land Use Branch. Horses were rounded up largely by chasing them into wing-corral traps or by roping during winter, and by use of salt baited corral traps in spring. During the period 1962-1972 up to 16 permits were in effect at one time, and over 2000 horses were removed from the Forest Reserve (Table 1.1).

A policy change instituted in early 1973 resulted in a phasing out of current letters of authority, and the last permit expired in March, 1974. According to this policy, further letters of authority would be issued only upon the express recommendation of a Forest Superintendent that action was necessary to alleviate conflict with game animals or other serious range or watershed problems. This policy was superseded by the Stray Animals Act (1977) administered by the Department of Agriculture, under which the Forest Superintendent and Land Use Officer in each Forest District are designated as inspectors with the power to authorize roundups.

Various other management strategies are in effect throughout the remainder of the range of these animals. In British Columbia feral horses occupying remote areas are being tolerated at present, but trespass grazing in the southern half of the province is closely controlled and a few feral animals are taken in the process of gathering strayed domestic horses (J.E. Milroy pers. comm.). Under the Grazing Act of 1960 trespass animals may be rounded up or

Table 1.1 Records of Horses Removed Under Permit from Alberta Forest Regions, 1962-1972

Year	Edson Forest		Clearwater-Rocky Forest		Bow-Crow Forest		Total	
	Permits	Horses Removed	Permits	Horses Removed	Permits	Horses Removed	Permits	Horses Removed
1962	-	-	9	73	5	no record	14	73
1963	-	-	11	67	4	75	15	142
1964	5	0	no record	no record	2	90	7	90
1965	4	27	3	12	4	276	11	315
1966	5	40	4	45	6	107	15	192
1967	3	55	5	89	7	174	15	318
1968	3	13	4	24	7	210	14	247
1969	2	27	4	37	8	279	14	343
1970	3	11	4	27	8	181	15	219
1971	4	40	4	65	8	101	16	206
1972*	3	3	-	-	8	-	11	3
Total		216		439		1493		2148

*Records subsequent to 1971 are incomplete. The last permit expired in 1974.

shot by persons holding a licence from the B.C. Forest Service. In contrast, the population of 200-300 feral horses on Sable Island (off the coast of Nova Scotia) is protected from harassment by federal statute (Bearcroft 1974). Feral horses on federal lands in the United States also are protected by law. The Wild Horse and Burro Management Act, passed in 1971 in response to public pressure, provided complete protection to all feral horses on whatever federal lands they then inhabited, including the Pryor Mountain Wild Horse Range established by previous government order in 1968. Provisions of the Act were so restrictive, however, that management was effectively prevented and problems of overpopulation soon were apparent (Cook 1975). The Act has been challenged in court by state agencies and various amendments providing for more effective management have been passed or are under consideration.

1.3 Current Status

There are now few if any feral horses in Saskatchewan and only one or two thousand in each of Alberta and British Columbia (Bearcroft 1974, this study). The total North American population, concentrated in the 10 westernmost states, numbers approximately 50,000 animals (Jacobs 1974, Anon. 1976).

In order to determine the current distribution and abundance of feral horses in Alberta, questionnaires were mailed to all Land Use Officers, Alberta Forest Service, and to all Fish and Wildlife Officers, Fish and Wildlife Division, in May 1975. Special effort was made to have the respondent differentiate feral horses from other categories of free-ranging horses, since this has been a prime source of confusion in the past. Four categories were established: 1) feral horses, defined as ownerless or unclaimed animals which forage for themselves year round (commonly known as 'wild' horses), 2) guide and outfitter horses, defined as horses running at large and foraging for themselves for all or most of the year, but rounded up and used periodically by their owners, or which would be claimed if rounded up under government permit, 3) horses owned by natives or Metis, defined as horses running at large and foraging for themselves for all or most of the year, but claimed by and nominally under the control of native or Metis people living in the area, and 4) other trespass horses which could not be classified into any of the above categories. A total of 43 replies, including responses from all Forest Service offices, were received from the 59 questionnaires distributed.

Results of the survey indicated that in 1975 all feral horses present in Alberta were inside the 'Green Zone', an area of primarily forest cover within which land use activities are administered largely by the Alberta Forest Service. The survey results were updated in January 1977 by recirculating the completed questionnaires to Forest Service Offices and requesting that any changes be noted. Data gathered during this most recent compilation are summarized in Figure 1.1 and Table 1.2, which show that the present centre of abundance of feral horses in Alberta is in the central foothills area.[1]

Feral horse populations were reported from seven of ten forest areas. Nearly 70% of these were in the Bow-Crow Forest, primarily between the Bow and Clearwater Rivers. As of January 1977, populations were considered to be increasing only in the Rocky-Clearwater and the Bow-Crow Forests. Population trend was considered to be stable or unknown in the Peace River Forest (1975), unknown in the Footner Lake Forest, and decreasing in the Slave Lake and Edson Forests (all 1977). Competition for forage was reported only for the Peace River Forest, where small herds (total 11 animals) were considered as potential competitors with elk in winter, and for the Bow-Crow Forest, where competition with elk (<u>Cervus elaphus</u>) in winter and with domestic stock in summer were identified. In the latter region, the respondent noted in 1977 that a number of the

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[1] Other investigations revealed that a herd of about 20 feral horses existed for several years in an area centering on Dry Island Buffalo Jump Provincial Park, in the Red Deer River Valley 60 km north of Drumheller. These animals were rounded up and disposed of by local ranchers in September 1976.

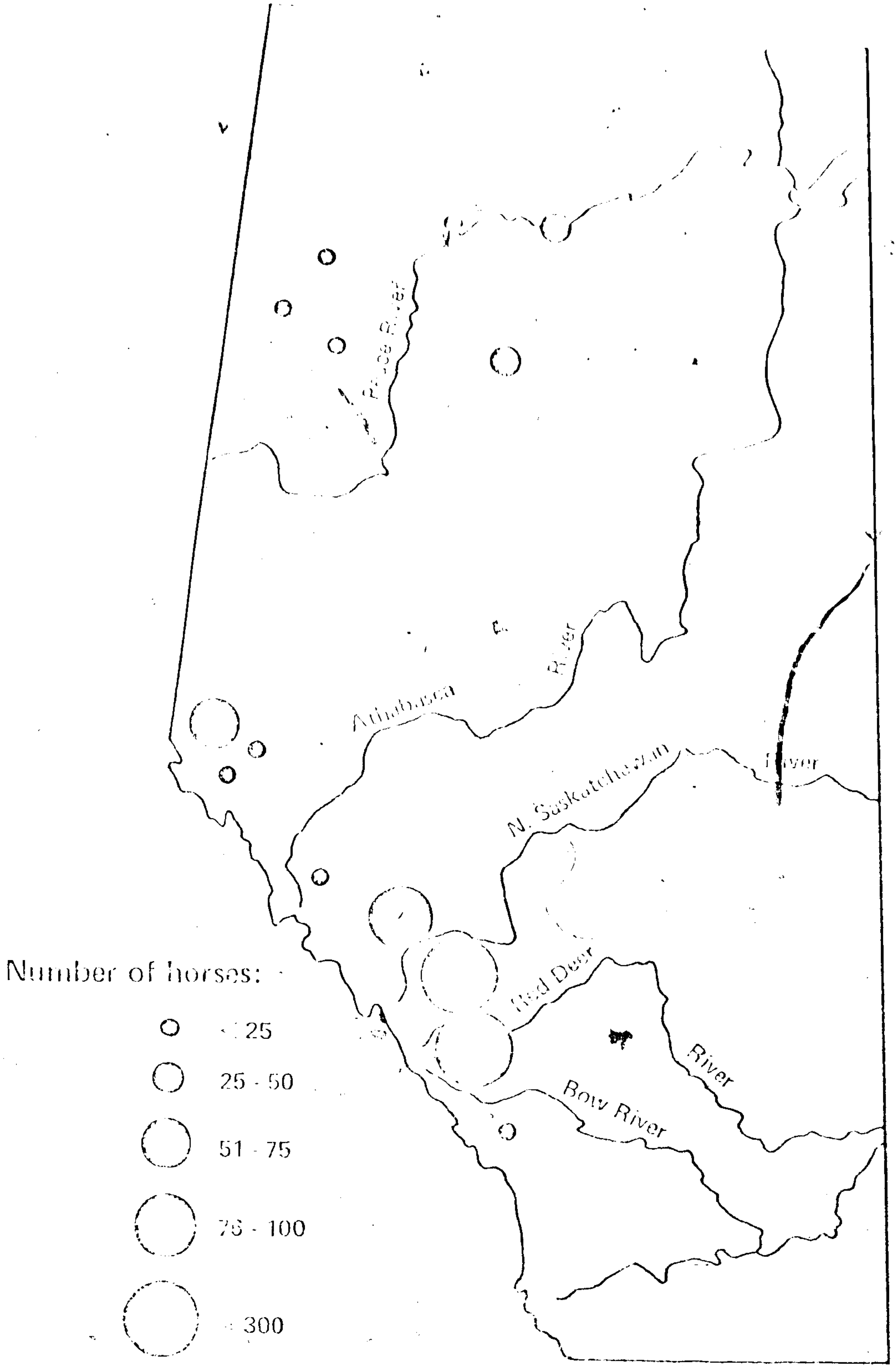

Figure 1.1 Distribution of feral horses in Alberta, January, 1977

Table 1.2 Numbers of Free-Ranging Horses in Alberta Forest Regions, as Reported by AFS Personnel, January, 1977

	Category and Estimated Number				
Forest	Feral	Native/ Metis	Guide/ Outfitter	Unclassified	Total
Footner Lake	60-61	35	-	-	95-96
Athabasca	-	10	-	-	10
Peace River	11+	140	-	9	160
Slave Lake	40	150	-	-	190
Lac La Biche	-	10-15	-	?	10-15
Grande Prairie	17-27	25-51	54-135	-	96-213
Whitecourt	-	-	-	-	-
Edson	62	220	-	20	302
Clearwater-Rocky	90	120	-	-	210
Bow-Crow	606	-	-	-	606
Total	886-897	710-741	54-135	29	1679-1802

cattle grazing allotments appeared to be overgrazed before the cattle entry date, and that early season grazing by horses on pipeline right-of-ways was having a detrimental effect on slopes. This was the only Forest for which environmental damage (defined in the questionnaire as watershed damage, trampling damage to young conifers, overgrazing or overbrowsing) attributable to feral horses was reported.

Chapter 2: Study Area

2.1 Choice of Study Area

In order to fulfill all objectives of the study the area chosen for field work had to be used by large numbers of feral horses as well as by populations of other ungulates (especially elk and cattle). Information from several sources indicated the presence of a number of possible sites in the Bow Forest, and based on a reconnaissance of the region a study area was chosen in late May, 1975. This area supported an accessible horse population (over 70 seen on a one-day reconnaissance) as well as elk, moose (Alces alces), mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus) populations, and was subjected to grazing by cattle in summer. Another key factor was that access was good along an all-weather road following one boundary, and on logging roads and seismic lines into the interior. Horses were rounded-up from the area under a permit which expired in 1973. Records of these removals provided some background knowledge of the population.

2.2 Physical Features and Vegetation

The study area encompassed approximately 200 km^2 of the outer foothills of the Rocky Mountains west-southwest of Sundre, Alberta (Figure 2.1). Boundaries were chosen to include a maximum diversity of vegetation types created by fire, logging and edaphic factors, and a balance between 'closed' forest and 'open' meadow communities (Figure 2.2).

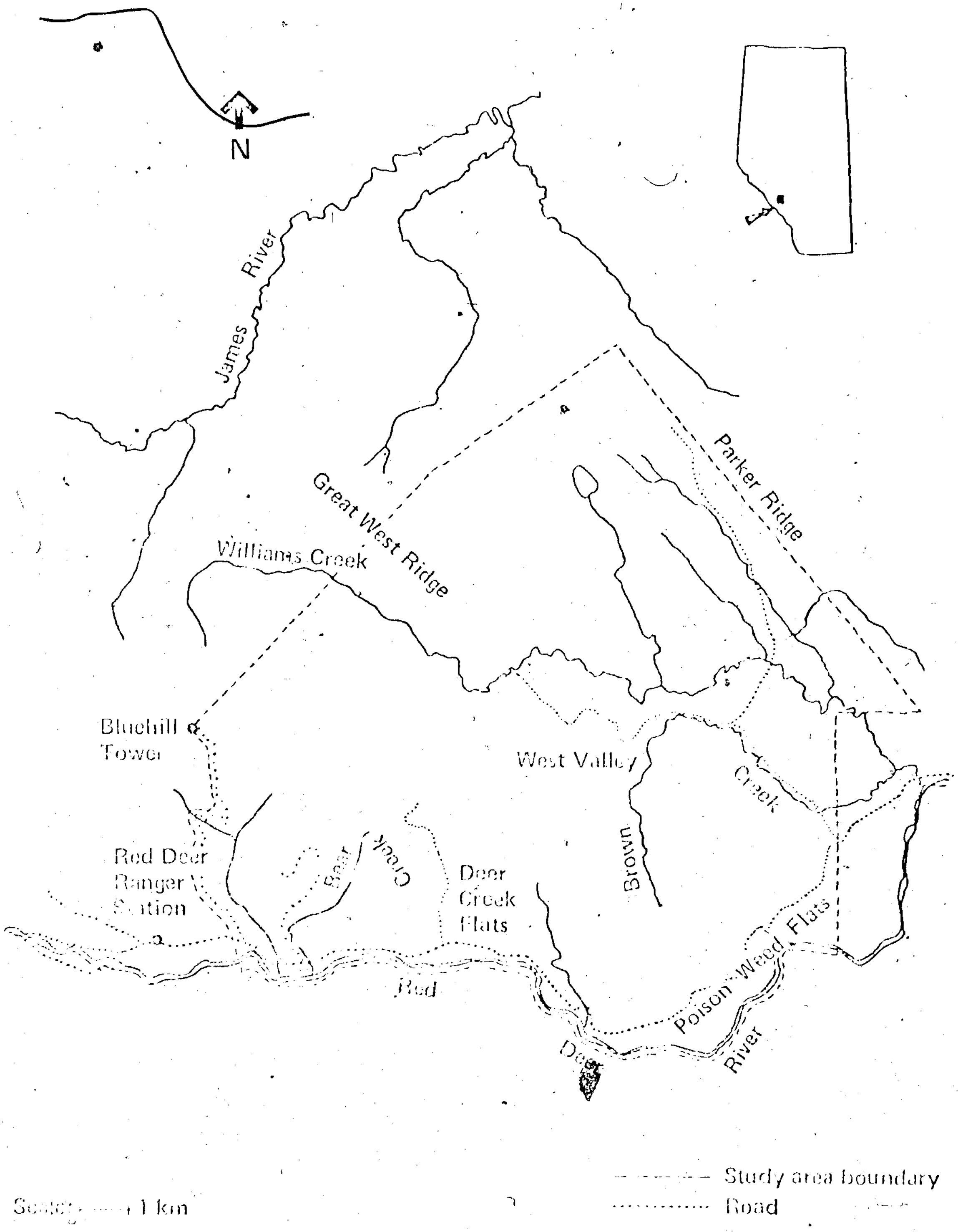

Figure 2.1 Map of the study area

Figure 2.2 Aerial view of part of the study area, looking west toward the Rocky Mountains.

The area was within the Upper Foothills section of the Boreal Forest as defined by Rowe (1972). Elevation varied from 1300 to 1900 m. A series of roughly parallel, forested ridges oriented along a NW-SE axis were the predominant topographical feature. Drainage was through numerous permanent streams emptying into the Red Deer River to the south or the James River to the north.

Upper Cretaceous and Paleocene material of the Brazeau and Paskapoo Formations formed the underlying bedrock (Olerenshaw 1966). Sandstone, siltstone and mudstone predominated; shale, conglomerate, coal and bentonite formed minor components. Soil-forming parent materials consisted of glacial tills, alluvium, colluvium, lacustrine deposits and organic materials (MacKenzie-Grieve 1970). Soils belonging to the Luvisolic, Brunisolic, Regosolic, Chernozemic, Gleysolic and Organic Orders were mapped within a small part of the present study area by Beke (1969), but within the area as a whole Luvisols, Organics and Chernozems predominated.

Forest cover consisted largely of lodgepole pine (Pinus contorta) with smaller stands of white spruce (Picea glauca), black spruce (P. mariana), alpine fir (Abies lasiocarpa), aspen (Populus tremuloides) and balsam poplar (P. balsamifera). Mixed woods formed a major forest component. Meadow vegetation types on a moisture gradient from flooded to dry comprised the non-forested cover. Sedge and low shrub fens with smooth to hummocky microtopography were characteristic of mesic conditions, such as occurred in flat or gently sloping valley bottoms. Associations dominated by bearded wheatgrass (Agropyron subsecundum), June grass (Koeleria cristata) and intermediate oatgrass (Danthonia intermedia) were developed on south-facing slopes and in gently rolling meadows. Meadow and scrub vegetation covered approximately 20% of the study area.

2.3 Land Use

Parts of three cattle grazing allotments (Williams Creek, Upper Red Deer, Lower Red Deer) were located within the study area. The combined carrying capacity was rated at approximately 1500 animal unit months over a grazing season of 1 June - 31 October.

Approximately 10% of the area was subjected to diameter-limit logging prior to 1964. Logged sites were located primarily in a large block in the northwest corner. Approximately 75 ha were clearcut on Parker Ridge, on the extreme eastern boundary, in the early 1970s. Logging roads provided access to the interior of the study area.

Three producing natural gas wells were located in the southwestern corner and drilling was active within this circumscribed region. Seismic lines criss-crossed the area and seismic exploration, over established lines, occurred during late winter in 1976.

Significant tourist traffic occurred along an all-weather road following the Red Deer River. Hunters and snowmobilers used logging roads and seismic lines for access into the interior.

2.4 Climate

The climate of the region is cool and subhumid (Alta. Dept. Lands and Forests 1973). Mean annual precipitation at the Red Deer Ranger Station, only two km west of the study area, totals 57.6 cm, an average 38% (220 cm) of this occurring as snow with much of the remainder falling during summer thunderstorms. Measurable snowfall occurs on average during 47 days of the year. March and April are the months of peak snowfall, averaging 49 and 48 cm respectively although the monthly mean is between 12 and 21 cm throughout the period September - May (Environment Canada 1973a).

Only about 94 days each year are frost-free. Mean daily temperature during January, the coldest month, is -10.8° C and during July, the hottest month, +12.4° C. Daily minimum temperatures average above 0° C only during June - August. Extreme maximum temperatures of 32° C have been recorded during August and September, while extreme minimum temperatures of -42° C have occurred during December (Environment Canada 1973b). Mild spells accompanied by warm west winds (Chinooks) are a prominent feature of the winter climate of this region.

Chapter 3: The Study Population

3.1 History and Origin

The study area was within the former hunting ground of tribes of the Blackfoot Confederacy, central figures in the equestrian culture which flourished in western Canada during the 18th and 19th Centuries (Jenness 1933, Bryan 1967). The Blackfoot acquired horses between 1725 and 1750 (Johnston 1958) and it is tempting to speculate that the first feral horses in the region originated as strays from herds kept by these tribes.[1] Scott (n.d.) believed that wild horses found along the Ghost River (40 km to the south of the study area) in the early part of this century were descended from Spanish horses, although there is no direct evidence for this. Horse ranching in the region dates hack to 1905, when the Brewster brothers grazed as many as 300 horses on the Ya Ha Tinda, 25 km to the west (McGillis 1976). Scott (n.d.) implied that many of the feral horses seen or rounded up on this ranch in 1917 were descended from Brewster stallions, and it is likely that others had dispersed from the immediate ranch area. Horses were used in forestry operations within the present study area during the early 1900s, but it is unknown whether these contributed to feral stock. Certainly feral horses were present in numbers by the late 1930s, when roundups took place in the immediately

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[1] - This was documented in adjacent British Columbia by the explorer David Thompson, who in 1807 found several herds of 'wild' horses along the upper reaches of the Columbia River, attributing their presence to losses from local Indian herds (Tyrrell 1916).

surrounding region (C. Chiswick pers. comm.). A horse rancher located just outside of the Forest Reserve reportedly pastured several hundred horses over a large region (including the present study area) up until less than 10 years ago and extending back over a 30 year period. These animals were essentially unmanaged and it is likely that the origin of many of the feral horses present at the time of the study could be traced back to this source. Virtually all ranches near the Forest Reserve lost horses at one time or another, especially during the late 1940s when demand for horses was low (R. Logan pers. comm.).

As noted above, roundups have occurred in the region since the early part of this century, partially counterbalancing natural reproduction and influxes of animals from other sources. During the most recent roundups (1965-1973) over 350 horses were removed from a permitted region centred on the present study area (Alberta Forest Service Records 1965-1974).

3.2 Physical Appearance

Adult horses observed during the study exhibited a wide variation in height and conformation, probably reflecting the mix of breeds from which the population has been derived. Most individuals were compact in build but several tall, stocky horses were described, reflecting recent draught background. Adult males removed from the area prior to the study ranged between 800 and 1200 lbs (364-545 kg) in weight, while adult females were slightly smaller at 700-1000 lbs (318-454 kg) (R. Logan pers. comm.).

Manes of adults were long and the full tails usually reached the ground. The forelock was particularly long in mature stallions, in extreme cases extending down the nose to midway between the eye and nostril. Mature stallions had noticeably heavier, more muscular necks and deeper chests than did mares.

Tails of yearlings reached down to the hocks or slightly below, and the short forelock had a 'bobbed' appearance. At close range these animals were readily distinguishable on the basis of body size. The length of mane and tail and body size of two year olds approached those of adults but they were much lighter in build.

Facial profiles varied from slightly dished (concave) to roman-nosed (convex). Examination of a skull collection from the area indicated characteristics typical of Occidental or cold-blooded horses (D. Welsh pers. comm.).

Nearly one half of the horses were bays, the remainder being a variety of other colour patterns (Table 3.1). Coat colour of bay horses ranged from light tan (sandy bay) to medium red (blood bay) to dark (mahogany bay). Several horses were noticeably lighter in colour in summer as compared to winter, some even changing from sandy or blood

Table 3.1 Coat Colour of Yearlings, Two Year Old and Adult Horses Described During January - December, 1976.

Colour	No. of animals	% of animals
Bay	77	45.6
Black	24	14.2
Red roan	22	13.0
Chestnut	18	10.6
Brown	14	8.3
Gray	12	7.1
White	2	1.2
TOTAL	169	100.0

bay to red roan. These are listed as roans in Table 3.1. Grays tended to have black stockings with a black mask covering the face, and also showed some variation in winter and summer coats. Some of these would likely be called blue roans by other authors. All chestnuts were shades of red brown, with manes and tails either matching the coat colour or being light golden in coloration.

Chapter 4: Social Organization, Behaviour and Productivity

4.1 Introduction

Knowledge of both behavioural and ecological adaptations are essential for management of ungulates in the wild state (Geist 1971) but attempts at synthesizing ideas on the relationships of ecology and social behaviour have been made only recently (Geist and Walther 1974, Jarman 1974, Leuthold 1977). These accounts have highlighted the interdependencies between social organization, distribution and resource utilization.

Leuthold (1977) tentatively defined social organization as "the result of all social interactions and spatial relations among members of a single species population." Thus social organization refers to sex and age composition and sizes of social groups, as well as to relationships of individuals and groups to space and to each other. Social organization may be viewed both as a determinant of how a species uses the environment, and as a product of the environment in which a species evolved. Terrain type and available food are considered to be the external factors which have had the most influence on the evolution of social relations (Ewer 1968). Not surprisingly, modern ungulates exhibit a variety of organizational patterns, many of these varying seasonally in response to environmental influences. Even within species, social organization may be different in sedentary and migratory populations, or in populations in open versus forested habitat (Leuthold 1977).

Social organization is maintained through "a complex system of communication" (Eisenberg 1966). Thus, within the context of a specific field study, it is important not only to describe a social system but also to examine mechanisms which function to maintain it. It may also be instructive to examine the system with regard to adaptive advantages within a given environment (Franklin 1974, Jarman 1974).

Social behaviour and organization of equids have been studied well enough to permit some generalizations. Two basic types of social organization have emerged: Type I, a non-territorial system characterized by permanent harem groups composed of adult females, their offspring, and an associated adult male, and by open bachelor groups comprised of excess males; and Type II, a territorial system in which animals may occur in open mixed herds, but characterized by territorial defence by adult males in the presence of an oestrous female, and by seasonal separation of the sexes (Klingel 1974, 1975). Among wild equids, the plains zebra (*Equus quagga*) and mountain zebra (*E. zebra*) belong to the first group; the Grevy's zebra (*E. grevyi*), the African wild ass (*E. africanus*) and possibly the Asiatic wild ass (*E. hemionus*) to the second. Populations [illegible] feral horses studied to date (Welsh 1975, Feist and McCullough 1975, 1976, Berger 1977) conformed to the harem-type organization. Studies on domestic or semi-domestic horses (Tyler 1972, Clutton-Brock et al. 1976) have also provided insight into social structure.

In this chapter aspects of social behaviour and organization are examined in relation to the use of space and effects on the productivity of the population. Particular attention is given to an examination of how reproductive units are maintained over time. Interrelationships between social organization and antipredator behaviour also are considered.

4.2 Methods

All or part of 208 days were spent on the study area between January and December, 1976 (11 to 24 days each month) during which time horses were observed over a cumulative 298 hours. Individual herds were kept under continuous observation for up to 12.5 hours. Herd locations were determined by searching a specific area or by opportunistic sightings during the course of other activities. Particular attention was paid to locating and watching herds during April to mid-July, the period when the animals were most visible. Detailed notes were maintained whenever possible on various aspects of social behaviour, with an emphasis on agonistic interactions among herd members and between members of different herds.

Individual horses were readily identifiable on the basis of coat colour and facial and leg markings, and an attempt was made to describe each animal seen on the study area during 1976. Descriptions of each individual were recorded on prepared forms and each was assigned a number the first time a herd was sighted. Data recorded were date of description, sex, age, relative height, coat colour, facial markings, leg markings, scars and maternal relationship (from suckling bouts). Identifying markings were drawn to scale on prepared outline drawings. Classification of coat colour was based on descriptions in Simpson (1951). Although secondary sexual characteristics were evident in mature males, sex was determined in all age classes on the basis of external genitalia. Yearlings were distinguished from two year olds on the basis of body size and length of mane and tail. Yearlings were defined as animals born in 1975, two year olds as animals born in 1974 - thus each animal was considered to be in only one age class throughout 1976. Three year olds were considered to be mature.

A file keyed to herd stallions but containing all descriptions was carried in the field to ensure rapid and accurate identifications during subsequent sightings. Occasionally an animal was not described completely enough on the first sighting to permit positive reidentification, but this proved to be a minor problem. Suspect partial descriptions were culled prior to data tabulation. A total of 206 descriptions were obtained, these forming the main body of data for analysis of population characteristics.

Data on location, time of day, general behaviour patterns and sex, age class and identification numbers of animals in the herd were recorded on prepared forms during 373 observations (actually somewhat more sets of descriptions were obtained, since new information was recorded when a herd was sighted two or more times in one day). Locations were determined at the time of sighting from 1:21,120 scale aerial photographs and were recorded to the nearest 50 m.

4.3 Social Organization

The horses exhibited a Type I social organization as defined by Klingel (1975): "adults live in non-territorial and cohesive one male family groups and in stallion groups." Twenty-three such family or harem groups were identified, ranging in size up to 17 animals. The majority of the groups consisted of a single dominant adult male and a variable number of adult mares, two year olds, yearlings and foals, although subordinate adult males were present with four of the groups when first described.

Figure 4.1 presents data on maximum size of individual herds during June, when 78% of all herds were sighted at least once. The mean group size of 7.7 is somewhat greater than that reported for the Pryor Mountains in mid-May by Feist and McCullough (1975) but modal group size and range are reasonably similar. Welsh (1975) reported an average herd size of 5.2 over the course of his study. Differences

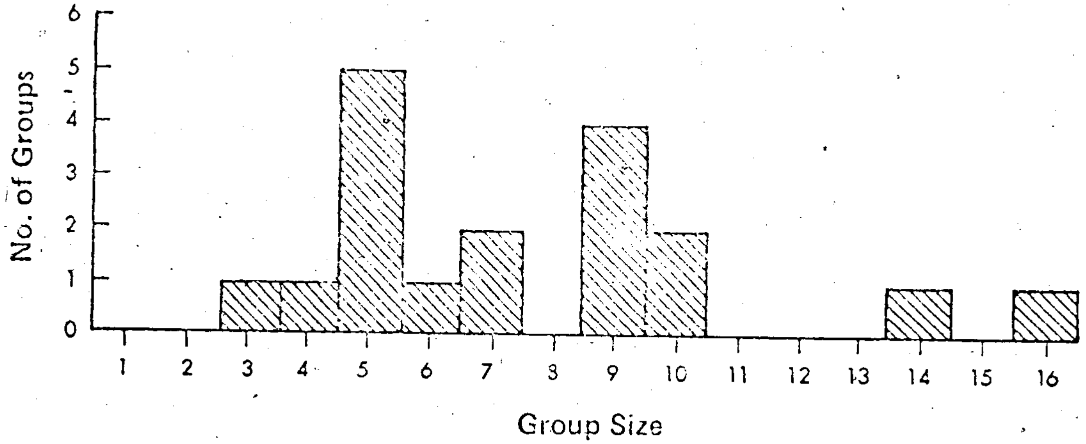

Figure 4.1 Size of 18 harem groups in June, 1976, based on the maximum number of animals observed in the group during the month.
Mean size = 7.7

in group size among areas must be interpreted with caution, however, since criteria for defining harem groups and the period lengths over which records were obtained were variable.

These stallion-mare groups constituted the basic reproductive unit, and except for births, deaths, and changes primarily involving younger animals (see following section on herd changes) they were essentially permanent, thus differing fundamentally from the seasonal reproductive units formed by native ungulates. Welsh (1975), quoting local sources, indicated that some stallions on Sable Island were known to have kept herds for more than 10 years, but his data indicated that average longevity of herds was much shorter.

Surplus stallions were organized into bachelor herds of one to six animals. These groups were rather unstable, although some long-term associations (19+ months) were observed. One bachelor group included a yearling female who joined the herd with a two year old male from the same original harem. Other associations between single bachelor males and females (usually immature, but including two mares with foals) were intermediate between harem and bachelor groups, representing attempts by single males to begin their own herds. These associations often were temporary and the stallions are considered as bachelor males in the following discussions.

4.4 Home Range

Home range sizes were determined by plotting individual herd sightings, joining the outlying points and measuring the enclosed area with a dot-grid overlay. Home ranges were plotted only for those herds satisfying an arbitrary criterion of eight sightings spanning an eight month period. This procedure provided an approximate measure of size of home range as defined by Jewell (1966): "the area over which an animal normally travels in pursuit of its routine activities." It is recognized that the home range is not necessarily a continuous area enclosed within defined boundaries (Ewer 1968) and that not all parts of a home range are of equal significance (Leuthold 1977). It also should be emphasized that home range is not synonymous with territory, the latter implying exclusion of certain conspecifics from a fixed area.

Both harem and bachelor groups remained within home ranges of less than 15 km² throughout 1976 (Table 4.1). Results from other studies indicate a great deal of variability in home range size, probably depending largely on availability of water and forage in the various vegetation types. Pellegrini (1971) reported harem home range sizes of around 31 km² in Nevada, while Feist and McCullough (1976) found that in Montana-Wyoming harems ranged over an average 15 km² (varying from 3-32 km²). The largest home range size reported by Berger (1977) for the

Table 4.1 Home Range Size and Number and Time Span of Observations of Seven Harems, One Bachelor Herd and One Single Bachelor, 1976.

Group No.		Home Range Size (ha)	No. of Observations	Period of Observation
Harems:	092	262	14	Apr - Dec
	040	1128	33	Jan - Dec
	030	1308	13	Apr - Dec
	027	656	23	Jan - Dec
	023	307	20	Jan - Aug
	007	1442	32	Jan - Dec
	001	786	28	Jan - Dec
Bachelors:	006	468	11	Jan - Dec
	021	1244	32	Jan - Dec

Grand Canyon area was 48 km². In contrast, on Sable Island the average home range size of family herds was 2.8 km² (Welsh 1975).

Welsh (1975) suggested that bachelors ranged over a larger area than did family herds, but Pellegrini (1971) reported just the opposite situation. In this study, home range sizes of bachelor herds appeared to be similar to those of harems (Table 4.1).

Theoretically, habitat quality - i.e. the dispersion of resources in the form of food, shelter, etc. - is a primary determinant of home range size (Leuthold 1977), small size being correlated with high quality habitat. It is noteworthy that in the studies quoted above home range sizes tended to be largest in desert and semi-desert areas, typified by a dispersed food resource, and were lowest on Sable Island, where forage grew in dense stands. The limited size of the island also may have been a factor in the latter situation, however. Home ranges on the present study area all included both meadow and woodland habitat, and were intermediate in size as compared to other areas. In general, feeding occurred primarily in meadows, where preferred forages were concentrated, but extensive feeding also took place in woodlands where forages were more dispersed.

Dominant stallions of both harem and bachelor herds appeared to remain within the same home ranges from year to year. Welsh (1975) also found evidence of stable ranges for herds on Sable Island. The evidence for stable home areas is consistent with prevailing theory on the functional aspects of home range. The chief advantages may be familiarity with the locations of resources and of escape routes from predators, although as yet there is little direct evidence to support this (Leuthold 1977).

Harem groups, bachelor groups and single bachelors overlapped considerably in their use of space (Figure 4.2). Similar overlap was found in studies by Welsh (1975), Feist and McCullough (1976) and Berger (1977), all of these concluding that feral horses occupy non-exclusive home ranges.

Overlap occurred in time as well as in space. For example in May, 1976, up to six herds were present simultaneously on a 20 ha area in the West Valley region. West Valley received particularly heavy utilization between April and June, during which time it was not unusual to see two, three or more herds grazing in the area. A similar situation occurred at Deer Creek Flats, where as many as three herds were observed at one time. Even though herds grazed in close proximity no mixing was observed.

4.5 Scent-marking

Many species of animals mark their home areas with scent from their own bodies, using urine, feces, saliva or secretions from specialized scent glands. The functions of

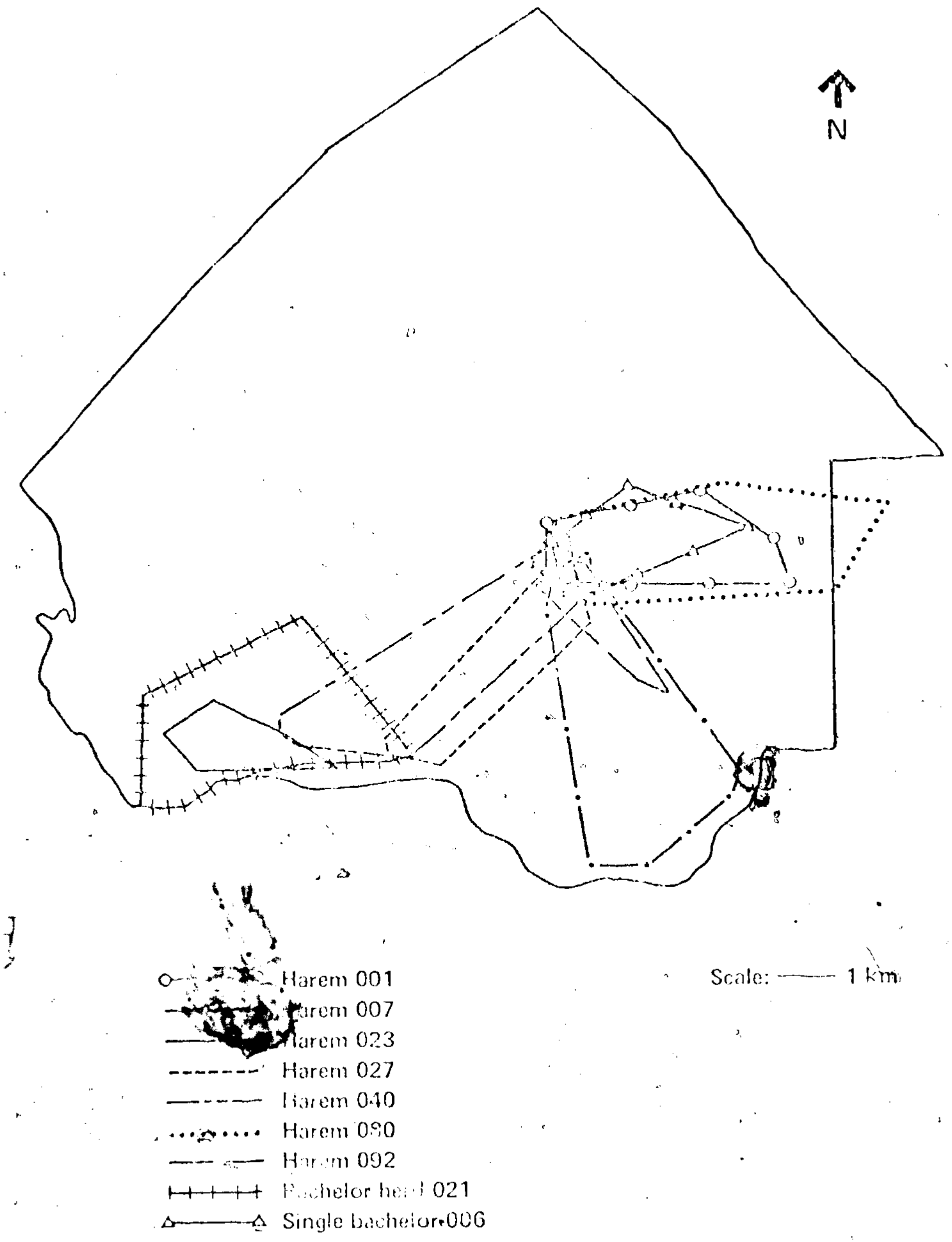

Figure 4.2 Home ranges of seven harems, one bachelor herd and one single bachelor, 1976. All herds observed on at least 3 occasions over an 8 month period.

scent-marking are poorly understood, apparently being related to territoriality in some species but not in others. Defecation or urination on eliminations of conspecifics, sometimes resulting in formation of large communal fecal piles, is a feature of the behaviour of both territorial and non-territorial equids; Klingel (1974) considered it to be relict behaviour in the latter, but this was disputed by Feist and McCullough (1976) at least for feral horses. Since scent-marking in feral horses appears to function in both spatial and social relationships, it provides a natural link between the previous discussion of home range and the following one on intra- and inter-group behaviour.

Scent-marking by stallions was a prominent feature of social interaction. Marking centred around communal fecal piles (stud piles), eliminations of other herd members, and defecations of one or both interactants during stallion encounters. Of 146 observed instances of scent-marking 87% involved marking with feces while 13% involved marking with urine (Table 4.2). Stallions commonly smelled their own feces after marking (70% of instances, n=127), less commonly their own urine (21%, n=19). Mature stallions only rarely eliminated outside of the context of marking behaviour (Table 4.2).

Marking occurred under various circumstances but was most apparent during interactions between stallions, these involving fecal as opposed to urinary marking almost

Table 4.2 Situations in Which Eliminations by Stallions Occurred, 1976.

Situation	Marker	Harem stallion		Subordinate male in harem		Bachelor stallion	
		Defacation	Urination	Defacation	Urination	Defacation	Urination
Scent-marking:							
On elimination of other herd member (during undisturbed activity)		0	3	1	3	0	1
After sniffing ground (no elimination products visible)		3	7	0	3	0	0
During courtship or tending		2	0	0	0	0	0
On stud pile in normal movements		5	0	3	0	1	0
During alert/escape to human disturbance		16	1	7	0	12	0
During undisturbed stallion interactions		26	1	10	0	33	0
No apparent external stimulus[1]		6	0	0	0	2	0
	Total	58	12	21	6	48	1
No immediate scent-marking context:							
While grazing		1	0	1	0	0	0
After rest period		0	0	0	0	0	1
	Total	1	0	1	0	0	1

[1] Included under scent-marking since normal activity was interrupted to defecate; stallions usually moved a few steps, assumed exaggerated defecation posture, and commonly sniffed feces after deposition.

exclusively. Sixty-two percent of all observed stallion interactions (n=82) involved fecal deposition and/or sniffing, indicating the importance of marking behaviour in these circumstances. Eighty-eight per cent[1] involved marking and/or some form of olfactory exploration of the opposing stallion, further emphasizing the role of scent during these encounters. Stallions commonly sniffed their own feces within this context (85% of defecations, n=66) but also took great interest in the feces of their opponent. Feist and McCullough (1976) found that order of elimination was related to dominance in interactions between rival males and within bachelor groups, the dominant animal defecating last. This was observed in this study during interactions within groups (harems including a subordinate male, bachelor herds) for which the dominance hierarchy was known from other evidence, but observations of interactions between stallions from different harems were too few to discern dominance relationships.

Feces often were deposited during escape from human disturbance, usually during the alert phase when the stallion(s) stood and stared at the intruder. In a few instances other animals also defecated during this period. Although on most occasions it could not be determined whether defecation occurred on a pre-existing fecal pile

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[1] 96% when seven interactions terminated by staring are excluded

(66%, n=35), it is noteworthy that both harem and bachelor stallions were observed defecating on fresh feces deposited by another herd member. Both dominant and subordinate stallions within harems were observed defecating on stud piles during escape, and although this was not seen in bachelor males it may have been due to the small sample size. Bachelors marked stud piles in other situations.

Stallions also marked eliminations of other herd members during undisturbed activities. Most of these involved urination as opposed to defecation (88%, n=8), primarily by stallions in response to defecation by mares, but also including one instance of a bachelor male urinating on the fresh urine of another bachelor. The only stallion interaction involving urination was initiated when a subordinate male urinated on the fresh feces of a mare; the dominant stallion then sniffed the marked fecal pile and urinated on it himself. Several observations of marking were preceded by the stallion walking around and sniffing one to several spots on the ground before eliminating; most of these also involved urination rather than defecation (77%, n=13) and were probably stimulated by prior urination of other herd members, particularly mares. Urination was reported by Feist and McCullough (1976) to be the primary response (70/76 observed) of harem stallions to eliminations of other group members. They concluded that such intraband marking was an expression of possession or association rather than of dominance *per se*.

Defecation on stud piles during undisturbed activity was actually observed on only nine occasions, but was probably a very common occurrence as evidenced by numerous additions of fresh feces to these piles throughout the year. Stud piles were located primarily along trails just inside the forest edge, along little-used roadways and beneath lone pine trees and on open, grassy sites in rolling meadows. Heavily used trails and sites beneath lone trees often had several large piles in close proximity, but it appeared that only one was in use at any one time. Stallions marking a stud pile would approach, sniff the pile, step over it, defecate and turn and sniff their own feces. Sniffing a stud pile without subsequent defecation was observed on only a few occasions. As noted above, stud piles also were marked during escape and in interactions with other stallions; sniffing following defecation was observed on 60% (n=5) and 65% (n=23) of occasions. Marking of stud piles by stallions has been documented in all extant North studies of feral horses (Welsh 1975, Feist and McCullough 1976, Berger 1977).

Only four observations were made of horses other than mature stallions showing an interest in scent-markings. On two occasions harem members (one mare and yearling male, one mare) appeared to sniff a fecal pile which had just been marked by the stallion; on another a two year old male sniffed at a stud pile encountered while grazing but did not defecate. The other observation involved a yearling nibbling briefly on a large dung pile shortly after the herd entered a meadow. A second horse sniffed the pile but showed no further interest. Mares in Montana - Wyoming were never seen to show an interest in excretory products, and the rarely observed response of foals and immatures was believed to be an early sign of sexual behaviour (Feist and McCullough 1976). New Forest Pony mares often sniffed feces and sometimes urinated on them (Tyler 1972).

Fecal and urinary marking is a common feature of the behaviour of other equids, including both territorial and non-territorial species. Klingel (1974) noted that in the former dung piles were found mainly along territorial boundaries, but believed that marking behaviour of non-territorial equids had no obvious function. This was disputed by Feist and McCullough (1976) whose studies suggested that marking represented a form of chemical communication.

Data from this study support the contention of Feist and McCullough (1976) that urinary marking is primarily an expression of intra-band association. With regard to marking of feces, Berger (1977) proposed that fresh scent on dung piles may lead to avoidance behaviour by other horses, thus minimizing contact among bands at more commonly used areas. However, Tyler (1972) found no evidence that marking exerted any repelling effect on rival stallions in New Forest Ponies, and no evidence of avoidance was found in the present study. Even in territorial equids scent-marking of dung piles is used for the orientation of the territorial animal itself rather than to warn away potential intruders (Klingel 1974).

Ewer (1968) pointed out that marking may have several intergrading functions - even the same mark may function in both reassurance and threat. In feral horses, it appeared that scent-marking had considerable importance for the animal performing the act, in the sense of creating "olfactorily familiar surroundings" (Leuthold 1977) and thus increasing the level of confidence, both in movements about the area and in interactions with other horses. The existence of solitary fecal marking behaviour, and the common practice of sniffing fecal piles before and after both solitary deposition and in stallion interactions all suggest that, in conjunction with dominance related aspects, a primary function of scent-marking may be one of orientation in space, time and in relation to other herds. This is further suggested by the location of the largest stud piles along well-used paths and under prominent, solitary trees in open areas. Stud piles thus may function as reference points for the individual and also in signaling the recent presence of other groups in the area. The foregoing interpretation and the views expressed by Feist and McCullough (1976) that marking "has immediate visual and olfactory importance in terms of dominance relationships" and that fecal deposits contain chemical information which persist over time all are consistent with data reported from other areas (Pellegrini 1971, Berger 1977). Nevertheless, it must be emphasized that evidence for the importance of scent-marking in the social relations of feral horses is all circumstantial, and in the absence of experimental data other interpretations, such as that marking is merely relict behaviour, cannot be discounted.

4.6 Stability of Reproductive Units

Harems were maintained year-round by herding of other group members by harem stallions, by stereotyped interactions between stallions when groups came into contact, and possibly by within-group bonding.

4.61 Herding and intragroup bonding

Herding or driving occurred under various circumstances but was most evident during alert and escape behaviour resulting from human intrusion. A typical sequence followed the progression alert / stare (stallion or mare) - trot several steps toward source of disturbance, stare (stallion) - gather behind stallion (other herd members) - move away from source of disturbance (all herd members, often initiated by a mare). Except for the most sudden escapes, when the alert sequence was shortened or eliminated, the harem stallion almost invariably remained in the rear position, either continuing to stare at the intruder while the other herd members retreated, or directing the escape from behind. This appeared to serve a dual function, both ensuring that the stallion remained between the source of disturbance and his herd during the alert/escape phase, and enabling him to control other herd members during escape. The herding or driving posture (illustrated by Feist and McCullough 1976), wherein the ears were laid back with the head low and stretched forward, was used in the escape context if subgroups began to split off from the main line of movement or if animals lagged behind. Assumption of the rear position was clearly related to dominance over the herd, as illustrated by escapes of herds containing subordinate males. Attempts by these animals to take over this position, to drive the herd from the rear, or to mark fecal piles during escape all resulted in interactions with the dominant stallion.

Herding also was used by stallions to retrieve herd members who wandered away or attempted to leave the group, and to move the herd away from other harems or bachelor males. During movements away from other groups the harem stallion assumed the rear position even if the herding posture was not used. Bachelor males herded newly acquired females away from disturbance on some occasions but led the retreat on others.

Some form of group bonding also may function in maintaining harem stability. On one occasion, the second ranking male in a harem containing three stallions attempted to drive the herd away while the dominant animal was interacting with two bachelors, but was unsuccessful. The other group members appeared reluctant to leave the area, possibly as a result of bonding to the dominant male. A second example is provided by a large harem group whose winter range was not shared by other herds. Subgroups of mares and immatures were observed on at least nine occasions, with no evidence that the stallion or other herd members were in the vicinity, but the harem invariably reunited within a few days. This is consistent with the suggestion by Berger (1977) that female-female bonding may be a factor in group stability.

Mutual grooming may be an important form of social contact (Tyler 1972), possibly reinforcing group bonds. Eight mutual grooming bouts were recorded in the following combinations: foal-foal (1), foal-yearling (2), yearling-yearling (2), yearling-mare (2), and mare-harem stallion (1). Not all instances of grooming were recorded and the above distribution is given as documentation only. An additional seven observations of non-mutual grooming between stallions and mares (three stallion-mare, four mare-stallion) were related to reproductive behaviour. Feist and McCullough (1976) documented mutual grooming among all combinations of group members except dominant stallions and foals. Similarly, Welsh (1975) reported initiation and reciprocation of grooming among all members of herds, except that harem stallions did not initiate grooming with foals.

4.62 Interactions between harem stallions

Display and threat behaviour by dominant stallions largely prevented serious fighting and competition for mares among family groups. No attempts by harem stallions to obtain mares from another group were seen.

When two harems were feeding in proximity to one another the stallions usually maintained positions at the periphery of their respective herds, such that each was positioned between his own group and the second harem. This may have represented a low level broad-side display directed towards the other stallion, even though feeding activities often continued. Its effectiveness is attested to by numerous observations of herds feeding in the same area without interaction. Welsh (1975) believed that stallions could discriminate between males and females on the basis of physical dimorphism and postures adopted by the stallion, and could thus determine whether or not a herd was protected by a dominant male.

Stallions often stood and stared, or approached and stared at passing herds or at herds moving closer while grazing. Of 16 harem male interactions for which details were recorded, seven did not proceed beyond this stage. The actual proportion is probably somewhat higher since many such low-level displays may have been missed when several herds were under simultaneous observation.

On other occasions harem stallions left their herds and approached each other, typically with head held high and tail partially outstretched, and met on a usually flat, open site between the two harems. Interactions often centred around a fecal pile, which was sniffed, defecated on and resniffed by one or both animals. The order and number of times these acts were performed varied, but some form of fecal marking or smelling was documented during eight of nine observed meetings. Mutual naso-nasal, naso-genital, and/or naso-anal explorations occurred during four meetings, prior to fecal marking on two occasions and subsequent to marking on two others. Biting and kicking were observed during three meetings, chasing of one stallion by another during only one. Postures assumed during these acts are illustrated by Feist and McCullough (1976).

Interactions usually were terminated after a fecal marking display (62%, n=8) or mutual olfactory exploration (38%). The stallions then returned to their respective herds. Both stallions moved their herds away from the area subsequent to two interactions, while one herd moved away following five interactions (n=16).

The predominance of display behaviour during these meetings and the absence of serious fighting is consistent with Klingel's (1975) observation that in species with Type I social organization "the presence of a family stallion is respected by the other stallions and there is little or no fighting over adult mares." Similar display and marking behaviour have been described for widely separated feral horse populations by Pellegrini (1971), Welsh (1975), Feist and McCullough (1976) and Berger (1977). Berger (1977) documented numerous fights but attributed this to increased contact due to drought conditions.

4.63 Interactions between harem stallions and bachelors

Interactions between harem stallions and bachelor males were more intense than those between two harem stallions, apparently as a result of increased vigilance by the harem males and greater persistence by the bachelors. Display again centred on fecal marking and olfactory investigation, but often several sequences were carried out before the interaction was terminated. Nearly all harem stallion-bachelor male encounters involved biting and/or kicking. In addition, usually more than one bachelor became involved in displays and fighting with the harem stallion. These interactions tended to be prolonged, as compared to the brief meetings between dominant males from two harems. The longest of these was a series of interactions lasting nearly 1.5 hours, during which a harem stallion spent the entire period exchanging greetings and aggressively interacting with a herd of predominantly young bachelors at a salt lick. The harem stallion actively prevented access of the bachelor males to the other herd members but was unsuccessful in driving them away.

4.64 Changes in herd structure

As a result of stallion dominance over the group and the largely ritualized nature of stallion-stallion interactions, established harems were relatively stable (Table 4.3). Most changes appeared to occur during the spring and summer months, but this may have been an artifact resulting from increased frequency of sightings during the early part of this period. In other areas, changes have occurred primarily during the breeding season (Feist and McCullough 1975) or following a severe winter (Welsh 1975).

Two year old and yearling males frequently left harems and either joined bachelor groups or were not resighted, the latter possibly indicating movement out of the area. Observations suggest that some young males, and perhaps females, may be driven out of their parental herds. One example is provided by harem 061, within which 11 instances of threat involving one animal chasing another, sometimes at full speed, were observed. These chases involved a total of six animals, including the dominant stallion, an associated bachelor, a three year old, a two year old and a yearling male, and a female yearling and foal. All but the harem stallion were chased by at least one other animal, and all but the yearlings and foal chased a subordinate. Once an animal had been chased it was sometimes actively kept away from the main group. This behaviour may have discouraged subordinates from remaining with the herd and it is of note

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Table 4.3 Sex and Age Class of Animals Involved in Observed Changes in Harem Group Structure, January - December, 1976.

No. animals	subord. adult ♂	adult ♀	2 yr. old ♂	2 yr. old ♀	yearling ♂	yearling ♀	unid. yearling	foal	Total
Leaving[1]	1	4	2	3	4	3	3	2	22
Joining	1	1	1	2	0	4	1	2	12
Total	2	4	2	3	4	4	3	4	26

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[1] only those animals absent during at least two consecutive observations of original herd and/<u>or</u> joining another herd after initial description were considered to have left.

that the yearling female and two year old male subsequently left together. Intraharem chasing was relatively rare, however, being observed on only one other occasion when a harem male engaged in an aggressive chase with his two year old son. This young stallion subsequently remained with the herd, however. No immature males left their family herds during the six month study reported by Feist and McCullough (1975), their presence being tolerated due to their submissive behaviour. Welsh (1975) documented that young Sable Island stallions left their family herds of their own accord when between six months and four years old, and were accepted back after temporary absences. However, in the Przewalski horse (Equus przewalskii), herd stallions drive off the juvenile males as they start to mature (Dobroruka 1961, cited by Ewer 1968).

Four harems in the Red Deer River area had males older than two years associated with them, some of these probably the offspring of the dominant stallion. All five[1] engaged in fecal marking behaviour and interacted with the herd stallion, but were clearly subordinate as evidenced by avoidance behaviour. A linear dominance hierarchy developed in a harem with a dominant male, two subordinate males, a mare and her female yearling offspring, the lowest ranking male avoiding threats even from the mare. Only one subordinate adult male left a harem during the study; this

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[1] two in one group

animal was later observed attempting (unsuccessfully) to join a bachelor herd.

Immature females leaving harems joined either single bachelors, bachelor groups or other harem groups. At least one left her family group in the company of another herd member, and one changed herds while foaling. In New Forest Ponies, young fillies sometimes left their mother's groups as yearlings, but more commonly as two, three or four year olds, the break being attributable to the birth of new siblings, the onset of sexual maturity, or the presence or absence of other siblings or young animals (Tyler 1972). Feist and McCullough (1975, 1976) found that most changes in harem groups involved immature females, and they speculated that young mares may leave voluntarily.

Permanent changes involving adult mares occurred only rarely, and appeared to have been associated primarily with the foaling period in spring when mares left the harem group to give birth. Most mares were subsequently resighted with their original group after this temporary absence, but on one occasion a stallion was observed in the process of incorporating a passing mare and foal into his harem, with which they remained. Two mares which had foaled and returned to their original harems were subsequently observed with single bachelor males, both accompanied by their foals and one accompanied as well by her yearling colt.

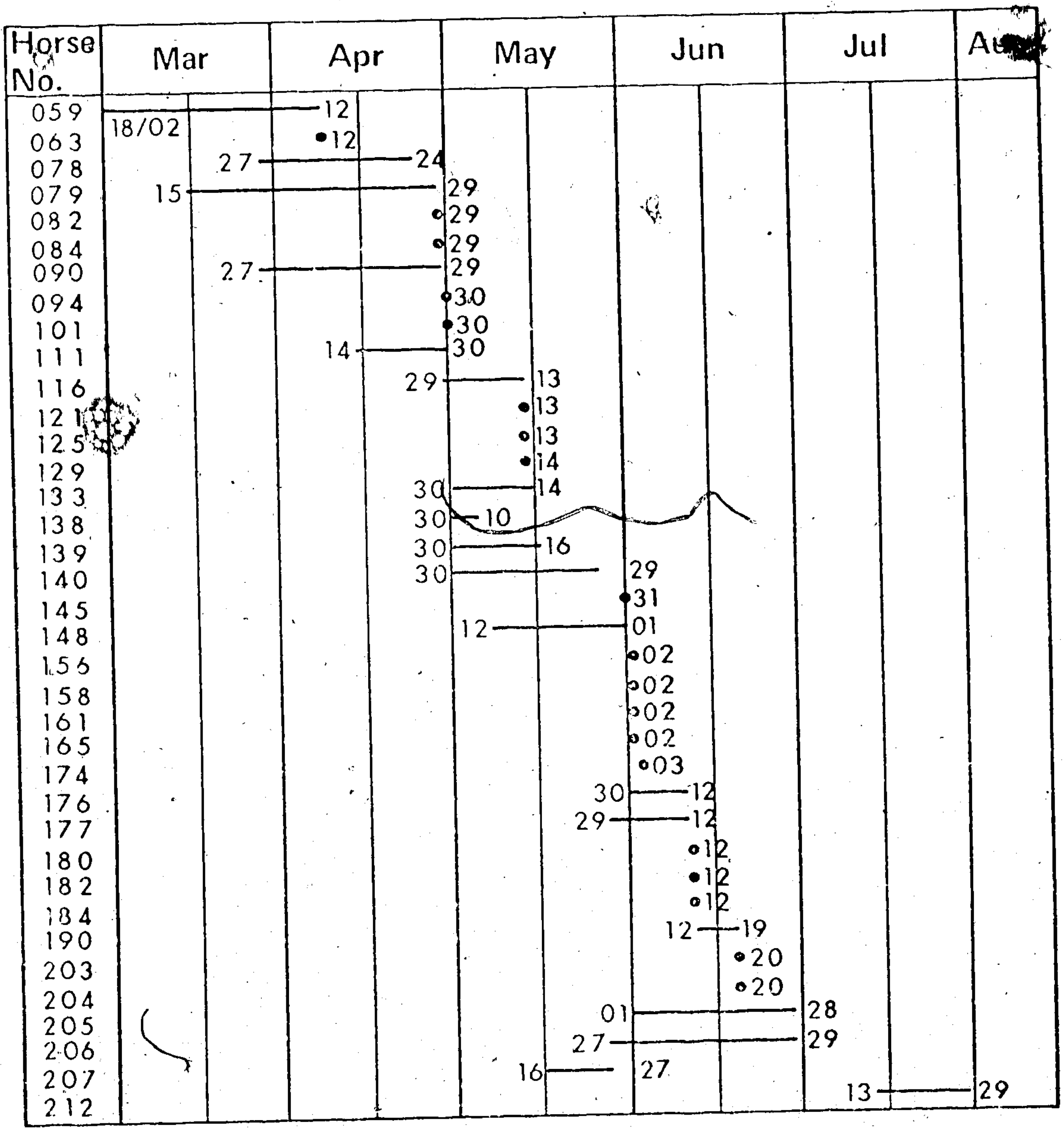
Single bachelor males appeared to pose the greatest threat to harem stability. One strategy used by single bachelors was to follow a harem and force the dominant stallion into frequent interactions, both by interfering when the stallion was marking dung piles or interacting with other herd members and by attempting to assume the rear position when the herd was escaping from disturbance. These all led to exchanges between the two stallions similar to those described above. One such association involving harem 061 was observed between 12 April and 27 May, 1976, and although several interactions were observed the harem stallion eventually appeared to tolerate the close proximity of the bachelor, on one occasion even lying flat on his side and resting while the other was with the herd. On both 12 and 14 April the bachelor maintained a close association with the same pregnant mare (apparently belonging to the harem), both grazing 50 to 75 m away from the main herd but joining the group when disturbed. The bachelor remained with the harem even though this mare left the group to foal and did not return. Subsequent to 15 May the bachelor obtained a mare and foal from another harem in the area, but still maintained his association with harem 061, following their movements closely during an observation on 27 May. When next observed on 25 June the bachelor, mare and foal were still together but the association with harem 061 appeared to have dissolved. Welsh (1975) discussed this 'tagging' behaviour of bachelors in detail and noted that some of these associations may persist for years.

Associations between single bachelor males and young females probably represented attempts by bachelors to start harems of their own but they often were unsuccessful. For example, one yearling female was seen with two different bachelors before joining a harem. Bachelor male 0C6, who was variously seen 'tagging' a harem in summer 1975, and alone and 'tagging' a single bachelor and recently acquired two year old mare in summer 1976, had acquired an adult mare and her yearling and foal offspring by November 1976 but had lost them and formed another association with an immature mare by June, 1977.

4.7 Reproductive Behaviour

Observations of stallions tending mares extended from 10 April to 29 June in 1976. Almost all foals were also born within this time period (Figure 4.3). Tyler (1972), Welsh (1975) and Feist and McCullough (1975) all reported that the birth of most foals occurred during April, May and June, indicating development of marked seasonality of breeding in both feral and free-ranging populations.

Stallion behaviour patterns confined solely or largely to the breeding season were exploratory sniffing of mares (14/14 instances) and flehmen or lip-curl (21/25 instances). Seven observations of stallions sniffing a mare's genital area involved harem stallions, five involved subordinate stallions in a harem, and two involved a yearling male.



Cumulative % of foals present at end of two week intervals:

5.4	27.0	43.2	54.0	83.8	97.3	97.3	100.0

Figure 4.3 Birthdates of foals during 1976. ——— :period between when dam last seen without foal and when first seen with foal.
•:foal already present when dam first described.

Observations of flehmen, each involving one or more lip-curls, were distributed among harem stallions (12), subordinate stallions in a harem (4), a yearling male in a harem (2) and bachelor males (3 - one by a two year old). Seven instances were accompanied by urinary marking. Flehmen occurred most commonly after sniffing the ground (nine instances) but also followed sniffing of a mare's vulva (4), smelling of a mare's urine (2), courtship or tending (2) and smelling of a bachelor's urine (one, by the dominant bachelor). The cause of flehmen was not determined in two instances, and was observed in association with a stallion interaction once during the breeding season and once following (July 12). Only three other instances of flehmen were seen, all involving bachelor males sniffing the ground in December. These observations agree with those of Feist and McCullough (1976) who found flehmen to be used only by males, most frequently during the breeding season. Tyler (1972), however, reported flehmen in female New Forest Ponies.

Although stallions most commonly followed mares and were the primary initiators of breeding activity, mares approached stallions on six occasions, nuzzling their flanks during at least three of these, and turning and 'presenting' during three. An additional three mares were observed raising the tail and 'presenting' without approaching the stallion. None of these resulted in copulation. All sexual behaviour initiated by mares was directed toward dominant stallions. Conversely, all approaches by subordinate stallions were rejected. Tyler (1972) found that mares played a more active part than stallions in initiating copulation, repeatedly approaching and displaying oestrous posture. Feist and McCullough (1976) observed this only once, believing it to be more characteristic of groups with unbalanced sex ratios.

Eight observations of actual or attempted copulation were made between 29 April and 28 June, five involving harem stallions mounting adult females, two of bachelor males mounting yearling females, and one of a subordinate harem male mounting a yearling female within the same herd. None of the yearling females were receptive, and although the latter raised her tail and permitted the stallion to sniff her, she moved forward during each of three attempts at copulation and intromission was not achieved. The stallion dismounted after the final attempt and interacted with another subordinate male and the harem stallion, after which the dominant male drove his only mare and the yearling female away from the area. Four of the five instances of mounting by harem stallions appeared to be triggered by the proximity of other herds. Feist and McCullough (1976) found that 70% of the observed breeding activity occurred during some form of disturbance, and theorized that this behaviour was adaptive since it maximized chances of reproductive success prior to potentially dangerous interactions.

Some mares apparently came into oestrus as yearlings as evidenced by sniffing behaviour directed toward them by stallions, and by attempted copulations. Only one mare considered to be a two year old foaled during the study, however, and the birth-date of mid- to late July was the latest of the 36 documented during 1976. Breeding by two year olds was somewhat more common, as four mares aged as two year olds in 1976 were observed with foals in early June, 1977. Tyler (1972) found that a small number of mares came into oestrus as yearlings but only one out of 107 foaled as a two year old, most foaling for the first time when three or four. The youngest animal observed copulating by Welsh (1975) was just over two years old, and Feist and McCullough (1976) did not record foals with mares younger than three years of age. Puberty in domestic horses is reported to begin between 10 and 24 months, with an average of 18 months of age (Frandson 1974).

The known reproductive histories of 12 adult mares observed with foals in early June, 1977 are given in Table 4.4, which shows that 83% of them also foaled the previous year. At least one of these, and probably more, also foaled during 1975. Although based on a very small sample size, these data tend to agree with Welsh (1975) who found that most mares on Sable Island foaled two or three times in three years, and that of those foaling twice 80% did so in consecutive years. Tyler (1972), however, found that very few New Forest Pony mares foaled in each of three years, but

Table 4.4 Reproductive Histories of Adult Mares Observed With Foals During Early June, 1977.

Mare No.	Foaled		
	1975[1]	1976	1977
081	?	yes	yes
083	?	yes	yes
087	?	no	yes
016	?	yes	yes
062	?	yes	yes
065	?	no	yes
154	?	yes	yes
155	?	yes	yes
157	?	yes	yes
043	?	yes	yes
044	?	yes	yes
045	yes	yes	yes

[1] based on observation of suckling yearling during early 1976.

it was common for a mare to foal in alternate years. It is believed locally that within the present study area mares generally foal every year, but that many foals are lost early in life (R. Logan pers. comm.).

4.8 Sex and Age Composition

Table 4.5 summarizes the sex and age composition of the population of 206 horses reliably classified between January and December 1976. Nearly half of the animals were immatures (born 1974-1976), probably indicating a high rate of recruitment. The foal to adult mare ratio was 62.1:100[1], within the range of 42.4:100 to 71.4:100 reported for Sable Island (recalculated from Welsh 1975, p.259) but much higher than the 43.2:100 (excluding most three year old mares) reported for Montana-Wyoming by Feist and McCullough (1975). Three foals are known to have died during the study period, and the high first week mortality (13-25%) reported by Welsh (1975) raises the possibility that more may have died early in life before they could be described. Domestic horses raised under western range conditions produced between 43.5 and 73.7 foals per 100 adult mares, with an average of 59.6 over a 14 year period (Speelman et al. 1944). In the northern U.S.S.R. foal to mare ratios of 62:100 are achieved in horse herding operations (Andreyev 1971).

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[1] excluding a late foal born to a mar considered to be a two year old.

Table 4.5 Sex and Age Class of Feral Horses Described During January - December, 1976.

	Number in age class					
	adult	2 yr. old	yearling	foal	total	%
Male	49	11	15	18	93	45.1
Female	58	13	14	9	94	45.6
Unidentified	2	1	6	10	19	9.2
Total	109	25	35	37	206	
% of total	52.9	12.1	17.0	18.0		

Seventeen per cent of the animals were yearlings, also higher than the 11% reported for this population segment by Feist and McCullough (1975). The winter of 1975-76 was exceptionally mild, however, and no mortality in this age class was documented.

Accurate male:female ratios could not be calculated since not all animals were sexed. This problem was most apparent in the younger age classes in which external genitalia were difficult to see. Feist and McCullough (1975) reported a nearly balanced sex ratio and considered variation of the ratio in younger age classes to be random.

4.9 Reaction to Predators

Although predators are not believed to control the ultimate size of mammalian populations, they may affect population structure by preferentially culling animals from the youngest and oldest age classes (Errington 1946). Also, herd formation in ungulates is considered to be primarily an evolutionary response to predation pressure (McCullough 1969, Hamilton 1971, Kitchen 1974). Coyotes (Canis latrans), wolves (C. lupus) and cougars (Felis concolor) were all present in the study area, and although no actual incidents of attacks on horses were documented several interactions were noted. These are interpreted both in terms of social behaviour and potential as mortality factors.

Coyotes elicited very little response from horses, even when in close proximity. Although coyotes were heard nearby during observations of five herds only one response was seen, this involving a brief glance toward the source of the calls by the stallion and two mares. On 27 March two coyotes passed less than 100 m in front of a herd of 12 horses which were alert and staring at me, but neither species appeared to take any notice of the other. During an observation on 11 November a single coyote approached a herd of four horses to within 25 m before noticing them, at which point he made a wide circuit of the herd and continued on his way. A lactating mare stared at this animal as he approached but showed no other reaction.

The only observed response by horses to the presence of a wolf occurred on 29 June, when a bachelor male and a harem comprised of 14 animals (including four foals) were under simultaneous observation at the edge of a large meadow. A single wolf approached both herds to within 25 m while walking along a trail just inside the forest edge, but showed no apparent interest in the horses. Nevertheless, the harem group bunched up and left the meadow, trailing along the edge of the woods (with the stallion in the rear), re-emerging and resuming grazing activity less than 100 m away. No response was observed from the bachelor, who was resighted at a nearby salt lick later in the morning. The response observed in this instance may have been due to the fact that only a single wolf was present, and that it showed no inclination to attack. Although Carbyn (1974) observed a successful group defense strategy in a herd of 15 horses under attack from 10 wolves (the horses staying together and rushing the wolves each time one moved closer), wolves are believed to be important predators of horses when wolf numbers are high (R. Logan, J. Stelfox, pers comm.).

No interactions with cougar were observed, but fresh cougar tracks were found in winter in the vicinity of at least two herds. Depredations on domestic horses by cougars have been reliably documented in Manitoba (Nero and Wrigley 1977), and they are believed to be efficient predators, especially on young horses, in the Alberta foothills (R. Logan pers. comm.).

4.10 General Discussion

The social organization of feral horses appears to be remarkably stable over a wide range of habitat types. All studies conducted in North America have shown the basic social grouping to be the harem, a permanent reproductive unit dominated by an adult stallion and consisting of a number of females and immatures. In many other ungulates males gather and defend harems on a seasonal basis, but the permanent, non-territorial harem system is unique to equids, and in North America to feral horse populations. The conservatism of social organization within this species has been discussed elsewhere (Feist and McCullough 1976).

Recent studies have documented some flexibility in the evolution of social organization in some species of bovids and cervids, group size and behaviour varying between sedentary and migratory populations and between populations occupying 'open' vs. 'closed' habitats, but this flexibility either is not present or is unnecessary in the case of non-territorial equids. Feral horses represent a unique case in that, by virtue of their previous association with man, they have been 'imposed' on habitats which are often greatly dissimilar to those in which their social system is thought to have evolved. The fact that populations of horses have become established over a large geographical region suggests, however, that their basic social organization is adaptive to a broad spectrum of habitat conditions.

4.101 Group Size

Jarman (1974) suggested that for African antelopes, and possibly for other ungulates as well, the likelihood of intragroup competition for forage imposes an upper limit on group size, whereas the lower limit is set by antipredator considerations. While these two factors may also operate to some extent within feral horse populations social factors are likely as important (or possibly more important) in determining group size. Within harems, maximum group size may be dependent upon the limited ability of the stallion to maintain herd integrity, and by limits to within-group bonding and mutual recognition. Minimum group size is set by the ability of the male beginning a harem to obtain and keep mares under his control. Within bachelor herds there may also be limits to within-group bonding, but more likely group size is determined primarily by the conflicting tendencies of gregariousness and for bachelors to leave and attempt to start harems of their own. Dominance hierarchies were well-developed in at least some bachelor herds, and may also have functioned to limit group size. On one occasion a single bachelor was observed attempting to join a bachelor herd (which also contained a yearling female) but was actively prevented from doing so by the dominant animal.

4.102 Spatial relationships

Both bachelor and harem groups occupied non-exclusive home ranges throughout the year, permitting exploitation of the best grazing areas by a number of herds. As noted by Klingel (1975), the social system of non-territorial equids is well-adapted to areas with changing ecological conditions, [illegible] the permanent reproductive units do not restrict movement. In the present study area overlap in the use of space was particularly evident during spring but occurred to some extent throughout the year. Comparison with other studies indicates that feral horses may also adjust home range sizes in relation to available resources, as is the case with other ungulates.

Scent-marking appeared to be an important aspect of space-related behaviour. Spacing between herds was also maintained by a hierarchy of threats among dominant males, and involved only a minimum of fighting, even during the breeding season. This is in marked contrast to some native ungulates, in which severe wounding or killing is not uncommon in intraspecific combat (Geist 1974, Wilkinson and Shank 1976).

4.103 Productivity

On superficial inspection the permanent reproductive units formed by feral horses might seem to promote inbreeding between a stallion and his daughters, or between siblings of opposite sex. In this study, however, young animals of both sexes tended to leave their parental herds, effectively preventing breeding between a stallion and his female offspring and resulting (usually) in the separation of siblings. Furthermore, there is evidence that young stallions of breeding age within a family group are prevented from breeding by the dominant male. In Plains zebras young females leave the parental harem at an earlier age than do males, and the separation of young mares from their families is believed to maintain the gene flow within the population (Klingel 1975).

The segregation of young males into bachelor groups is a common feature of the social organization of many ungulates. In territorial species, only the strongest of these eventually establish territories and are able to breed, their position in the bachelor male hierarchy apparently being a strong determinant of eventual success (eg. Kitchen 1974). This has its parallel in the social organization of horses, in that not all bachelors are successful in establishing and maintaining harems. During this study several attempts by bachelor males to gain females were documented, but the proportion of the bachelor population which eventually obtain their own harems is not known. Kirkpatrick et al. (1976) documented lower testosterone concentrations in an eight year old feral bachelor stallion than in two harem stallions, but whether this was a cause or an effect of this animal remaining a bachelor was not determined.

Examination of mare:foal ratios indicated that productivity during the study [illegible] comparable to that achieved under domestic manage[illegible]elman et al. 1944, Andreyev 1971). [illegible] comprised 18% and yearlings 17% of the population, but [illegible] percentage of yearlings (animals surviving their [illegible]st winter) is the more important figure for estimating recruitment since this is usually considered to give a better indication of the number of animals entering the breeding population. Although recruitment rates would be expected to vary [illegible] year to year, the available data suggest that feral horse populations are at least as potentially productive as those of some native ungulates (e.g. compared to bison (<u>Bison bison</u>) with 10% yearlings (Fuller 1966)) but less so than others which commonly twin (e.g. moose, 25% yearlings (Simkin 1974)).

It has been suggested that in the United States numbers of feral horses are increasing at about 20% annually (Anon. 1976), but data on recruitment and mortality were not presented. The effect of recruitment on population growth is of course moderated by mortality of animals already in the population. Mortality rates were not determined in this study, but evidence from other feral horse populations indicates that mortality is concentrated among the very young and the very old (Feist and McCullough 1975, Welsh 1975), as is the general rule for other mammalian populations. This situation occurs even in the absence of predation (Welsh 1975), which is probably a highly variable mortality factor on the present study area. Welsh (1975) also found that males had a longer life expectancy than did females, due to reproductive stress in the latter. He presented long-term data showing alternate peaks and crashes in population size.

Chapter 5: Feeding Ecology

5.1 Introduction

Horses are primarily grazers (Hafez et al. 1969) but until the recent interest in feral horses little else was known of their foraging behaviour or food preferences on natural range. Tyler (1972), Welsh (1975), Feist and McCullough (1976) and Berger (1977) discussed various aspects of feeding behaviour in free-ranging and feral horse groups, all concluding that horses spend the majority of their time foraging. Odberg and Francis-Smith (1976, 1977) discussed the formation of grazed and ungrazed areas in fields used by horses, and compared their findings to the available information on feral horses and other equids. Dietary studies now available are those by Hansen (1976) from New Mexico, Hubbard and Hansen (1976), Hansen and Clark (1977) and Hansen et al. (1977) for Colorado, and Olsen and Hansen (1977) for Wyoming. These showed that a major proportion of diets of feral horses are comprised of grasses and grass-like species.

Despite the intimate interrelationship of food habits with nutrition and over-winter survival the latter remain poorly understood in free-ranging animals. Welsh (1975) discussed aspects of the nutrition of feral horses on Sable Island, especially as these related to winter starvation, and Dieterich and Holleman (1973) discussed the physiology of environmentally and nutritionally stressed horses in Alaska, both reports providing background information pertinent to the present study.

Patterns of feeding behaviour, including drinking, the use of salt licks and adaptations for feeding in snow, are discussed in this chapter. Data on diet composition throughout one annual cycle also are presented. These data are discussed in terms of palatability, availability and quality of major forages. Habitat selection in relation to food habits is discussed in the following chapter.

5.2 Methods

5.21 Feeding behaviour

Information on feeding behaviour was obtained primarily during 298 hours of observation in 1976 (see section 4.2). Examination of feeding areas and salt licks throughout the year provided supplementary data.

Records of the number of animals engaged in specific, undisturbed activities were obtained by scan sampling (Altmann 1974) at regular intervals during 99 of the 298 hours of observation to obtain quantitative information on activity cycles in relation to weather, time of day and season of year. Records were maintained at 15 minute intervals during 25 hours, and at five minute intervals during 74 hours. These were summed on an hourly basis for the periods January-March and April-June, inclusive. Time spent feeding and resting was calculated as the percent of animals recorded in each activity. Activities such as walking, agonistic interactions, play and grooming were noted in the field but were tabulated in the category 'OTHER' for purposes of this analysis. Mountain Standard Time was used throughout the year.

5.22 Diet composition

Diet composition was determined by identification of plant fragments in the feces. Fifty samples of fresh horse feces were collected during the last three weeks of each month in 1976, each consisting of one or two pellets. All samples were obtained within two areas (total 30 ha) utilized for quantitative assessment of habitat utilization. An attempt was made to collect horse feces from several sites during each month, and not more than 15 samples were obtained from any one site. The samples were kept as cool as possible in the field in order to limit bacterial and fungal action and were transported to the laboratory and frozen as soon as practicable.

In preparation for analysis the feces were thawed and combined on an approximately equal dry weight basis into 12 composite samples representing monthly diets. The composite samples were oven-dried at 55°C for 48 hours, then ground in a Wiley mill using a 1.5 mm screen. Approximately 10 gm of each thoroughly mixed composite sample were sent to the Composition Analysis Laboratory, Colorado State University, for analysis at 400 microscope fields per sample (Hansen et al. n.d., Sparks and Malechek 1968). This technique provides results which approximate the relative dry weights of food categories in the diet (Hansen et al. 1973, Todd and Hansen 1973, Dearden et al. 1975, Reynolds 1976). Correction factors for over- or underestimation of certain species are sometimes applied but rarely provide additional precision (Hansen et al. n.d.).

5.23 Diet quality

Seasonal changes in diet quality were estimated indirectly through fecal analysis. Crude protein and acid detergent fibre levels in each of the 12 monthly fecal samples were determined by the Agricultural Soil and Feed Testing Laboratory, Alberta Department of Agriculture.

5.3 Feeding Behaviour

5.31 Adaptations for foraging in snow

During winter, horses pawed away the overlying snow to expose food plants. Snow was cleared by repeated downward and front to back motions of the foreleg, the hoof acting as a 'shovel'. The head was usually kept down while pawing, with the body weight shifted to the opposite foreleg. In a typical sequence a horse pawed snow away from a selected spot, took several bites interspersed with more pawing, slowly walked forward several steps (head down), then repeated the cycle. Feeding was usually begun before the end of the initial pawing phase. Downward motions of the head assisted in biting off forage, these motions probably also functioning to keep the crater clear of snow. Although observed at all snow depths pawing was resorted to more frequently in deep as compared to shallow snow cover, and each pawing bout tended to involve more strokes (Table 5.1). Up to 19 strokes per bout were used in deep snow cover. The animals appeared well able to cope with the snow depths encountered on the study area during January-March and craters were found in snow as deep as 60 cm.

Horses also were able to feed in shallow snow without pawing. In these situations snow was 'plowed' away by pushing the muzzle through the snow at a selected spot, and subsequent snow clearing was accomplished by thrusting the muzzle forward while feeding. It appeared that this technique also was used to enlarge or clear snow from craters already created by pawing; it was used without pawing only at the shallowest snow depths (Table 5.2).

In addition to these behavioural adaptations for feeding in snow horses took advantage of reduced snow depths at tree bases in woods, and on hummocks and around shrub bases in open areas. Steep south-facing slopes remained snow-free or had reduced snow depth throughout the winter and also were exploited as feeding habitat. However, bare

Table 5.1 Frequency of Pawing by Foraging Horses in Relation to Snow Depth, 1976.

Snow depth (cm)	No. 5 min observation periods	Mean no. pawing bouts/5 min ± s.d.	Mean no. strokes/ pawing bout ± s.d.
< 10	16	1.44 ± 2.00	5.39 ± 1.80
40 - 50	9	9.11 ± 3.79	9.67 ± 3.55

Table 5.2 Number of Observations During Which Pawing Was Utilized by Horses and Relationship to Snow Depth, 1976.

No. observations involving:	Snow depth (cm) 1 - 10	11 - 20	21 - 30	31 - 40	40+	Total
Pawing	10	7	4	5	2	28
No pawing	6	2	0	0	0	8

areas were not always favoured as evidenced by an observation on 28 January of two bachelor males feeding in an isolated snow-patch on a steep slope above Bear Creek. This may have been related to selection of less weathered forage from beneath the snow, as shown by Bruns (1977) in a study of pronghorn antelope (<u>Antilocapra americana</u>) feeding behaviour.

5.32 Time spent foraging

About three-quarters of daylight hours were spent foraging during winter (Figure 5.1). Yearling and older horses continued to spend nearly 75% of daylight hours feeding in spring (Figure 5.2), and except for a two hour lull in mid-morning, feeding activities predominated from dawn to dusk during both seasons. Foals spent an average 41% of their time foraging, 13% standing resting, 26% lying resting, 4% suckling and 15% in other activities.

Quantitative observations during the last six months of 1976 were too few to permit similar calculations, but a decline in the frequency of horse sightings subsequent to June suggests a decrease in feeding time, at least in open areas, during summer. Welsh (1975) found that family herds grazed almost constantly in winter and spring but spent only about half of the summer daylight hours feeding, with time spent grazing again increasing during fall. Berger (1977) also reported a low in feeding time in summer as compared to

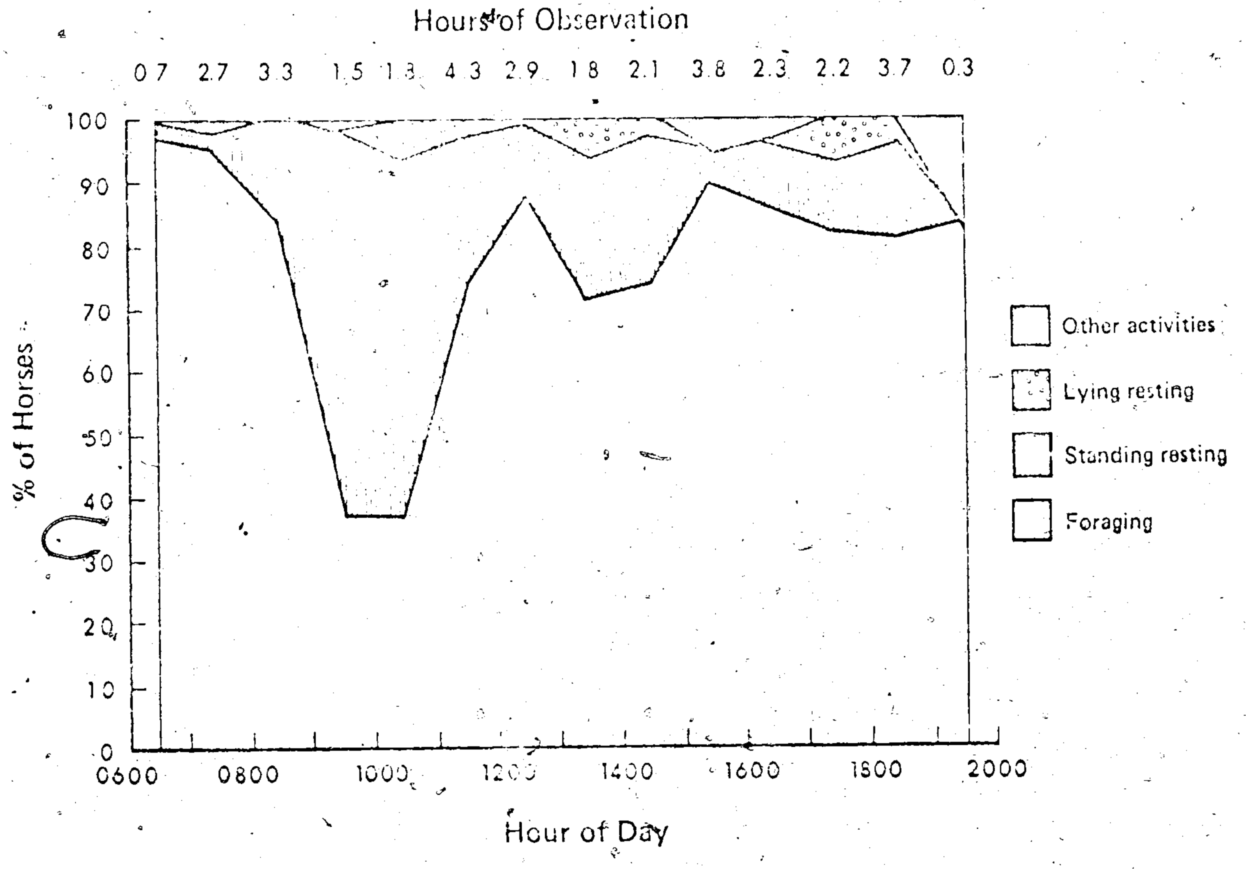

Figure 5.1 Activity patterns of horses during daylight hours, January - March, 1976.

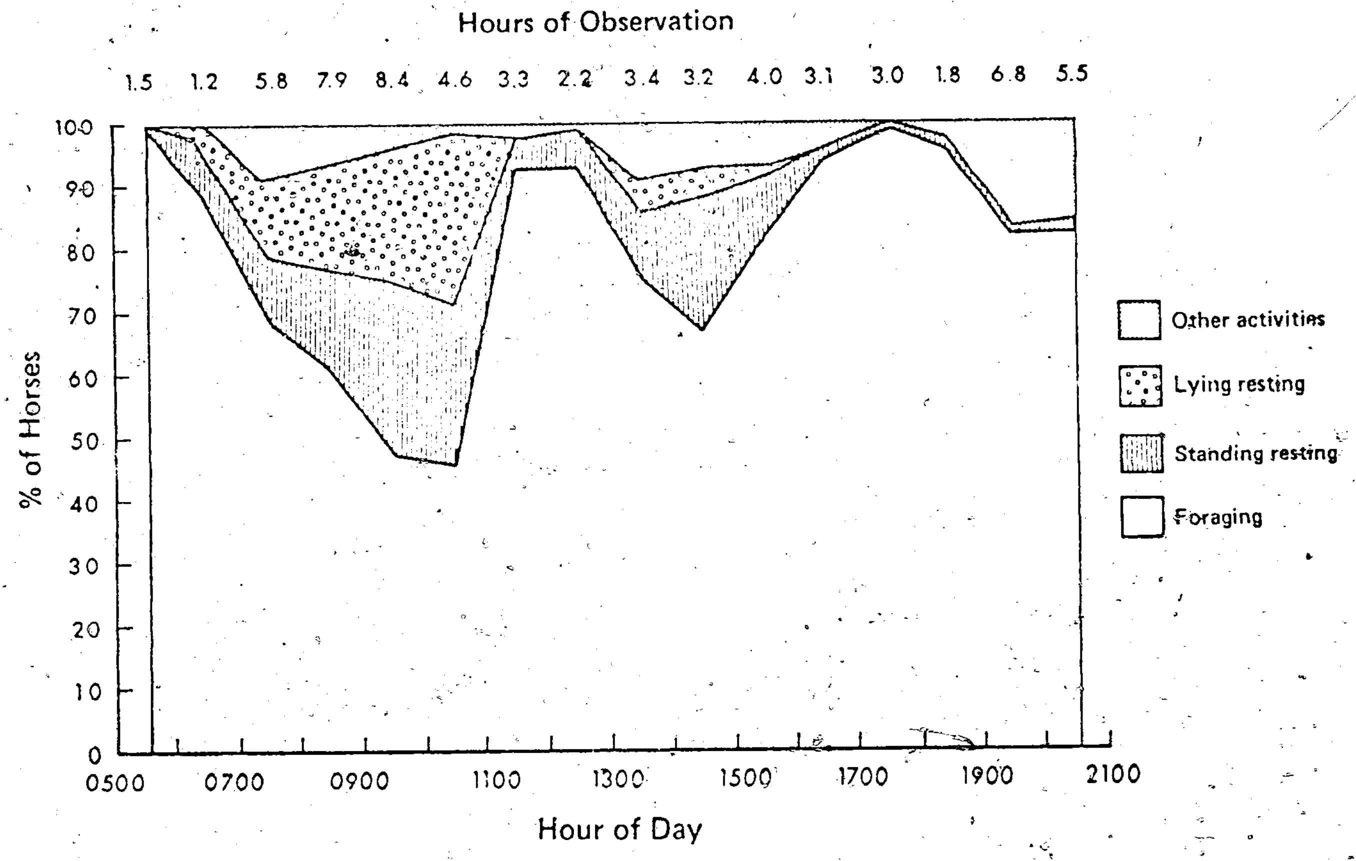

Figure 5.2 Activity patterns of horses (exclusive of foals) during daylight hours, April - June, 1976.

spring and fall.

Limited evidence suggests that foraging continued throughout the night during all seasons. On 11 March nine horses were observed, with the aid of a nightscope, feeding on an open slope above Deer Creek Flats, and on 13 March three horses were observed under moonlight feeding at the same location. On other occasions observations of feeding horses were discontinued due to darkness but the animals were still present, feeding, the following morning. Tyler (1972) believed that in all seasons New Forest ponies spent most of the night feeding, but provided no quantitative data.

Herd members usually remained in proximity to one another while feeding, although individual distances were maintained. On occasion animals were dispersed over an area of 100 m diameter or more; the largest recorded distance between foraging animals was 200 m. Herd integrity was maintained when two or more groups grazed the same area. Feist and McCullough (1976) reported similar dispersion patterns.

5.33 Drinking

Horses were seen drinking on only seven occasions. Water was readily available from the numerous streams in the study area, and consequently horses did not gather at specific sites to drink as reported for more arid areas.

Five of the observations involved drinking from streams (one while disturbed by human presence), one involved drinking from a puddle on a road (while disturbed), and one involved drinking from a puddle in a salt lick. The latter may have been related to salt hunger.

Three instances of undisturbed drinking during summer occurred in the evening between 19:00 and 20:00 MST. These observations suggest an evening watering period but the data are too few to confirm this. Feral horses in Montana-Wyoming visited watering holes throughout the day (Feist and McCullough 1976) as did horses in the Grand Canyon (Berger 1977). Pellegrini (1971), however, reported that in Nevada horses visited water holes at night.

Water requirements in winter were probably met largely by ingestion of snow, but one observation was made of a mare and yearling drinking from a small hole in a stream overflow area in December.

5.34 Use of salt licks

Horses ingested quantities of soil at both natural mineral licks and cattle salt licks throughout much of the year. These areas also were used for a variety of other maintenance and social activities, including rolling, resting, play and stallion interactions.

At the natural licks vegetation and soil were chewed away primarily from the southeast, south and southwestern faces of large hummocks. Fresh toothmarks were found on a number of these, and were particularly evident when the soil was frozen or semi-frozen. Soil was removed from flat areas between the hummocks only during the snow-free period. Sign of soil-eating was found in January and February but soil ingestion was not actually observed until April, when a mare and subordinate harem male were observed eating soil for a short period. Soil ingestion also was observed in May and June. There appeared to be a peak in this activity in May - during this month a number of sites were found, not necessarily in association with established licks, where quantities of soil had been chewed away from the sides of hummocks. Lick use appeared to be minimal during July-October, except at one lick which was an important locus for social interaction. Sign of soil ingestion at the natural licks was again observed in November and December.

Although other activities were observed at cattle salt licks soil-eating predominated. At these sites horses removed soil either by gouging the surface with the teeth or by licking. In one instance horses were seen drinking from a small pool of standing water within a lick, and on other occasions animals were seen pawing at the soil, presumably to loosen it prior to ingestion. Some soil ingestion occurred in January but this activity did not peak until April-June. During June-September several herds were observed at the West Valley Lick, a site where large numbers of horses had been seen in previous years, attracted by the salt put out for cattle (I. Sorenson pers. comm.). Horses had eaten soil at all four licks examined during November and December.

Observed movements toward licks from grazing areas were very purposeful, horses visiting licks at various times of day and for periods of varying length (Figure 5.3). The four soil-eating bouts observed on natural licks were all less than 10 minutes in length. Undisturbed periods of soil-eating at artificial licks lasted up to 40 minutes and possibly longer, as some observations had to be terminated due to darkness.

Over a quarter of the total population of horses (58/206) were observed eating soil at licks. That this high a proportion was observed during non-systematic observations indicates the likelihood that most, if not all, of the population were involved in utilization of these areas. All sex and age classes were represented in the observed sample.

Soil ingestion by feral equids is a widespread phenomenon, occurring in a variety of environmental settings. Horses were observed eating old, heavy organic soils on Sable Island off the coast of Nova Scotia (Welsh 1975), and in Montana-Wyoming Feist and McCullough (1976) observed a lone stallion eating "mud of a dark grey color from a nearly dried up water puddle" in spring. Feral burros (Equus asinus) in California spent approximately 10-20

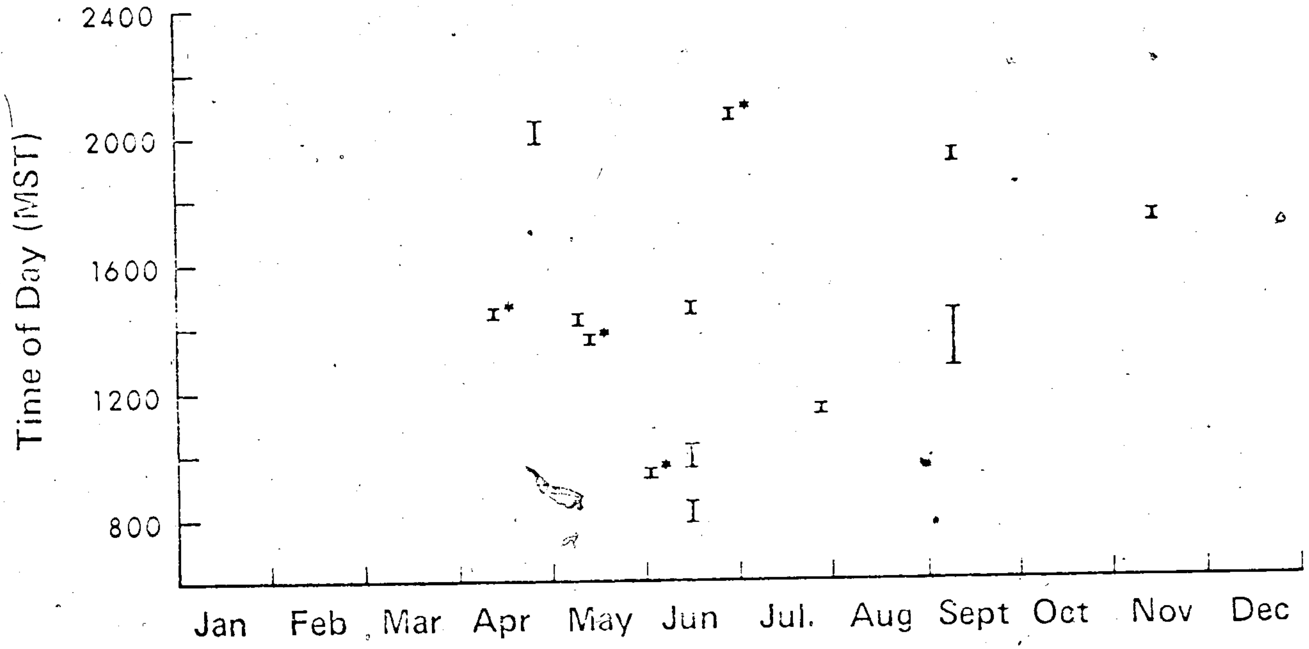

Figure 5.3 Seasonal and diurnal distribution of observed soil-eating bouts, January - December, 1976. Those marked with an * occurred in natural licks, all others in artifical licks.

minutes every three days eating salt-encrusted soil (Woodward and Ohmart 1976). Chemical analyses of soil, feces and vegetation indicated that soil- eating observed in the Red Deer River area likely was related to Na deficiency (unpubl. data).

5.4 Diet Composition

A total of 43 plant categories (species and species groups) were identified in horse feces collected between January and December, 1976, from 17 to 21 of these being found in each monthly diet (Table 5.3). Grasses, sedges and rushes constituted the bulk of the diet throughout the year, never occurring at a level of less than 83% during any one month. Within this group grasses were most important. Elymus innovatus was utilized throughout the year, constituting on average over 25% of the monthly diet with a seasonal decrease in utilization, probably related to increased availability of more palatable forage, during May-July. Festuca sp. (likely scabrella) was the second most important grass at an average of 20% of the diet. No other grass constituted more than a mean of 2.2% of the monthly diet although Agrostis scabra, Danthonia intermedia, Deschampsia caespitosa, Koeleria cristata, Poa spp., Schizachne purpurascens and Stipa spp. approximated or surpassed this figure during one or more months. Sedges were important throughout the year, ranging between 18% (September) and 56% (May) of diet composition. Juncus balticus was consistently

Table 5.3 Percentages of Plant Fragments in Monthly Samples of Feral Horse Feces, January-December, 1975.

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Annual
Grasses													
Agrostis scabra (Hair Grass)	-	0.1	0.1	0.6	0.7	0.8	0.2	0.4	0.6	2.0	0.4	0.3	0.5
Agropyron spp. (Wheat Grass)	0.4	0.3	-	-	0.1	0.1	0.2	0.2	-	-	-	0.1	0.1
Bromus spp. (Brome Grass)	0.1	0.1	-	-	-	0.2	0.2	0.6	0.1	[illegible]	-	0.1	0.2
Calamagrostis spp. (Pine Grass)	-	-	0.6	-	0.2	0.2	-	0.1	-	0.5	-	-	0.1
Danthonia intermedia (Timber Oat Grass)	0.9	0.9	-	2.1	2.7	0.6	4.1	2.2	4.0	1.8	2.1	1.1	1.9
Deschampsia caespitosa (Tufted Hair Grass)	1.8	-	0.6	0.6	1.7	1.6	1.7	1.0	[illegible]	2.3	1.2	2.2	1.3
Elymus innovatus (Hairy Wild Rye)	18.2	23.8	40.6	29.4	7.2	11.8	12.3	39.3	46.5	17.4	33.8	41.5	26.8
Festuca spp. (Fescue)	20.9	16.7	8.1	19.4	24.7	22.1	28.6	21.5	25.1	19.9	18.4	19.6	20.4
Glyceria spp. (Manna Grass)	-	-	-	-	-	-	0.1	-	-	-	-	[illegible]	T
Helictotrichon hookeri (Hooker's Oat Grass)	-	-	-	-	0.2	-	-	-	-	-	-	-	T
Koeleria cristata (June Grass)	2.3	0.6	0.1	1.9	-	-	-	-	0.4	2.6	1.6	3.3	1.1
Muhlenbergia spp. (Muhly Grass)	-	-	-	-	-	-	-	0.2	-	-	-	-	T
Phleum spp. (Timothy)	-	0.1	-	-	-	-	-	-	-	-	-	-	T
Poa spp. (Bluegrass)	0.9	0.8	0.1	0.4	4.1	4.4	1.6	1.7	0.4	9.9	1.1	0.5	2.2
Schizachne purpurascens (False Melic)	2.4	1.5	1.3	2.3	0.2	-	0.2	0.6	0.4	1.3	1.5	0.4	1.0
Stipa spp. (Needle Grass)	-	0.1	-	0.8	0.5	0.2	0.2	-	-	3.1	0.2	0.3	0.4
Trisetum spicatum (Spike Trisetum)	0.1	-	0.1	-	-	-	-	-	-	-	-	-	T
Total grasses	48.0	45.0	51.6	57.5	42.3	42.0	49.6	67.8	78.3	61.6	60.3	69.4	56.1
Sedges and Rushes													
Carex spp. (Sedge)	39.5	37.2	29.1	28.7	56.1	49.7	45.0	28.5	17.6	30.3	21.7	23.4	33.9
Eriophorum viridi-carinatum (Cotton Grass)	0.6	0.5	0.1	-	0.2	6.0	-	-	0.3	0.5	-	-	0.7
Juncus balticus (Wire Rush)	6.6	2.3	1.8	-	0.1	1.0	4.0	1.8	0.7	1.0	2.2	1.6	1.9
Scirpus caespitosus	-	-	0.1	-	0.1	-	-	-	-	-	-	-	T
Total sedges and rushes	46.7	40.0	31.1	28.7	56.5	56.7	49.0	30.3	18.6	31.8	23.9	25.0	36.5
Total grasses, sedges and rushes	94.7	85.0	82.7	86.2	98.8	98.7	98.6	98.1	96.9	93.4	84.2	94.4	92.6
Forbs													
Artemisia spp. (Sagewort)	-	-	-	-	-	-	-	-	-	-	0.1	-	T
Astragalus frigidus (Milk Vetch)	-	-	-	-	-	0.1	-	-	-	1.3	-	0.1	0.1
Mertensia paniculata (Tall Mertensia)	-	-	-	-	-	-	-	0.1	0.1	-	-	-	T
Petasites spp. (Sweet Coltsfoot)	-	-	-	-	-	-	-	-	-	-	0.2	-	T
Potentilla-Geum spp. (Cinquefoil-Avens)	0.7	0.1	0.1	0.8	0.3	0.8	0.2	-	0.1	0.5	0.2	0.1	0.3
Solidago spp. (Goldenrod)	-	-	-	-	-	-	-	-	-	-	0.1	-	T
Stellaria spp. (Chickweed)	-	-	-	-	-	-	0.2	0.2	-	-	-	-	T
Vicia americana (Wild Vetch)	-	0.3	-	-	-	-	-	-	-	0.8	-	-	0.1
Unidentified forbs	0.1	0.3	0.3	0.2	0.3	0.2	-	0.5	0.9	-	-	-	0.2
Total forbs	0.8	0.7	0.4	1.0	0.6	1.1	0.4	0.8	1.1	2.6	0.6	0.2	0.8
Browse													
Picea spp. (Spruce)	-	1.3	1.3	0.4	-	-	-	-	-	-	-	0.5	0.3
Pinus contorta (Lodgepole Pine)	3.2	3.8	7.0	4.0	-	-	0.1	0.2	0.5	2.3	6.2	3.5	2.6
Populus spp. (Poplar)	-	-	0.7	-	-	-	-	-	-	-	-	-	T
Salix spp. (Willow)	0.4	-	-	0.6	0.1	-	-	-	-	-	-	-	0.1
Shepherdia canadensis - Elaeagnus commutata (Canadian Buffalo-berry - Silver-berry)	-	-	0.1	0.9	-	-	0.3	0.3	-	0.2	-	-	0.2
Total browse	3.6	5.1	9.1	5.9	0.1	-	0.4	6.4	0.5	2.5	6.2	4.0	3.6
Miscellaneous													
Equisetum spp. (Horsetail)	0.6	2.8	4.5	2.7	-	0.2	0.4	0.4	0.8	0.2	5.7	1.2	1.6
Lichen	-	-	-	-	-	-	-	-	0.4	-	0.1	-	T
Moss	0.5	6.3	3.0	4.4	0.5	-	0.1	0.1	0.2	1.3	2.7	0.1	1.6
Total miscellaneous	1.1	9.1	7.5	7.1	0.5	0.2	0.5	0.5	1.4	1.5	8.5	1.3	3.3

present but averaged less than 2% of the monthly diet, as did *Equisetum spp.*

Forbs were utilized very little by horses and were found at a total level of less than 3% during each month. Species in the *Potentilla*- *Geum* group were the only ones which appeared consistently.

Browse was a highly variable dietary constituent, ranging from 0% in June to 9% in March. Although *Salix spp.*, *Populus spp.*, and *Shepherdia canadensis* (or possibly *Eleagnus commutata*) were all identified, none reached a level of 1% during any one month and all were inconsistent in occurrence. In contrast, *Pinus contorta* needles and to a lesser extent *Picea spp.* needles were consistently found in the feces; both were absent only during May and June. Since no evidence of browsing on living conifers was found at any time during the study, it seems most likely that the material in the feces represented fallen needles ingested accidentally while grazing other forage. This hypothesis is strengthened by the fact that levels were highest during the winter months when snow cover presumably decreased the ability of the horses to graze selectively. Mosses and lichens present in the feces may have been ingested under similar circumstances.

The predominance of grasses and sedges in the diet is consistent with reports from other areas. Hansen (1976) found that grasses and grass-likes constituted approximately

50% of the average annual diet of feral horses in New Mexico, but noted that this percentage was lower than in diets from other areas. In Wyoming, approximately 87% of the average annual diet of feral horses was grass, while 5% was sedge (Olsen and Hansen 1977). Grasses made up between 39 and 84% and sedges between 6 and 46% of the average diet of horses in three vegetation zones in the Piceance Basin of Colorado (Hubbard and Hansen 1976). In two other regions of Colorado grasses constituted 63 and 92% and sedges 27 and 2% of average annual diets, but composition even within regions was highly variable (Hansen and Clark 1977, Hansen et al. 1977). In the USSR, under conditions more comparable to the present situation than the desert and semi-desert conditions in the above reports, grasses and sedges were considered to be among the best plants for winter feeding (Andreyev 1971).

5.5 Diet Quality

Fecal crude protein levels showed strong seasonal variation (Figure 5.4), likely reflecting seasonal changes in diet quality as shown by Hebert (1973) for bighorn sheep (Ovis canadensis). Gates (1975) and McFetridge (1977) interpreted similar variation in fecal crude protein as indicating seasonal shifts in vegetation quality on bighorn sheep and mountain goat (Oreamnos americanus) ranges, respectively. In the present study, acid detergent fibre in the feces was used as an additional measure of the seasonal quality of vegetation ingested (Figure 5.4). Klein (1962)

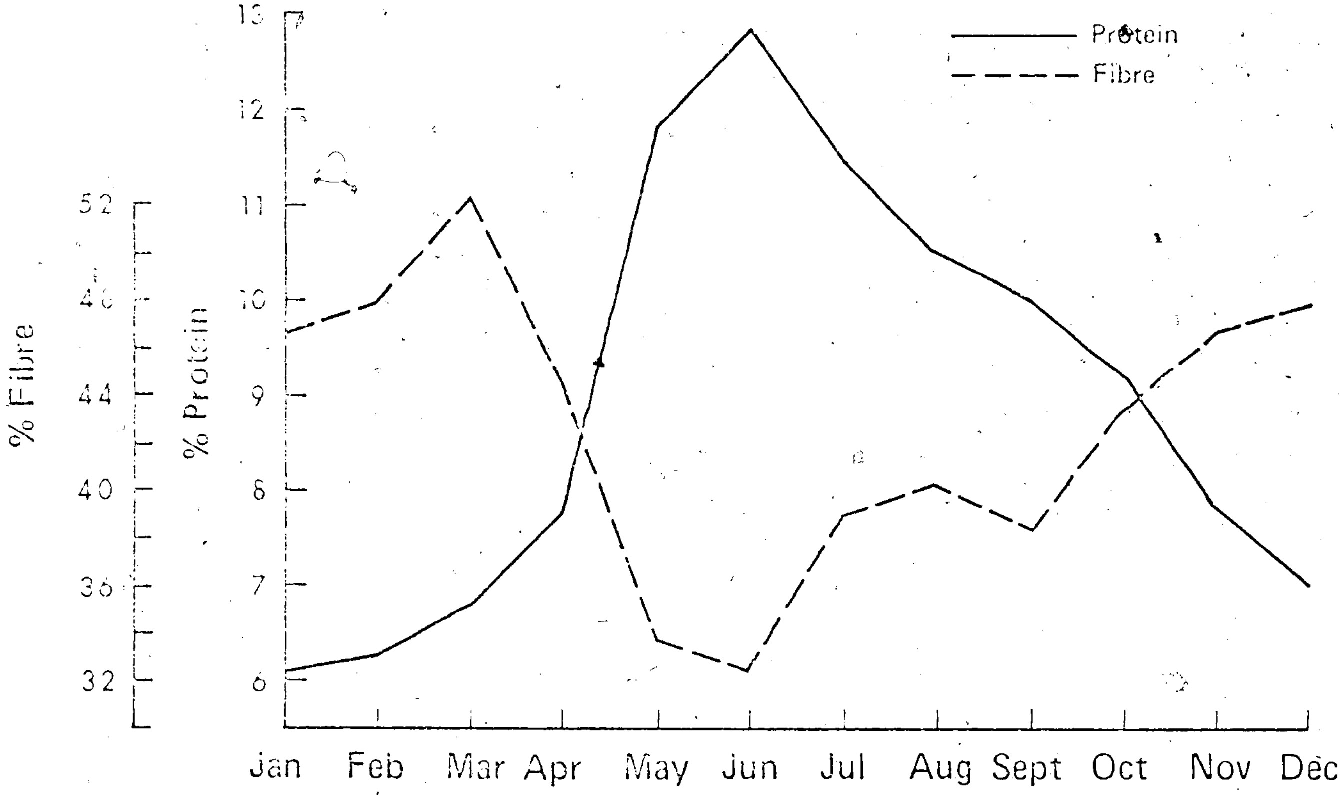

Figure 5.4 Monthly variation in levels of protein and fibre (% DM) in composite samples of feral horse feces, January - December, 1976.

suggested a negative correlation between fibre content in the feces and the quality of range used by black-tailed deer (Odocoileus hemionus columbianus).

Assuming that low values of fecal crude protein and high fibre levels indicate a poor quality diet, and that the opposite situation indicates a relatively higher quality diet, the curves in Figure 5.4 can be interpreted both in terms of botanical composition of the diet and growth stage of forages selected. During winter only weathered forages were available and diet quality appeared to be low. Greenup began in March (first noted 13 March) and the slight increase in diet quality during this month, and again in April, was probably due to the selection of some green material. The increasing availability of new growth was reflected in a rapid rise in diet quality between April and May, with a peak in June. Quality declined steadily thereafter as forages matured, cured and began to weather. It is noteworthy, however, that protein levels appeared to be as high in the November diet as in April, when at least some green material was available. Johnston and Bezeau (1962) showed that major forages (including Elymus innovatus and Festuca scabrella) in the Alberta foothills were highest in protein content and lowest in crude fibre during the leaf stage, prior to flowering, while the reverse was true for weathered plants, prior to spring growth.

Overall, diet quality was highest during May-July, when sedges averaged 50%, fescues (Festuca spp.) 25% and hairy wild rye (Elymus innovatus) only 10% of the diet, and was lowest during December-March when sedges averaged 32%, fescues 16% and hairy wild rye 31% of the mean monthly intake. These changes in diet composition likely were related to both palatability and availability factors. Hairy wild rye and rough fescue (Festuca scabrella) have comparable protein contents in spring (Johnston and Bezeau 1962) but wild rye is considered unpalatable (Campbell et al. 1966) probably explaining the low level in the diet at this time. Rough fescue contains more protein and less crude fibre at the weathered stage than does wild rye (Johnston and Bezeau 1962), but in this study fescue received heavy utilization by both cattle and horses during summer, and during winter was not readily available. Conversely, wild rye received little use during summer but was heavily used in winter, probably because it was a widespread and readily available forage. Sedges also were widespread and formed an important dietary constituent throughout the year, although utilization was heaviest during early growth stages in May, June and July. McLean and Tisdale (1960) found that sedges on wet meadows in British Columbia were close to maturity at the end of July, crude protein dropping from approximately 11% at this time to 6% in mid-September. Most sedges are moderately palatable and are comparable to grasses in forage value (Hermann 1970).

5.6 General Discussion

Cratering, removal of snow cover with the muzzle, frequent utilization of salt licks, and ability to utilize low quality forage can be viewed as adaptations of feral horses for maximizing forage and nutrient intake. As expected, these are all within the behavioural and physiological abilities of domestic horses, but may be more critical to the survival of animals in the feral state. Although published information is scanty, some differences in grazing behaviour of domestic and feral horses were noted.

5.61 Formation of grazed areas

Pastures utilized by domestic horses typically develop a patchy pattern of heavily grazed and ungrazed areas (Taylor 1954). Odberg and Francis-Smith (1976) observed that captive horses fed preferentially on areas where the grass had been closely cropped and eliminated most often in ungrazed patches. They concluded that this behaviour was the result of captivity in small fields, since no similar behaviour had been described in studies on free-living or feral horses or wild equids. The formation of extensive ungrazed areas was believed to be related to the avoidance of feces during foraging (Odberg and Francis-Smith 1977).

Although the formation of grazed areas was not specifically examined during the present study, it was apparent that horses preferentially grazed and regrazed certain areas while other sites of similar species composition were untouched. There was no evidence that horses defecated in these ungrazed areas; in fact only stallions stopped feeding to defecate, in marked contrast to all sex and age classes of domestic horses which may stop feeding and move to a preferred defecation site (Odberg and Francis-Smith 1976). Feral stallions frequently defecated on stud piles but these were along pathways or on grazed sites. Clearly, the formation of preferentially grazed areas on range used by feral horses was not related to avoidance of feces in ungrazed stands, since most horses defecated even while grazing. More likely, the accumulation of plant litter in the ungrazed areas formed a barrier to grazing, whereas the only limitation to forage availability in grazed areas was the extent of plant regrowth. There is evidence that protein levels are higher and crude fibre levels lower in regrowth than in undisturbed plants (Corns and Schraa 1962, Corns 1974).

Although the relationship was not specifically tested, a combination of availability and palatability factors likely influenced the preferential use of previously grazed sites by feral horses. This was particularly evident in spring, when disturbed areas such as roadsides or ditches and previously grazed areas, all lacking litter, were heavily utilized. It was estimated that less than 5% of non-forested habitat was grazed during spring, but destruction of forage through close cropping and trampling was severe on a limited number of sites (section 7.7). Utilization of ungrazed areas appeared to occur primarily during the period of snow cover.

5.62 Winter feeding strategy

Among northern ungulates different strategies are employed for obtaining food during periods of snow cover. Caribou (Rangifer tarandus) and bison primarily resort to cratering, moose resort to a browse diet (which is distributed largely above snow), while muskoxen (Ovibos moschatus) and wild sheep select windswept areas (Hudson and Bunnell 1978). Recent studies have shown that in some species a combination of strategies are employed, and this is likely the case to some extent in all species forced to cope with snow cover. Pronghorns select areas of shallower and softer snow than the average available, and are adept at pawing for forage (Bruns 1977). Caribou utilize different habitats and plant species in different snow conditions (Miller 1974). Elk utilize cratering and also select windswept areas (Hudson and Bunnell 1978).

Data gathered during this study show that horses are well adapted to obtaining forage from beneath snow, primarily utilizing the cratering strategy also used by some ungulates which have evolved under northern conditions. Areas of shallow snow cover also are selected. The influence of snow cover on habitat selection by feral horses will be covered in more detail in the next chapter.

5.63 Suitability of diet

Estimation of diet quality from feces illustrated a clear seasonal trend which correlated with trends in crude fibre and protein levels in major forage plants as reported in the literature (Johnston and Bezeau 1962). Since dietary nitrogen was not measured on an absolute basis, it could not be determined from the data presented if protein requirements were met during winter. However, forages available from grasslands such as occur within the study area are characterized by high crude fibre and low protein content in winter, and do not meet the maintenance requirements of beef cows (Johnston and Bezeau 1962).

Daily levels of forage intake were not measured during this study, but it has been shown in experimental situations that voluntary intake by domestic horses is positively correlated with crude protein content; ie. that intake is lowest at low protein levels (Fonnesbeck et al. 1967). The relationship in feral horses has not been established experimentally, but Welsh (1975) believed that horses on Sable Island compensated for low food quality by eating more, citing the time spent feeding in winter as possible evidence of increased intake. Extensive feeding time may have been due to increased selectivity and would not necessarily result in increased intake, however. In any case, it is well known that horses are capable of successfully utilizing low quality roughages (Slade et al. 1970). Slade and Robinson (1970) have suggested that feral equids may excrete less metabolic fecal protein than their domestic counterparts as an adaptation to low protein diets.

Horses can survive even subarctic winters if forage of sufficient quality is available (Andreyev 1971, Dieterich and Holleman 1973). Dieterich and Holleman (1973) suspected a degree of cold acclimation in horses surviving a severe winter in subarctic Alaska. Horses raised in the northern USSR may rely entirely on pasture for several years at a time, although additional fodder has to be provided during critical periods (Andreyev 1971).

Although both domestic and feral horses lose weight when maintained on native range over winter (Dawson et al. 1945, Andreyev 1971, Welsh 1975), starvation and die-offs may be due more to a combination of low forage quality and climatic stress than to low forage quality <u>per se</u>. Welsh (1975) found that on Sable Island forage quality was similar between years and was not limited in quantity, suggesting that weather, particularly the number and intensity of spring storms, determined the susceptibility of horses to starvation. In the study reported by Dieterich and Holleman (1973), horses had difficulty feeding due to deep snow and several died by mid-winter. On the present study area, widespread starvation of horses has occurred during long, cold winters with deep snow. Deaths occurred primarily during the latter part of winter (February onward) and it is believed that up to one half of the population may die-off under such conditions (R. Logan pers. comm.).

Chapter 6: Habitat Utilization

6.1 Introduction

Within their present North American range feral horses are found in desert grassland (Hansen 1976), semi-desert vegetation (Feist and McCullough 1976), mixed mountain shrub and pinyon-juniper woodland (Hubbard and Hansen 1976), sand-dune grassland (Welsh 1975) and coniferous forest-meadow complexes (Storrar et al. 1977) but, with few exceptions, little is known regarding habitat utilization or selection within these broad types. Welsh (1975) provided some indication of factors influencing the use of various plant communities on Sable Island, and Hubbard and Hansen (1976) briefly mentioned the relative abundance of horses in three vegetation zones in the Piceance Basin of Colorado. The study in central British Colombia reported by Storrar et al. (1977) appears to be the first attempt to relate feral horse distribution to features of habitat.

Moen (1973) pointed out that evaluation of habitat requires recognition of what is present that the animal responds to, and of what kinds of responses are made. The approach adopted in many studies has been to classify a given area into a number of habitat or vegetation types and then to describe animal distribution within these types, either by direct census or by counts of sign left by the animal. Other studies have attempted to define specific features of the environment which might influence animal distribution; sometimes the two approaches are combined. In this chapter habitat utilization by feral horses is described both in terms of available habitat types and of specific features of habitat, based on quantitative analyses of sign within plots, on data from animal sightings, and on indirect evidence from food habits.

6.2 Methods

6.21 Habitat classification

A reconnaissance method was used to develop a habitat classification system upon which subsequent distribution studies could be based. The original technique was developed by Franklin et al. (1970) for use in forest site classification in Oregon, and a modification of the method was used successfully by Douglas (1974) in sampling montane zone vegetation in the Yukon. The modified field methodology described by Douglas (1974) was followed quite closely.

Sampling sites were selected with the aid of 1:31,680 scale forest cover maps and 1:21,120 scale aerial photographs. The objective was to obtain a representative sample of the major cover types delineated on the maps, and of minor types discerned from direct observation. Homogeneous stands were selected for sampling based on their appearance on the aerial photographs and from the ground, and on the proximity of other similar stands (an attempt was made to distribute sampling effort over the entire study area). Once a sampling site had been selected, crown cover of each vascular understory species within a 15 m diameter circle was recorded using the cover classes of Daubenmire (1959). In forested stands, all trees within the circle were counted and recorded by species, height class and diameter at breast height, and the ages of up to four of the dominant trees in the sample were determined using an increment borer. Abundance of lichens and mosses was recorded using the same cover classes as used for vascular plants. A total of 150 sites were sampled during the period 4 July to 28 August, 1975. An additional two sites were sampled on 8 September, 1976. Identifications of vascular plants were verified by comparison with specimens in the University of Alberta Herbarium.

A subjective habitat classification developed while sampling agreed closely with descriptions of the vegetation types reported by MacKenzie-Grieve (1970) for Deer Creek Basin, within the present study area. A preliminary key to habitat types was constructed based on these two sources of information. This classification was used in the field and later tested and refined by numerical analysis of the original data from the 152 vegetation plots. Cluster analysis and principal components analysis techniques were applied to the data using the CLUSTAN IC cluster analysis package (Wishart 1975). Since details of these techniques are not important to the present discussion they are given in Appendix 1.

6.22 Quantitative assessment of habitat utilization

Two areas considered representative of the 200 km^2 Red Deer River study site were selected for intensive assessment of habitat utilization beginning in January 1976. The combined extent was 30 km^2, or approximately 15% of the total study area.

Habitat utilization by horses during winter was determined by quantifying sign (tracks, pellet groups, feeding sites) within 15 m diameter circular plots spaced at 100 m intervals along straight line transects. Because it was necessary to minimize the time spent in locating and traveling between transects a random location system was not used; rather starting points and directions of transects were selected to provide representative coverage of major habitat types. An approximately even spatial distribution was obtained by dividing the two areas into a total of nine subsections, each of which was visited one day a month during January - March. In total, 493 plots were examined during this period. Indicators of animal use and physical and vegetational parameters recorded at each plot are given in Appendix 2. At least two days were allowed to elapse between the most recent snowfall and sampling. Pellet groups deposited on bare areas were counted only if they were completely frozen (feces deposited prior to winter were at least partially dried and therefore 'flaky' on the outside).

To further explore factors influencing habitat selection by feral horses, total pellet group counts within 490 circular plots were conducted between 15 July and 31 August, 1976. Plots were again 15 m in diameter, spaced at 100 m intervals along straight line transects across the same two study areas as used during the winter period. Transects were oriented east-west, at 500 m intervals from a randomly selected base line in each area. Parameters recorded at each plot are summarized in Appendix 2. Horse pellet groups were aged as spring-type (amorphous, often bleached and insect riddled), fresh (moist, greenish), or unknown.

6.23 Supplementary data on habitat utilization

Pellet group counts are widely used to determine numerical trends and distribution of herbivores, but their relationship to actual habitat use is usually unclear due to a lack of behavioural data (ie. knowledge of the animal's activities within each habitat). This short-coming was recognized in the present study, and a body of data on observed habitat use behaviour was developed to assist in interpretation of the pellet group counts. Habitat descriptors similar to those used in the plot surveys were recorded for each horse sighting. During extended periods of observation new parameters were recorded each time a significant change in habitat occurred (usually considered as a movement of 100 m or more). A total of 546 sets of descriptors based on 372 sightings were obtained during

1976. This information is considered primarily qualitative in nature since the probability of sighting a herd was strongly biased toward open or treeless cover types, but coupled with additional observations of horse sign during winter (tracks, feeding craters) and spring-summer-fall (grazed areas) it provided valuable supplementary information on habitat use patterns over one complete annual cycle.

6.24 Data analysis

Environmental descriptors recorded in conjunction with examination of macroplots for horse pellet groups and sign provided 490 records of independent variables describing spring and year-long (multi-season) distribution and 493 records of variables describing winter distribution of horses. Difficulties arose in deciding the appropriate form of the dependent variables, however, since important biases were present during both periods. On plots examined during summer a major source of variation in total pellet group counts was differential rate of decay and disappearance of feces under various habitat conditions; thus on plots where conditions were favorable for preservation of pellets counts were biased upward, while on plots where decay occurred at an accelerated rate counts were biased downward. The winter data were biased to the extent that variability in completeness of snow cover and differences in length of time between snowfall and sampling resulted in differential probabilities of detecting sign within any two plots. These problems were obviated by categorizing the dependent variable in terms of presence/absence of sign for purposes of analysis. In addition, total pellet group counts were categorized into four abundance classes since most plots contained at least one pellet group and use of the presence/absence dichotomy consequently yielded limited information.

Occurrences of winter sign, spring pellet groups and total pellet groups were tabulated initially on the basis of habitat type. Expected distributions were calculated on the basis of availability of each habitat, and compared to observed distribution using chi-square:

$X^2 = (0-E)^2/E$ where

0 = number of plots in habitat type containing sign

and $$E = \frac{\text{number of plots sampled in habitat type}}{\text{total number of plots sampled}}$$

$$\times \text{ total number of plots containing sign}$$

Habitat types contributing most to the tabulated X^2 values were assumed to be highly favored or avoided following Irwin (1975).

Distributions of winter sign in relation to each of 15 independent variables and of spring pellet groups in relation to 21 independent variables were similarly evaluated using chi-square. Because the number of categories of each independent variable was small (≤ 9) it was possible to calculate confidence intervals on each category (Neu et al. 1974) and thus determine the statistical significance of preference or avoidance.

Distributions of winter sign, spring pellet groups and total pellet groups were evaluated within the context of a multivariate model using Multiple Classification Analysis (Andrews et al. 1967). Restrictions imposed by the program necessitated reduction of the number of independent variables, and three preliminary THAID analyses (Morgan and Messenger 1973) were conducted each using presence/absence of sign as a nominal dependent variable. THAID outputs "a subset of predictors and possible interactions (non-additivities) which provide an explanatory model for the particular variable chosen" (University of Michigan 1973). Based on the THAID analyses nine predictor variables were chosen for input into MCA. Individual MCA runs were conducted using winter sign, spring pellet groups and total pellet groups as dependent variables, the first two based on presence/absence, the latter based on a scaling of counts as outlined above. In order to simplify interpretation the same predictor variables were used for each model.

6.3 Resource Base - Identification of Basic Habitat Units.

Habitats in the area were classified into seven meadow/shrub types, nine forested types and one miscellaneous (disturbed) category (Table 6.1, Figures 6.1-6.16). Based on frequency of occurrence during the plot

Table 6.1 Description of Habitat Types Found Within the Study Area.

Habitat Type and Estimated Extent (% of area)	Description
Meadow and shrub types:	
dwarf birch meadow (4%)	Flat, wet meadows with a dense growth of *Carex spp.* and an open, low (< 5 dm) scrub layer dominated by *Betula glandulosa*. Microtopography often hummocky.
sedge meadow (< 1%)	Small, seasonally flooded meadows or patches within the above habitat, characterized by almost pure stands of *Carex spp.* on a moss base, and by complete lack of shrubs.
mixed shrub meadow (7%)	Rolling and gently sloping meadows often associated with dwarf birch meadows but drier and with greater grass cover; *Salix spp.* dominant or co-dominant in low, open scrub layer. Usually hummocky.
willow thicket (2%)	Tall (8-15 dm), dense thickets of *Salix spp.* on dry, flat benches adjacent to streams or (patchily) within other meadow types.
dry grassland (6%)	Warm south and southwest facing slopes (up to 50%) and dry flats. Major grasses *Agropyron subsecundum*, *Koeleria cristata* and *Danthonia intermedia*.
dwarf birch thicket (3%)	Dry, shrub covered flats and slopes of rolling meadows, characterized by a dense, relatively tall (to 15 dm) growth of *Betula glandulosa*.
silver-berry thicket (< 1%)	Periodically flooded sand and gravel flats along the Red Deer River, with *Elaegnus commutata* to 15 dm.

.../continued

Table 6.1 Continued.

Habitat Type and Estimated Extent (% of area)	Description
Forest types:	
mesic pine woods (< 1%)	*Pinus contorta* dominated woodland on moderate slopes (0-20%) of NE to SE aspect. Shrub understory sparse but dwarf shrub layer (*Vaccinium vitis-idaea*, *Ledum groenlandicum*) well developed.
dry pine woods (17%)	Similar to mesic pine woods but drier, tending to occur more on westerly and southwesterly exposures, and with *Ledum groenlandicum* lacking or nearly so.
black spruce woods (3%)	Mesic, dense woodlands typically dominated by *Picea mariana* but with *P. glauca* and *Pinus contorta* also present, occurring on west to northerly facing moderate slopes, and along the edges of some wet meadows.
white spruce woods (6%)	Woodlands co-dominated by *Picea glauca* and *Pinus contorta*, typically on flat to steep slopes (0-40%) of NW to easterly exposure. Deadfall moderate to heavy.
poplar woods (4%)	Deciduous woodlands dominated by *Populus tremuloides* but also with *P. balsamifera*, on dry, moderate to steep (10-50%) south and west facing slopes.
mixed woods (15%)	Open canopy woodlands with a mixed *Pinus contorta* - *Populus tremuloides* - *Picea glauca* tree layer, on flat to slight (0-10%) slopes.

.../continued

Table 6.1 Continued.

Habitat Type and Estimated Extent (% of area)	Description
alder thicket (30%)	Woodlands dominated by *Pinus contorta*, and characterized by a dense (> 50%), tall (up to 25^{+} dm) *Alnus crispa* shrub layer. On slight to moderate slopes with south and western exposures.
alpine fir woods (< 1%)	Mature woodlands dominated by *Abies lasiocarpa*, but also with *Picea glauca*. A shaded, species poor habitat occurring only at the highest elevations, on 5-50% slopes of NE and easterly exposures. Deadfall moderate-dense.
forested watercourse (2%)	Wooded ravines and swales, primarily with *Picea glauca* tree cover but also including *Populus balsamifera*, *P. tremuloides* and tree-sized *Salix spp*.
Disturbed sites: (< 1%)	Includes logged areas and sites where original vegetation cover has been removed or disturbed by road-building, seismic exploration, and well-site (natural gas) preparation.

Figure 6.1 Dwarf birch meadow.

Figure 6.2 Sedge meadow.

Figure 6.3 Mixed shrub meadow.

Figure 6.4 Willow thicket.

Figure 6.5 Dry grassland.

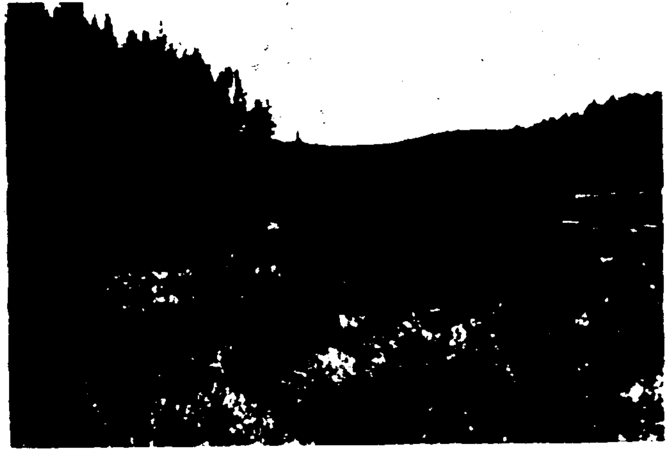

Figure 6.6 Dwarf birch thicket.

Figure 6.7 Silver-berry thicket.

Figure 6.8 Black spruce woods (in background).

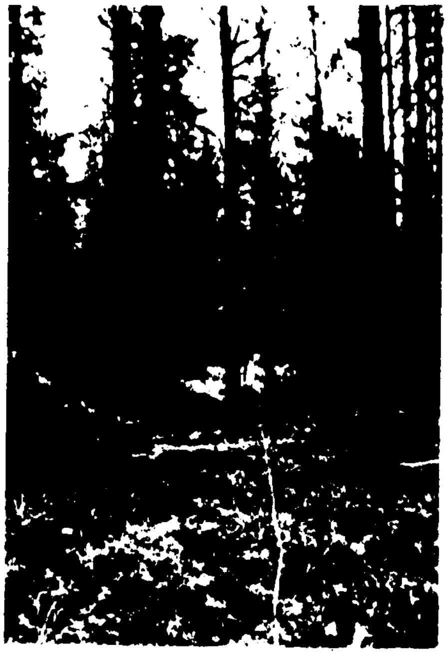

Figure 6.9 Mesic pine woods.

Figure 6.10 Dry pine woods.

Figure 6.11 White spruce woods.

Figure 6.12 Poplar woods.

Figure 6.13 Mixed woods.

Figure 6.14 Alder thicket.

Figure 6.15 Alpine fir woods

Figure 6.16 Disturbed habitat (seismic line).

surveys the alder thicket type was the most widespread, constituting an estimated one third of available habitat. Dry pine woods and mixed woods also were major components; other woodland types were relatively minor constituents. Mixed shrub meadow was the most abundant non-forested type, followed by dry grassland. Dwarf birch meadow, dwarf birch thicket and willow thicket were about equally abundant. Sedge meadows and silver-berry thickets were very limited in extent, while disturbed sites were widespread but covered a small area.

One or more major forages occurred in at least trace amounts in all habitats, although there was a distinct tendency toward greater variety and cover in the non-forested types (Table 6.2). As an extreme example dry grasslands contained up to 14 potential forages while alpine fir woods contained only two.

6.4 Patterns of Habitat Utilization

Consideration of cumulative (multi-season) distribution of feral horses provides a first approach to understanding habitat occupancy by these animals. Seasonal patterns of habitat utilization can then be considered against this background. For purposes of this analysis the year was divided into four equal periods: late winter (January-March), spring (April-June), summer (July-September) and fall-early winter (October-December). While this division is

Table 6.2 Mean Cover and Frequency of Occurrence Within Habitat Types of Major Forages Used by Horses.

Forage species	dwarf birch meadow	sedge meadow	mixed shrub meadow	willow thicket	dry grass-land	dwarf birch thicket	silver-berry thicket	mesic pine woods	dry pine woods	black spruce woods	white spruce woods	poplar woods	mixed woods	alder thicket	alpine fir woods	disturbed
	Mean cover and frequency ( ) on sample plots															
No. plots sampled	24	3	19	8	9	6	4	10	18	7	13	8	4	8	6	5
Agrostis scabra	*(5)	-	*(6)	1(4)	1(5)	1(4)	-	-	*(1)	-	-	-	-	-	-	*(2)
Danthonia intermedia	-	-	-	*(1)	2(4)	1(3)	-	-	-	-	-	-	-	-	-	-
Deschampsia caespitosa	1(22)	*(3)	3(19)	2(7)	-	-	-	-	-	-	-	-	-	-	-	-
Elymus innovatus	-	-	-	-	*(1)	1(1)	2(3)	4(10)	3(17)	*(4)	3(13)	5(6)	4(4)	4(6)	*(1)	3(5)
Festuca rubra	*(3)	-	1(14)	1(7)	-	-	2(4)	-	-	-	-	-	-	-	-	-
F. saximontana	-	-	*(1)	*(1)	1(3)	1(3)	*(1)	-	-	-	-	-	*(1)	*(1)	-	-
F. scabrella	-	-	*(1)	*(1)	2(5)	4(6)	-	-	*(4)	-	-	-	*(1)	-	-	-
Koeleria cristata	-	-	-	*(1)	2(9)	*(2)	-	-	-	-	-	-	-	-	-	-
Poa interior	-	-	-	-	*(3)	-	*(1)	-	-	-	-	*(1)	-	-	-	-
P. palustris	-	-	-	*(1)	*(1)	-	-	-	-	-	-	*(2)	*(1)	-	-	-
P. pratensis	*(2)	-	*(8)	*(5)	1(4)	*(5)	-	*(1)	-	-	*(2)	*(2)	*(2)	*(5)	*(1)	1(3)
Schizachne purpurascens	-	-	-	*(1)	-	2(4)	-	*(1)	-	-	-	*(2)	-	-	-	-
Stipa columbiana	-	-	-	-	1(4)	-	-	-	-	-	-	-	-	-	-	-
S. richardsonii	-	-	-	-	*(2)	-	-	-	-	-	-	-	-	-	-	-
S. spartea	-	-	-	-	1(3)	-	-	-	-	-	-	-	-	-	-	-
Carex spp.	5(24)	6(3)	4(19)	2(8)	1(5)	1(3)	*(2)	-	*(1)	1(2)	*(1)	-	-	[illegible]	-	*(3)
Eriophorum viridi-carinatum	*(9)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Juncus balticus	*(5)	-	2(13)	2(7)	*(1)	*(2)	-	-	-	-	-	-	-	-	-	*(1)
Equisetum arvense	-	-	-	-	-	-	-	-	*(1)	*(2)	-	-	-	-	-	-
E. fluviatile	*(6)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
E. scirpoides	*(1)	-	-	-	-	-	-	-	-	*(2)	-	-	-	-	-	-
E. variegatum	*(4)	-	-	-	-	-	*(1)	-	-	-	-	-	-	-	-	-
Astragalus frigidus	-	-	-	*(1)	-	-	-	-	-	-	-	*(1)	-	-	-	-
Total potential forages	10	2	8	13	14	10	6	3	5	4	3	6	5	4	2	5

Cover codes: *(mean canopy cover < 1%), 1(mcc 1-5%), 2(mcc 5-25%), 3(mcc 25-50%), 4(mcc 50-75%), 5(mcc 75-95%), 6(mcc 95-100%).

admittedly somewhat artificial, the periods correspond approximately to phenology of important events (ie. late winter - maximum snow cover and minimum forage quality and availability; spring - greenup and forage growth, breeding season and birth of foals; summer - maximum forage quality and availability, area occupied by numbers of cattle; fall/early winter - forage cures and quality begins to decline, forage less available beneath snow). Particular emphasis is given to quantitative determination of habitat use during late winter and spring, considered to be the most critical period in terms of survival (winter) and potential range damage (spring). An attempt is made to integrate sighting data and information on diet into the discussion of habitat use over all seasons.

6.41 Cumulative use

Horses made at least some use of nearly all habitats, pellet groups representing year-round deposition occurring on 85% of the macroplots examined during July-August, 1976. Pellet groups did not occur in any one habitat more frequently than expected but on the basis of total counts the dwarf birch thicket, mixed shrub meadow, dwarf birch meadow and black spruce woods types appeared to be most heavily utilized (Table 6.3).

Individual habitat features accounted for 25% of the variation in pellet group numbers found on the plots

Table 6.3 Seasonal Distribution of Horse Sign by Habitat Type, 1976.[1]

Habitat Type	% of sampled plots in habitat type (n=493)	% of plots containing sign in habitat type				% of sampled plots in habitat type (n=490)	% of plots containing sign in habitat type			mean no. all age pellet groups per plot
		winter feeding craters (n=52)	winter tracks (n=138)	winter pellet groups (n=169)	craters, tracks and/or p.g.s (n=185)		spring pellet groups (n=132)	summer pellet groups (n=28)	any age pellet groups (n=417)	
dwarf birch meadow	5.3	7.7	6.5	9.2	6.5	2.4	2.3	0.0	2.4	8.4
sedge meadow	0.4	0.0	0.0	0.0	0.0	-	-	-	-	-
mixed shrub meadow	8.5	17.3	11.6	15.6	11.4	6.3	$\underline{15.2}^{+}$	17.8	7.0	8.8
willow thicket	2.6	9.6	3.6	2.7	3.8	1.6	0.0	3.6	1.0	2.8
dry grassland	7.5	3.8	2.9	14.7	9.7	4.1	4.5	0.0	4.8	4.4
dwarf birch thicket	3.2	3.8	5.1	3.7	4.3	2.2	$\underline{6.8}^{+}$	10.7	2.6	8.9
silver-berry thicket	0.2	0.0	0.0	0.0	0.0	-	-	-	-	-
mesic pine woods	1.2	1.9	0.7	0.9	0.5	-	-	-	-	-
dry pine woods	14.4	1.9	5.8	5.5	$\underline{6.0}^{-}$	20.4	22.7	25.0	19.2	3.2
black spruce woods	3.0	3.8	5.0	1.8	3.8	2.4	2.3	3.6	2.9	6.5
white spruce woods	7.1	0.0	1.4	2.7	$\underline{2.2}^{-}$	4.3	3.0	17.8	3.8	3.2
poplar woods	4.2	11.5	5.1	9.2	$\underline{7.6}^{+}$	3.9	5.3	3.6	4.3	4.9
mixed woods	12.8	11.5	17.4	13.8	14.0	16.9	$\underline{25.8}^{+}$	3.6	18.4	4.2
alder thicket	26.8	23.1	30.4	19.3	27.0	32.9	$\underline{11.4}^{-}$	10.7	31.4	3.2
alpine fir woods	0.4	0.0	0.0	0.0	0.0	-	-	-	-	-
disturbed	0.4	0.0	0.7	0.0	0.5	1.0	0.0	0.0	0.7	4.0
forested watercourse	1.8	3.8	3.6	0.9	2.7	1.4	0.8	3.6	1.4	3.3
total %	99.8	99.7	99.8	100.0	100.0	99.6	100.1	100.0	99.9	
total X^2					28.95*		60.27***		4.97	

[1] Chi-square tests were performed on selected data sets on the null hypothesis that observed distribution during each season = expected distribution (as calculated from % of each habitat type in total plots sampled). Individual habitat types contributing 10% or more to significant total X^2 values are underlined and marked + or - to signify preference or avoidance during the appropriate season.

*probability of obtaining a greater X^2 value: .05>p>.01.

**.01>p>.005.

***p<.005.

(generalized R^2, model 1, Table 6.4). Of the nine variables, five accounted individually for 5% or more of this variation; these were major shrub species, major tree species, major grass species, shrub height and deadfall (eta^2 values, Table 6.4). Regression coefficients of the MCA model indicated that high pellet group counts tended to be most positively associated with either a lack of shrub cover or a shrub cover dominated by dwarf birch, with poplar cover or a lack of tree cover, with a grass cover dominated by *Festuca* or *Deschampsia*, and with a light to moderate amount of deadfall; they were negatively associated with a predominance of poplar regeneration or rose in the shrub layer, with shrub heights over 11 dm, with a cover of black spruce[1] in the tree layer, with a lack of grasses or a predominance of *Calamagrostis*, and with heavy to very heavy deadfall (Table 6.5). Taken together these variables suggest preferential use of meadow habitats, as was indicated by the absolute pellet group densities in individual habitat types. Relationships with grass cover suggest habitat selection on

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[1] The apparent discrepancy between this negative relationship and the observed high pellet group density in the black spruce woods type can be exlpained by examination of plots where black spruce was the major tree and/or the habitat was classified as black spruce woods. Black spruce was the dominant tree in 15 plots, seven of which were in habitats other than BSW - primarily dwarf birch and mixed shrub meadows which supported only a few scattered trees. Mean density of pellet groups in the seven plots was 3.0, compared to a mean of 4.9 in the eight BSW plots. Further, not all BSW plots were dominated by black spruce; 4/12 had a predominance of pine cover and a mean pellet group density of 9.8, twice the density found in BSW plots where black spruce was the major tree.

Table 6.4 Summary Statistics of MCA Models Relating Horse Pellet Group and Sign Counts to Habitat Variables.[1]

	Model 1 total distribution	Model 2 winter distribution	Model 3 spring distribution
Multiple Relationships			
Generalized R^2	.25	.21	.29
Multiple R	.42	.38	.48
Multiple R^2	.17	.14	.22
Major tree			
Eta^2	.09	.07	.05
$Beta^2$	.03	.02	.06
Major grass			
Eta^2	.08	---	.08
$Beta^2$	.01	---	.08
Major shrub			
Eta^2	.10	.06	.10
$Beta^2$	.07	.05	.01
Shrub cover			
Eta^2	.04	.04	.03
$Beta^2$	.05	.01	.03
Shrub height			
Eta^2	.05	.02	.09
$Beta^2$	.03	.01	.04
Deadfall			
Eta^2	.06	.06	.03
$Beta^2$	.01	.04	.01
Topography			
Eta^2	.04	.01	.10
$Beta^2$	.01	.02	.04
Slope			
Eta^2	.03	.01	.05
$Beta^2$	.01	.01	.01
Aspect			
Eta^2	.04	.07	.02
$Beta^2$	.03	.05	.02

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[1] dependent variables are: Model 1 - total pellet group counts in summer plots (none = 0, 1-5 = 1, 6-10 = 2, 10+ = 3).
Model 2 - presence (1) or absence (0) of feeding craters, pellet groups or tracks in winter plots.
Model 3 - presence (1) or absence (0) of spring pellet groups in summer plots.

Table 6.5 Coefficients of MCA Models Relating Horse Pellet Group and Sign Counts to Habitat Variables.

	Model 1	Model 2	Model 3
	yr. long distribution	winter distribution	spring distribution
Major tree			
no trees	.116	-.003	-.055
black spruce	-.416	-.091	-.391
white spruce	-.091	.161	-.295
pine	-.089	-.048	.021
poplar	.188	.154	.175
mixed conifer	.097	-.107	-.108
mixed con./dec.	.080	.089	.057
Major grass			
no grasses	-.088		-.167
Elymus	-.030		-.050
Calamagrostis	-.072		.077
Deschampsia	.130		.300
Bromus	.029		-.054
Festuca	.233		.278
Major shrub			
no shrubs	.529	-.158	.200
willow	.163	.125	-.044
dwarf birch	.502	.078	.080
Shepherdia	-.126	-.021	.063
poplar saplings	-.248	.023	-.104
alder	.047	.026	-.011
rose	-.165	-.058	-.004
Shrub cover			
no shrubs	-.836	.279	-.376
1-5%	-.051	-.031	-.020
6-25	.108	.016	.003
26-50	.055	.001	.077
51-75	-.125	-.069	-.093
76-95	-.527	.344	-.185
Shrub height			
absent	.273	-.144	.051
1-5 dm	.091	-.013	.099
6-10	.095	.019	.065
11-15	-.235	.003	-.140
16-20	-.073	-.035	-.088
21+	-.009	.078	-.060
Deadfall			
none-very light	.012	.060	.017
light	.034	.014	.035
moderate	.085	-.057	.001
heavy	-.129	-.213	-.082
very heavy	-.321	-.120	-.111
missing data		-.237	
Topography			
flat	.136	-.106	.056
rolling	.115	-.019	.082
steep	-.506	.071	-.109
Slope			
0-10%	.015	-.024	.027
11-20	-.076	.032	-.055
21-30	.118	.034	-.039
31+	-.199	-.032	-.015
Aspect			
north	.032	-.120	.039
N.E.	-.199	-.170	-.016
east	-.114	-.096	.009
S.E.	.055	-.085	.040
south	.058	.125	.058
S.W.	.250	-.030	.102
west	.056	.006	.004
N.W.	-.123	-.106	-.122
no slope	-.064	.104	-.105

the basis of forage availability, while relationships with deadfall and shrubs indicate that structural features may also have been important determinants of habitat use. Storrar et al. (1977) reported similar results from central British Columbia, feral horses there showing preferential use of sedge meadows and upland (aspen) forest on a year-long basis.

6.42 Seasonal use

6.421 Late winter (January-March)

Horses utilized a variety of habitats in late winter, sign occurring on considerably fewer plots than expected only in dry pine woods and white spruce woods. Frequency of occurrence of sign within the other habitat types was about the same as expected from their distribution within the study area, with the exception of poplar woods where frequency was high (Table 6.3).

Presence/absence of sign also was used to test preference or avoidance of individual features of habitat. Sign occurred more frequently than expected on plots with no conifer cover or with conifer cover less than one meter in height, with no or light deadfall, with southerly aspects, with less than 50% snow cover, or with only 1-10 cm of snow depth; features of under-utilized habitat were conifer cover of 51-75%, conifers 11-15 m in height, pine and mixed conifer cover, shrub cover of 1-5%, and shrub cover dominated by <u>Shepherdia</u>. Plots located in areas where there were no other major vegetation cover types within 100 m also tended to contain less sign than expected (Table 6.6). An MCA analysis conducted on a more limited set of variables confirmed the positive relationship with no or light deadfall and with southerly aspects, and the negative relationship with tree cover dominated by mixed conifers or pine and shrub cover dominated by <u>Shepherdia</u> (Tables 6.4, 6.5). As was the case with cumulative habitat use, results of these analyses suggest habitat selection primarily on the basis of forage availability and structural features of the vegetation.

Some habitats (and features within these) were clearly favored over others for winter feeding. Within forested types, feeding craters were found in over twice as many plots as expected in poplar woods. Utilization of this limited habitat may have been related to reduced snow depth due to southerly exposure, resulting in greater forage availability, as well as to heavy cover of <u>Elymus innovatus</u> and proximity to concurrently utilized grassy slopes. The foregoing analyses identified preference for several features of habitat associated with poplar woods, and observations of horses confirmed the exploitation of this habitat as a winter forage source in the Deer Creek and Bear Creek areas. Presence of feeding craters in plots and during independent observations also indicated extensive utilization of forested watercourses, especially at ravine sites where small grassy areas had developed on the slopes - this habitat was limited in extent, however. Black spruce woods, mixed woods and alder thickets also were used for winter feeding, the first primarily in association with dwarf birch meadow edge. Craters and actively feeding horses were sometimes found deep within the latter two habitats, where Elymus innovatus was the major available forage. Crater frequency data also showed that most meadow and thicket habitats were used for winter feeding, but underestimated the importance of the dry grassland type since craters tended to be obliterated by melt on the south facing slopes on which this habitat often occurred. The importance of dry grassland during winter was indicated by sightings of actively grazing animals (Table 6.7); these data also emphasize the importance of mixed shrub meadows, dwarf birch meadows, and to a lesser extent dwarf birch thickets. Fescue grasses and sedges, both important constituents of the winter diet of horses, were concentrated within these habitats.

Several habitats which received little or no use in winter were limited in extent (sedge meadow, silver-berry thicket, mesic pine woods, alpine fir woods). Dry pine woods and white spruce woods were the only widespread habitats which were clearly under-utilized. Both supported a mean cover of Elymus innovatus of 25-50% but this was apparently insufficient to attract feeding activity - only 1/106 plots

Table 6.7 Monthly Records of Habitat Use Involving Actively Foraging Horses, 1976.

Month	Records of habitat use involving actively foraging horses: monthly distribution (%) by habitat type									total records
	dwarf birch meadow	sedge meadow	mixed shrub meadow	willow thicket	dry grassland	dwarf birch thicket	silver-berry thicket	dis-turbed	undiffer-entiated meadow	
January	30.8	0	23.1	0	30.8	15.4	0	0	0	13
February	15.8	0	36.8	0	47.4	0	0	0	0	19
March	7.1	3.6	10.7	3.6	64.3	7.1	0	3.6	0	28
April	7.5	0	15.0	0	68.8	3.8	0	5.0	0	80
May	13.7	3.2	14.7	1.0	46.3	5.3	0	13.7	2.1	95
June	12.2	2.7	41.9	0	28.4	4.0	0	8.1	2.7	74
July	9.5	0	52.4	0	38.1	0	0	0	0	21
August	6.7	0	40.0	0	33.3	6.7	0	6.7	6.7	15
September	0	0	55.6	0	22.2	11.1	0	11.1	0	9
October	0	0	0	0	77.8	0	0	22.2	0	9
November	22.2	22.2	0	0	44.4	0	0	11.1	0	9
December	8.3	2.8	27.8	0	50.0	8.3	0	2.8	0	36

in these types contained feeding craters.

Multiple tracks or trails were found in several habitat types. Although trails appeared to be developed primarily in deep snow areas this relationship could not be tested, as single and multiple horse tracks were not differentiated during data collection.

The coniferous habitats (especially alder thicket) appeared to have high shelter value but the use of shelter was not documented during this study. The winter of 1975-76 was exceptionally mild, however, and it is possible that shelter might be an important determinant of habitat selection during more severe periods. Conversely, meadow habitats, especially those with south-facing orientations, probably afforded favorable microclimates during fair weather and this may have been a factor in their utilization.

6.422 Spring (April-June)

Coincident with the onset of snowmelt and the initiation of greenup, horses showed a distinct tendency toward greater use of meadow areas and decreased use of forested habitats. This was reflected in both increased frequency of horse sightings and by the distribution of spring-type pellet groups (Table 6.3). Observed distribution of pellet groups differed significantly from that expected on the basis of habitat availability, plots in alder thickets containing them much less frequently and those in the mixed shrub meadow and dwarf birch thicket types much more frequently than expected. In terms of individual features of habitat, spring pellet groups were found more frequently than expected on plots with features descriptive of open areas (meadow and thicket habitats) and less frequently than expected in pine and alder dominated habitats (Table 6.6). An MCA model constructed with a reduced set of variables confirmed positive relationships between spring pellet group occurrence and rolling topography, predominance of Festuca in the grass cover, predominance of dwarf birch in the shrub cover, shrub heights of less than 11 dm and slopes of less than 10%, and negative relationships with steep topography, slopes of greater than 10%, a predominance of alder in the understory, and shrub heights of greater than 11 dm (Tables 6.4, 6.5).

Habitat occupancy during this period appeared to be related primarily to stage of forage growth. Greenup began earliest on previously grazed meadows and was followed by an increase in diet quality as the animals switched to better forage. Horses were also frequently noted grazing on disturbed areas, such as roadsides and ditches, where the absence of litter permitted the rapid growth of new plant material. The positive association between frequency of spring pellets and dominance of the favored Festuca spp. in the grass cover, and a negative association with a predominance of forbs (a very minor dietary constituent) in the herbaceous biomass both likely were related to habitat selection on the basis of forage availability. The use of sedges increased during this period while utilization of Elymus innovatus decreased; sedges were available primarily from meadow habitats while Elymus reached its greatest extent under forest cover. The absence of pine and spruce needles from the feces in May and June also likely was indicative of decreased feeding in forested areas.

Evidence of decreased use of forested areas notwithstanding, 70% of plots containing spring-type pellet groups (n=132) were in forested habitats (in comparison 82% of all plots sampled were in forest; n=490), indicating that although meadow habitats were favored and may have been a primary forage source, they certainly did not receive exclusive use. On the other hand, frequency of occurrence of spring-type pellet groups in open areas was probably underestimated, as they tended to break down more quickly as a result of trampling, feeding by birds, and weathering.

6.423 Summer (July-September)

Beginning in July use of open habitats appeared to decline, as indicated by reduced frequency of horse sightings. Nearly 70% of plots containing fresh horse fecal groups were in forested habitats, but the frequency was too low for reliable statistical analysis. During the summer period horses were observed deep within wooded areas on at least four occasions, and frequently made use of shade at forest-meadow edges. Elymus innovatus increased in importance in the summer as compared to the spring diet (33% vs. 16%) reflecting increased utilization of woodland areas.

Predominance of Festuca and sedge in the summer diet indicated, however, that most forage continued to be obtained from meadow and shrub habitats. From observational and plot data the widespread mixed shrub meadow type appeared to be the most important feeding habitat, and was probably the primary source of sedge in the diet. The dwarf birch meadow type was the only other major habitat where sedges were readily available, but footing was poor prior to freezeup and this type was utilized very little. Observations of horses leaving meadows after early morning feeding periods and re-entering them in the evening suggested that much of the summer foraging activity may have been nocturnal, but observations were too few to confirm this.

6.424 Fall-early winter (October-December)

During early winter the pattern of use of both open and forested habitats continued, as revealed by food habits data. Diurnal use of open areas was minimal during October and November as compared to December, however. This may have been due to disturbance by big-game hunters, although there is no direct evidence for this.

Among open habitats dry grassland appeared to be the most important for feeding but other types also were utilized (Table 6.7). The importance of feeding in forested habitats was again emphasized by the level of Elymus in the diet (31%), which was comparable to the proportion observed during summer (33%) but much higher than that in spring (16%), when greater use was made of open areas.

Snowfall during early winter of 1976-77 was light and disappeared rapidly, and did not appear to have a great effect on forage availability. However, the reappearance of quantities of pine needles and moss in the diet during this period may have been due to decreased selectivity by horses while feeding beneath snow in both open and forested habitats.

6.5 General Discussion

Habitat selection by grazing animals is determined largely by the presence of a preferred food supply (Arnold 1964, Bell 1971, Ferrar and Walker 1974, Jarman 1974), although shelter considerations may be im[illegible]t for some species particularly in northern environments. In this study significant seasonal variation in habitat use appeared most strongly related to food supply with other factors being of only secondary importance. Horses utilized a variety of cover types but on a seasonal basis their utilization of various habitats was markedly non-random. Storrar et al.

(1977) studied habitat utilization by feral horses in a situation analagous to the present study area, in that the habitat was primarily coniferous forest interspersed with meadows. They found that horses responded positively to sedge cover, pine grass cover, aspen crown closure and to flat or very steep slopes. Although food habits studies were not undertaken, response to habitat variables was considered to be due primarily to forage availability.

Other studies of feral horses in North America provide only limited information on habitat utilization. Pellegrini (1971) found seasonal differences in habitat occupancy in Nevada related to snow cover and forage availability, and possibly to the presence of livestock. Welsh (1975) also found seasonal alterations in distribution, with most time spent in grass and heath communities. Hubbard and Hansen (1976) reported that in Colorado feral horses were resident in each of three vegetation zones throughout the year but were least abundant in a zone classified as pinyon-juniper.

Evidence from body morphology and tooth structure indicate that modern horses evolved primarily as animals of the open plains, with a diet dominated by grass (Simpson 1951, Groves 1974). It is not surprising, then, that the limited evidence now available indicates that within broadly divergent vegetation types and among widely separated geographical areas, the preferred habitats of feral horses are meadows or grasslands where their predominant food is most available. Perhaps just as important, however, is their ability to utilize a variety of habitat types, as shown by data from the present study. This may reflect an inherent flexibility in habitat use behaviour, and when viewed against the background of other studies, adaptability to a considerable range of habitat conditions.

Chapter 7: Resource Partitioning: Relationships with Other Ungulates

7.1 Introduction

The growing body of knowledge concerning the ecology of feral horses includes several comparative studies on diets of horses, domestic stock and native ungulates. A commonly expressed rationale is the need to estimate carrying capacities for various combinations of herbivores on land designated for multiple-use. Diets of horses have been determined in relation to those of cattle and mule deer in Colorado by Hubbard and Hansen (1976), to cattle, elk, domestic sheep and antelope in Wyoming by Olsen and Hansen (1977), to cattle and mule deer in Colorado by Hansen et al. (1977) and to cattle, elk and mule deer in Colorado by Hansen and Clark (1977). These studies are all somewhat limited, however, as evidence of dietary overlap is only important if shared foods are in short supply or if one herbivore otherwise limits the access of another to a preferred food source. Except for generalized accounts there appears to be little information regarding the effects of combined use by horses and other herbivores on range condition.

Analysis of range relationships of two or more ungulates requires consideration of the use of both food and space, ideally including observations on behavioural interactions and range condition. Traditionally, this has been accomplished by describing seasonal overlaps in habitat utilization and food habits (eg. Stevens 1966, Allen 1968, Constan 1972, Wilkinson et al. 1976). Indices descriptive of spatial overlap have received limited use (Telfer 1972, Irwin 1975, Anthony and Smith 1977). Recently, attempts have been made to evaluate resource division on the basis of vectorial response to habitat and functional interactions of coexisting species (Ferrar and Walker 1974, Hudson, 1976, Hudson et al. 1976, Hudson 1977). Storrar et al. (1977) adopted an analytical approach to a study of feral horses in central British Columbia, describing spatial relationships with moose and determining which features of the environment may have been responsible for resource division, then relating these to presumed differences in food habits. Animals were sighted only rarely, however, and functional interactions could not be determined.

In the present study a primarily descriptive approach was taken to the analysis of spatial, habitat use and dietary overlap of feral horses with cattle and native ungulates. Evidence of competition was sought from the condition of the range and from behavioural interactions of horses with other species.

7.2 Methods

7.21 Occupational patterns

Information on occupational patterns of cattle and native ungulates was developed primarily during inspection of 983 temporary macroplots for horse sign (section 6.22). Approximately one half of these were examined during January-March, 1976, providing information on winter distribution, while the remainder were examined from July-August, 1976, for data on year-long or multi-season distribution. In plots inspected during winter, tracks and pellet groups of deer, elk and moose were tabulated and habitat type and a number of habitat descriptors were recorded. Only cattle defecations were counted on the summer plots: pellet groups of deer, elk and moose were recorded on a presence/absence basis. Habitat descriptors additional to those obtained in winter also were noted.

Elk, moose and deer were seen frequently on the study area, and during each sighting in 1976 data similar to those obtained for horse sightings (section 6.23) were recorded. Only general notes were maintained on cattle distribution.

7.22 Food habits

As noted previously monthly diets of horses were determined through fecal analysis. Available literature suggested the possibility of dietary overlap with cattle and elk and seasonal diets of these species also were determined.

Seventy-five fresh elk fecal samples were obtained during January-March, 1976 (25 each month) and a further eight samples were collected during May-June. Each sample consisted of one or two individual pellets. Samples were frozen and stored as soon as practicable after collection. Two hundred samples of cattle feces representing deposition from mid-June to the date of sampling were obtained during 11-17 October, 1976, each consisting of approximately 10 gm of material. All collections were made from within the two areas (total 30 km²) covered by the macroplot surveys. Elk were distributed over a limited area and as many samples as possible were obtained each time an area of elk-use was found. Cattle feces were collected from four sites, two within each area.

In preparation for analysis elk feces were thawed and composited on an approximately equal dry weight basis into one group representing the January-March diet and a second group representing the May-June diet. Cattle feces were mixed at the time of collection into a single composite sample. Subsequent treatment and analysis were identical to those applied to the horse fecal collections (section 5.22).

7.23 Range use

Evidence of the effects of spatial overlap or of possible deleterious single species use was sought from surveys of range condition and level of utilization. Inspections carried out on the area since 1969 by Forest Service personnel provided background information on annual use, range condition and trend, and problem areas. During

11-18 October, 1976, an extensive survey method (Anderson and Currier 1973) was used to check zones of utilization on all the meadows within the two areas previously covered by the macroplot surveys, subsequent to season-long grazing by cattle and horses. The Deer Creek area, an important elk and feral horse winter-spring range and cattle summer range, was again examined on 1 June, 1977, to establish level of use by feral horses and native ungulates during spring.

Each meadow was traversed on foot in a zig-zag fashion with sufficient coverage to determine the gross pattern of utilization. Use zones representing five classes of herbage utilization were mapped on blown-up aerial photographs and the level of use, stubble height and plant community type were recorded for each zone. Herbage utilization was classified as none-very light (0-15% of herbage biomass removed), light (16-35% removed), safe (36-65% removed), heavy (66-80% removed) and severe (>80% removed, plants grubbed, trampling damage evident). Levels of use were determined by visual comparison with ungrazed plants. Since broad use classes are employed the procedure stresses consistency of judgement and is therefore an appropriate extensive survey method (Anderson and Currier 1973).

7.24 Data analysis

Presence/absence of deer, moose, elk and cattle sign on the macroplots examined during January-March and July-August

1976 was used as a measure of habitat occupancy by these species. Distribution in relation to habitat availability was examined using chi-square tests. A coincidence index, an association index (Dice 1945) and a coefficient of association, C8, (Hurlbert 1969) were used to evaluate the extent of mutual use of plots by horses and each other herbivore. To the extent that pellet groups and winter sign are reliable indicators of spatial distribution, coincidence indices provide a measure of how much of the combined area used by two species sustains mutual use (ie. what proportion of sites used by either species a or b are used by both), association indices indicate the degree of overlap (ie. what proportion of sites used by a are used by b, and vice-versa), and C8 values provide a frequency independent measure of association. Coincidence and association indices vary from zero, representing no association, to one, representing perfect overlap. A C8 value of zero indicates that two species are associated as expected by chance; C8 varies from -1 to +1.

Horse, cattle and elk diets representing various periods were compared using Kulcyznski's similarity index (Oosting 1956) which indicated what percentage of a pair of diets was identical, and Spearman's rank order correlation coefficient (Nie et al. 1975) which indicated to what degree species were chosen in the same or opposite orders by a pair of herbivores. One or both of these procedures have been used in previous studies of feral horse diets in relation to those of other ungulates (Hubbard and Hansen 1976, Hansen and Clark 1977, Hansen et al. 1977, Olson and Hansen 1977) and thus provide a standard means of comparison.

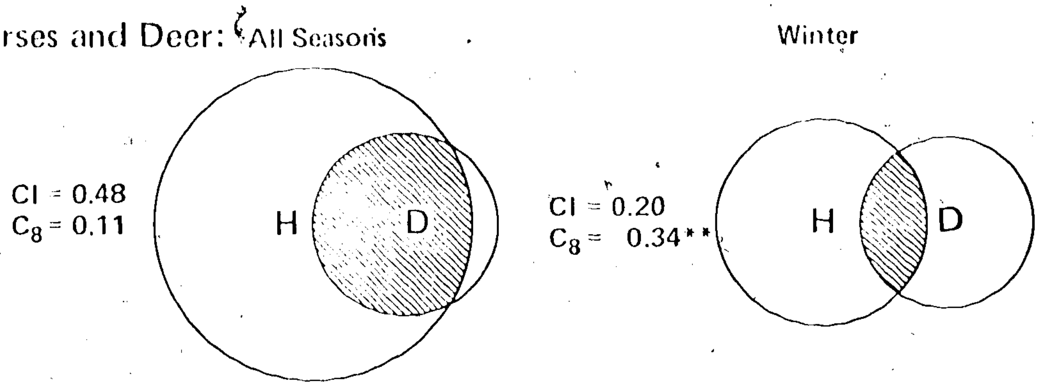
7.3 Horse-Deer Relationships

Both mule deer and white-tailed deer were found within the study area, but mule deer were probably about three times more abundant as indicated by number of observations (46/62) and total numbers seen (89/118) during 1976. The centre of abundance of the white-tailed deer population was east of the two areas used for quantitative assessment of habitat utilization and it is likely that only a very low proportion of deer sign in the macroplots was attributable to this species. The following discussion therefore refers primarily to mule deer.

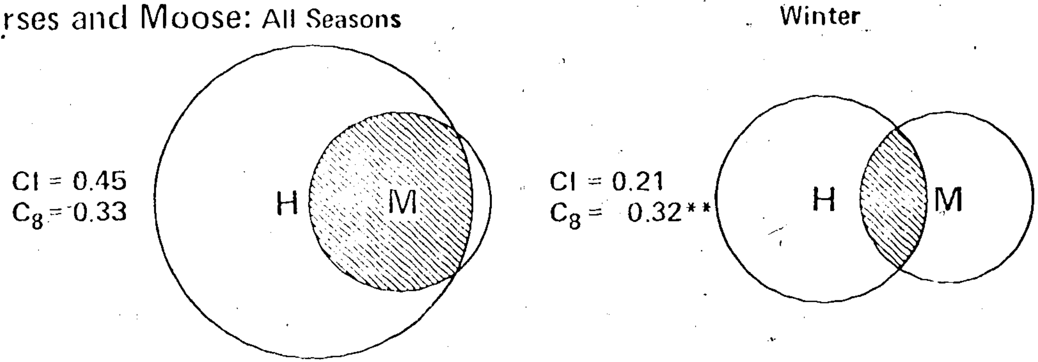
On a multi-season basis horses and deer shared somewhat less than half of their combined range within the two areas. However, horses were more ubiquitous in their distribution and occupied in the order of 85% of the sites used by deer while deer used only about 35% of the sites sustaining horse-use (Figure 7.1). Deer exhibited a degree of habitat selectivity, pellet groups being found in more plots than expected in dry pine woods and in less plots than expected in mixed shrub meadows (Table 7.1). In contrast, dry pine woods supported a relatively low level of horse activity while utilization of mixed shrub meadows was relatively

Figure 7.1 Diagrammatic representation of spatial overlap of feral horses with native ungulates and cattle. Circles are drawn to scale based on frequency of occurrence of sign or fecal groups in macroplots examined during January - March and July - August, 1976. Proportion of plots receiving mutual use (calculated as association and coincidence (C8) indices) are represented by cross-hatched areas. Each C8 value provides a frequency independent measure of association which was evaluated by chi-square (probability of obtaining a greater X^2 value given as: $^{*}0.05 > p > 0.01$; $^{**}0.01 > p > 0.005$; $^{***}p < 0.005$).

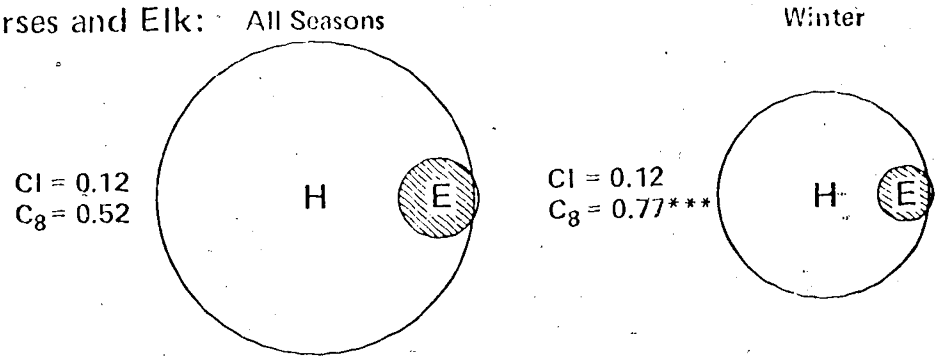
Horses and Deer: All Seasons



Horses and Moose: All Seasons



Horses and Elk: All Seasons



Horses and Cattle: All Seasons (H) - Summer (C)

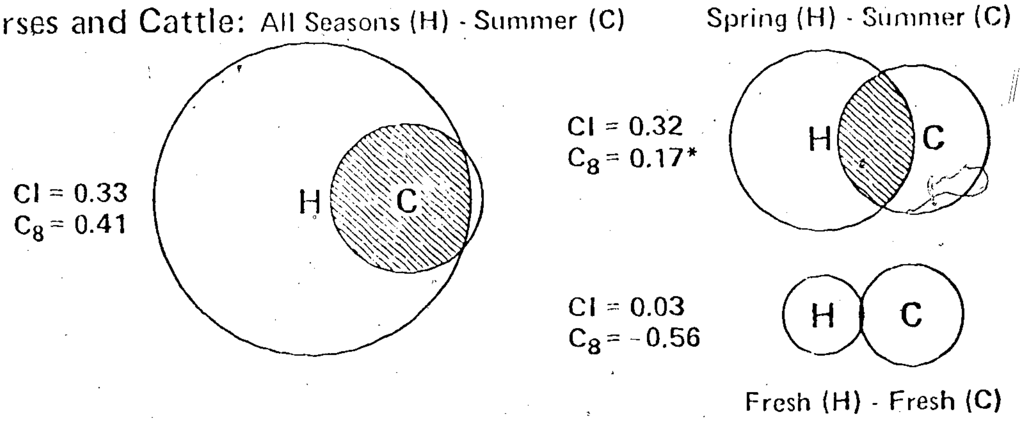


Table 7.1 Distribution of Deer, Moose, Elk, Cattle and Horse Sign by Habitat Type.[1]

	All Seasons						Late Winter (January - March)				
		% of plots containing fecal groups in habitat type						% of plots containing sign in habitat type			
Habitat Type	% of sampled plots in habitat type (n=493)	Deer (n=159)	Moose (n=140)	Elk (n=28)	Cattle (n=92)	Horses (n=417)	% of sampled plots in habitat type (n=490)	Deer (n=126)	Moose (n=126)	Elk (n=14)	Horses (n=185)
dwarf birch meadow	2.4	0.0⁻	4.3	0.0	0.0	2.4	5.3	0.0⁻	7.1	14.3	6.5
sedge meadow	-	-	-	-	-	-	0.4	0.0	0.0	0.0	0.0
mixed shrub meadow	6.3	0.0⁻	11.4⁺	0.0	9.8	7.0	8.5	2.4⁻	[illegible]⁺	0.0	11.4
willow thicket	1.6	0.0	1.4	0.0	8.7⁺	1.0	2.6	0.8	6.3⁺	0.0	3.8
dry grassland	4.1	1.9	0.7⁻	10.7	[illegible]⁺	4.8	7.5	0.8⁻	5.6	50.0⁺	9.7
dwarf birch thicket	2.2	0.0	5.7⁺	0.0	12.0⁺	2.6	3.2	0.8	7.9⁺	0.0	4.3
silver-berry thicket	-	-	-	-	-	-	0.2	0.0	0.8	0.0	0.0
mesic pine woods	-	-	-	-	-	-	1.2	2.4	0.0	0.0	0.5
dry pine woods	20.4	30.2⁺	27.1	39.3	15.2	19.2	14.4	15.1	19.0	7.1	6.0⁻
black spruce woods	2.4	1.3	1.4	0.0	2.2	2.9	3.0	1.6	2.4	0.0	3.8
white spruce woods	4.3	5.0	4.3	3.6	3.3	3.8	7.1	15.2⁺	4.0	0.0	2.2⁻
poplar woods	3.9	3.1	0.0⁻	10.7	6.5	4.3	4.2	3.2	0.8	14.3	7.6⁺
mixed woods	16.9	18.9	13.6	17.9	16.3	18.4	12.8	15.[illegible]	12.7	14.3	14.0
alder thicket	32.9	38.4	26.4	17.9	5.4⁻	31.4	26.8	35.7	15.1⁻	0.0	27.0
alpine fir woods	-	-	-	-	-	-	0.4	1.6	0.0	0.0	0.0
disturbed	1.0	0.0	0.7	0.0	4.4	0.7	0.4	0.0	0.0	0.0	0.5
forested watercourse	1.4	1.3	2.9	0.0	1.1	1.4	1.8	1.6	0.0	0.0	2.7
total %	99.8	100.1	99.9	100.1	100.1	99.9	99.8	100.1	99.9	100.0	100.0
total X^2		34.09***	33.66***	16.55	15[illegible]***	4.97		54.61***	53.55***	44.50***	[illegible]*

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[1] Chi-square tests were performed on the null hypothesis that observed distribution of each species = expected distribution (as calculated from % of each habitat type in total plots sampled). Individual habitat types contributing 10% or more to significant total X^2 values are underlined and marked + or - to signify preference or avoidance by the appropriate species.

*probability of obtaining a greater X^2 value: $.05 \geq p > .01$.

**$.01 \geq p > .005$.

***$p \leq .005$.

high, as judged by pellet group density.

These measures of spatial overlap and habitat selection are limited since they take no account of the temporal dimension; e.g., a site used by deer in winter might well be used by horses during some other period of the year. However, some indication of mutual use of habitat during the critical late winter period is provided by data gathered during January-March, 1976. During this time there was a highly significant lack of association between the two species, horse sign occurring on only 25% of sites used by deer. Deer sign occurred on plots in white spruce woods much more frequently than expected, and on dry grasslands and dwarf birch meadows much less frequently than expected, contrasting sharply with the pattern of winter habitat selection by horses wherein white spruce woods were avoided and dry grassland and dwarf birch meadows were among the preferred habitats.

Although deer remained in forested areas and avoided open habitats during winter they began to use the latter with the initiation of spring greenup. The number of deer sightings increased sharply during April and May (Figure 7.2); over half of these involved animals actively grazing on south-facing grassy slopes or along road edges. This change in habitat use behaviour was exhibited by both mule deer and white-tailed deer, and was clearly related to the availability of succulent green forage in the dry grassland

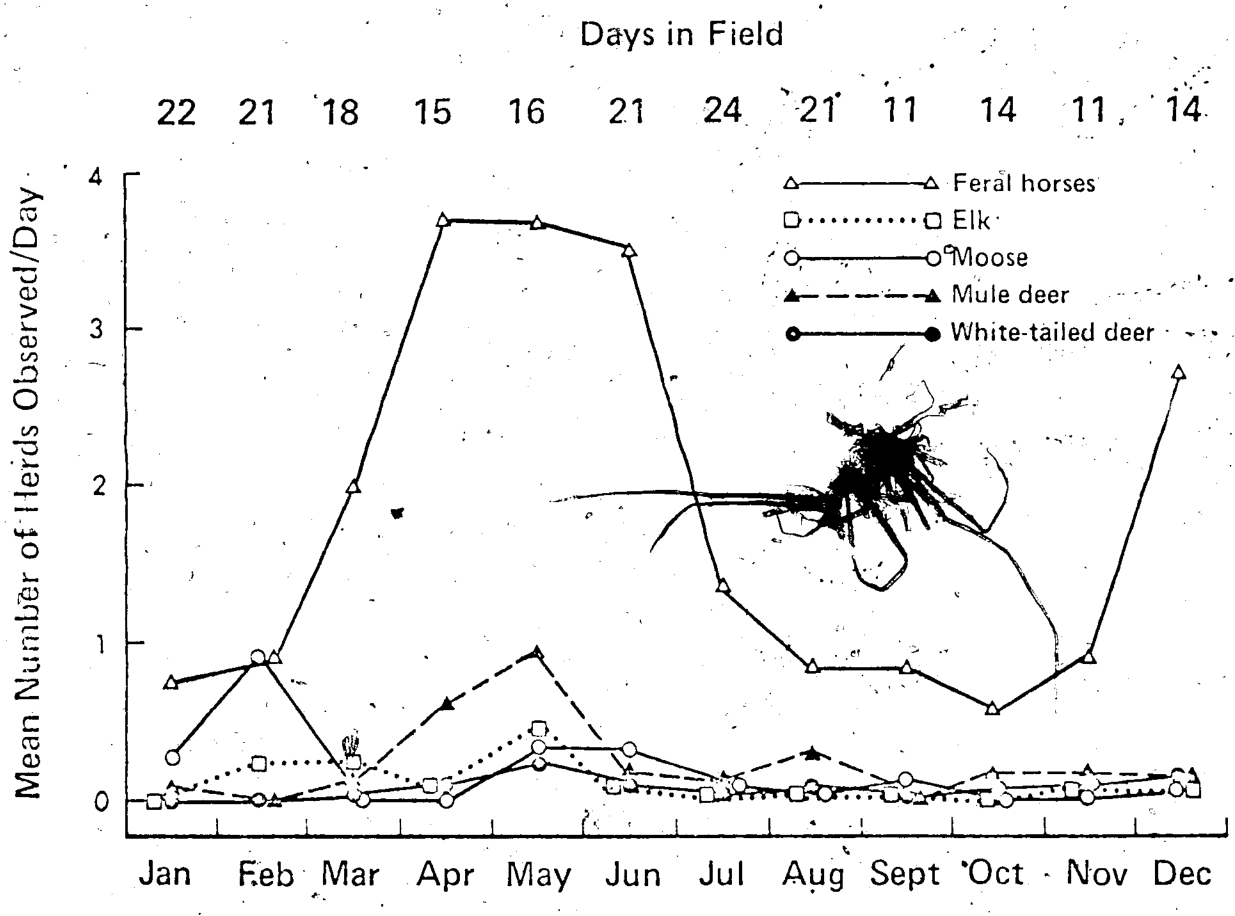

Figure 7.2 Mean number of herds (≥ 1 animal) of native ungulates and feral horses observed per day in field, January - December, 1976.

and disturbed habitat types. On four occasions during April and May, 1976, herds of mule deer and horses were observed feeding on the grassy slopes above Deer Creek Flats within 150 m of each other, but no interactions were observed. Deer were less frequently observed during summer, fall and early winter, but limited observations indicated that meadows continued to be used as feeding areas at least into August.

Dietary overlap of horses and mule deer was not determined during this study, but reports from other areas indicate that very little similarity would be expected. In three studies conducted in Colorado annual diet similarity ranged from one to 11%, and was usually less than 5% (Hubbard and Hansen 1976, Hansen and Clark 1977, Hansen et al. 1977). No comparative studies of the diets of white-tailed deer and horses have been reported.

7.4 Horse-Moose Relationships

On a multi-season basis these two species shared about half of their combined range, but due to a more catholic distribution horses infringed more onto sites used by moose than did moose onto sites utilized by horses (Figure 7.1). Moose pellet groups occurred on more plots than expected in dwarf birch thickets and mixed shrub meadows, both also preferred horse habitats (Table 7.1).

When considered on a seasonal basis, however, there is less evidence for spatial and habitat use overlap. During late winter only about 20% of the combined range [illegible] shared, and evidence of horse use was found on only 2[illegible] of sites used by moose. There was a highly significant lack of association between the two species during this period, and although moose preferred mixed shrub meadows, dwarf birch thickets and willow thickets - habitats also frequented by horses - observations suggest separation of the two species on the basis of food selection. Moose were most commonly observed in January and February (Figure 7.2) when they browsed during morning in extensive rolling meadows. Although meadow areas also were utilized for winter feeding by horses, different foods were chosen. The lack of direct evidence of browsing by horses was confirmed by fecal fragments analysis, sedges and grasses proving to be the most important dietary constituents. An observation on 12 February, 1976, of an adult moose and five horses feeding within 25 m of each other in a mixed shrub meadow - the moose on shrubs protruding above the snow and the horses pawing for sedges and grasses - serves to illustrate the ecological separation of these two species during winter even in shared habitats.

The paucity of moose sightings in spring was in direct contrast to the increased use of open habitats by horses during April-June. Limited observations suggested a mixed diet during this time - moose were observed feeding on new leaves and shoots of willow in mixed shrub meadows (two sightings) and on sedges in a sedge meadow bordering a lake (one sighting). The extent of diet similarity between moose and horses during spring is unknown, but the superabundance of food in mutually used habitats during this period, and continuing into summer, suggests that competition for this resource was unlikely.

Moose rely primarily on browse throughout the year although grasses occur in the spring and summer diet (Banfield 1974). No comparative studies of horse and moose diets have been reported, but Storrar et al. (1977) found significant ecological separation of the two species in central British Columbia and believed that this was due primarily to differing food habits.

7.5 Horse-Elk Relationships

Among the four species of wild ungulates occurring on the study area, elk had the narrowest distribution. During 1976, sightings were centred almost entirely around the Deer Creek - Bear Creek area, where herds of from one to twenty animals were seen between February and June. In 1975 animals were seen around Deer Creek Flats until the end of July, but their movements later in the summer and into the fall were not determined during either year. No mature bulls were seen but cast antlers were found at two locations.

Horses used in the order of 90% of the sites occupied by elk, whereas elk utilized only about 5% of those used by horses (Figure 7.1) reflecting the broader distribution and greater numbers of the latter within the study area. A similar situation occurred in winter when there was a highly significant association between the two species. During this time elk exhibited a preference for dry grassland habitat, as shown by a higher than expected frequency of sign (Table 7.1) and by observational data. Nine sightings of elk involving some 84 animals were made during February and March, 1976, all but two of these of herds feeding on south-facing grassland slopes in the Bear Creek and Deer Creek areas. Horses were observed feeding on the same slopes at this time (22 sightings, January-March). Evidence of mutual use of winter habitat also was found in two small muskegs (both classified as dwarf birch meadow) east of Bear Creek, where it appeared that elk had followed horses into the area and fed in the same feeding craters. Due to the paucity of elk sign in the study area as a whole it was not possible to determine the extent of this relationship, or whether it represented commensalism or competition. Winter diets of the two species were moderately similar (Tables 7.2, 7.3). _Elymus innovatus_, _Festuca spp._ and _Carex spp._ were important shared constituents. Both coniferous and deciduous browse were important in elk diets but were little used by horses.

Steep south-facing slopes above Deer Creek Flats continued to be used by elk during April-June, nine of ten observations involving actively grazing animals. Feeding occurred in both dry grassland and poplar woods habitats, both also used by horses; on three occasions elk and horses

Table 7.2 Percentages of Plants in Seasonal Diets of Feral Horses, Elk and Cattle, 1976.

	Horse				Elk		Cattle
	Late winter	Spring	Summer	Year long	Late winter	Spring	Summer
Danthonia intermedia (Timber Oat Grass)	1	2	4	2	1		5
Deschampsia caespitosa (Tufted Hair Grass)	1	2	1	1		<1	7
Elymus innovatus (Hairy Wild Rye)	23	10	33	27	19	25	7
Festuca spp. (Fescue)	15	23	25	20	21	4	41
Poa spp. (Bluegrass)	1	4	1	2		2	2
Carex spp. (Sedge)	35	53	30	34	9	11	27
Juncus balticus (Wire Rush)	4	<1	2	2		<1	<1
Mertensia paniculata (Tall Mertensia)			<1	<1	<1	3	<1
Potentilla-Geum spp. (Cinquefoil-Avens)	<1	<1	<1	<1	2	22	3
Pinus contorta (Lodgepole Pine)	5		<1	3	22	<1	<1
Salix spp. (Willow)	<1	<1		<1	19	26	<1
Equisetum spp. (Horsetail)	3	<1	1	2	<1		
Moss	3	<1	<1	2		<1	2

Other foods (< 3%) in horse, elk and cattle diets were *Agrostis scabra*, *Koeleria cristata*, *Schizachne purpurascens* and *Artemisia spp.*; in horse and elk diets, *Astragalus frigidus*, *Petasites spp.*, *Picea spp.*, *Shepherdia canadensis*-*Eleagnus commutata* and lichen; in horse and cattle diets, *Bromus spp.*, *Stipa spp.*, *Solidago spp.*, and *Vicia americana*.

Table 7.3 Percentage Similarities and Rank Correlations of Seasonal Herbivore Diets, Red Deer River Area, 1976.

Diets	% Similarity	Spearman's RHO	Spearman's P[†]
HWIN and EWIN	51	+0.38	0.011
HSPR and ESPR	28	+0.32	0.039
HSPR and CSUM	64	+0.57	0.001
HSUM and CSUM	67	+0.57	0.001

[†] two-tailed test

HWIN, EWIN = Jan-Mar

HSPR, ESPR = May-Jun

HSUM = July-Sept

CSUM = late June - early October

were observed grazing within 200 m of each other but no interactions occurred, and on 16 May, 1976, two elk were seen feeding at the same location utilized by 10 horses earlier in the afternoon. Although diet similarity of the two species appeared to decline in spring as compared to winter, forages still tended to be selected in the same order of importance - *Elymus innovatus* and *Carex spp.* continuing to be major shared constituents.

In the Red Desert in Wyoming, horse diets overlapped with those of elk by 52% in winter, 26% in spring, 14% in summer and 70% in fall (Olsen and Hansen 1977). This compares with figures of 51% and 28% for winter and spring respectively on the Red Deer River study area. In northwestern Colorado, dietary overlap of the two species averaged 42% on an annual basis (Hansen and Clark 1977).

7.6 Horse-Cattle Relationships

Horses and cattle shared about one third of their combined range (Figure 7.1) but cattle used the area for only four months during summer while horses were present year-round. Horses used in spring nearly 40% of the sites utilized by cows later in the year, but there appeared to be little overlap during the time when cows were actually present, the coincidence and association indices being low and the C8 value negative (although not statistically significant) when only fresh feces were considered in their calculation.

Cattle utilized the dwarf birch thicket, willow thicket and dry grassland habitat types more frequently than expected, and the alder thicket type less frequently than expected from their availability within the study area (Table 7.1). All habitats except dwarf birch meadow were used to some extent, plots in dry grassland, dwarf birch thicket, and disturbed areas containing the highest mean numbers of total cattle fecal groups. The general pattern of avoidance of the wettest habitats and concentration on dry, open sites, including roadsides, was confirmed by observations of cattle herds during 1975 and 1976.

Horse and cattle diets during the period of cattle occupancy in 1976 were nearly 70% identical (Table 7.3). Fescues and sedges together constituted over 50% of the horse diet and nearly 70% of the cattle diet during this time; the two species differed chiefly in that horses ate more <u>Elymus</u> (Table 7.2), indicating a greater use of forested habitats. However, as already noted, open habitats-chiefly mixed shrub meadows - appeared to supply most of the forage utilized by horses throughout the summer.

In order to determine whether horses ate preferred cattle foods in spring, prior to arrival of cattle on the study area, comparisons were made between the May-June diet of horses and the late June-early October diet of cattle. This pair of diets was nearly 65% identical although the order of the two most important forages was reversed - sedges being most important in the horse diet and fescues being most heavily utilized by cattle.

Cattle diets have been found to be very similar to those of feral horses throughout much of their combined range. Hubbard and Hansen (1976) reported dietary overlaps of 71, 75 and 59% in three vegetation zones in the Piceance Basin of Colorado. In two other Colorado based studies, average horse and cattle diets were 78% and 77% identical (Hansen and Clark 1977, Hansen et al. 1977). A comparable figure from this study, comparing cattle diets to the average annual horse diet, would be 65%. In cold desert habitat in Wyoming, horse and cattle diets overlapped 61% in summer, 69% in fall, 21% in winter and 28% in spring, for an annual mean of 45% (Olsen and Hansen 1977).

7.7 Effects of Combined Range Use

Evidence of interspecific competition between horses and other ungulates was sought from the condition of their range as well as from their habitat use behaviour. Range surveys were carried out during mid-October, 1976, to examine the range after summer long use by cattle and horses, and less intensively in early June, 1977, to determine if the range was over-used by horses in spring, prior to the arrival of cattle onto the study area.

Annual late summer inspections carried out by AFS personnel indicated that over the three allotments covering the study area range condition has been generally fair to good, with a stationary range trend. Current use since 1969 generally has been considered satisfactory, with only small areas of poor condition range associated with overgrazing (AFS Range Inspection Reports, 1969-76). Employing a somewhat different system, and including thicket and wetland habitats, I found that 75% of the area examined was used at a safe or lower level, most of the remaining 25% receiving heavy utilization (Table 7.4). This pattern varied according to habitat type, dry grassland clearly receiving the heaviest use and dwarf birch meadows the lightest, although grazing occurred in all habitats to some extent.

Within dwarf birch meadows, 'safe' and 'heavy' use areas tended to be associated with isolated, largely shrub-free patches where previous grazing had removed the litter, resulting in an open growth of sedges on a moss base. Grazing in sedge meadows was associated with similar conditions, and tended to occur on sites which had dried out over the summer. Extensive wet or saturated stands of either habitat were not utilized. Heavy grazing of mixed shrub meadows often occurred adjacent to streams; small areas of severe use were found within this habitat in low spots or where groundwater flow surfaced, several of these sites apparently being utilized as mineral licks. Most grazing in the above three habitats was attributable to horses, although cattle also made some use of the mixed shrub meadow

Table 7.4 Degree of Grazing Utilization in Non-forested Habitats, Mid-October, 1976.

Habitat type	% of habitat in use class[1]					habitat area (ha)	% of total
	none - very light	light	safe	heavy	severe		
dwarf birch meadow	73.3	20.8	3.9	2.0	0	68.9	17.5
sedge meadow	34.7	38.8	22.4	4.1	0	4.9	1.2
mixed shrub meadow	8.2	55.7	19.1	11.6	5.4	115.1	29.2
willow thicket	0	0	100.0	0	0	20.8	5.3
dry grassland	3.1	3.9	44.9	47.2	0.8	122.9	31.2
dwarf birch thicket	9.9	39.9	25.4	24.9	0	60.7	15.4
miscellaneous	0	0	0	83.3	16.7	0.6	0.2
total ha	71.4	109.3	117.2	88.7	7.3	393.9	100.0
% of total	18.1	27.7	29.8	22.5	1.8	99.9	

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[1] none - very light: 0-15% of herbage biomass removed; light: 16-35% removed; safe: 36-65% removed; heavy: 66-80% removed; severe: >80% removed; plants grubbed, trampling damage evident.

type.

The generally limited extent of utilization of wet and mesic sites is in direct contrast to the situation for dry grasslands, dwarf birch thickets and willow thickets - all preferred cattle habitats - which together received the heaviest grazing use. At the end of the 1976 grazing season nearly half of the dry grasslands were overgrazed and nearly all had received some degree of use. Although residual biomass was not measured, stubble heights (usually less than 5 cm) indicated that forage available on these areas over winter had been severely reduced. This was also true to a lesser extent for the closely associated dwarf birch thicket type.

Since horses also made extensive use of dry grasslands throughout the year potential for interspecific competition was probably highest within this habitat. The Deer Creek Flats area, which was used by at least five herds of horses and up to 12 elk during winter and spring, by several mule deer in spring and by approximately 50 cattle during summer 1976 serves as a case in point. By fall, over 60% of non-forested habitat was overgrazed while only about 5% was ungrazed or lightly grazed. Heavy use was concentrated in the dry grassland and dwarf birch thicket types. South-facing grassy hillsides were overgrazed on the lower and midslopes and were safely or lightly used only on the highest and steepest sites; all dwarf birch thickets and grasslands on the extensive flats associated with this area were subjected to heavy utilization. Previous observations indicated the following general pattern. Since cattle graze the area after the primary period of herbaceous growth, the amount of forage remaining for over-wintering herbivores is dependent largely on the degree of use by this species. Conversely, as a result of heavy utilization by cattle there is little litter to impede forage growth during spring and greenup is rapid, resulting in use of previously grazed sites as spring range by horses, elk and deer. Forage growth during this period is rapid, however, and it is unlikely that horses, the major user, could seriously impede the access of elk or deer, or subsequently of cattle, to this resource. Although it is recognized that early-season grazing is detrimental to subsequent forage production (Heady 1975, Stoddart et al. 1975), and could thus limit the amount of forage available to cattle, this effect was not measured during the study. When examined intensively in early June, 1977, just prior to initiation of the next cattle grazing season, utilization of new growth at Deer Creek was rated as none to very light over 95% of the area.

While spring grazing by horses on dry grasslands appeared to be moderate (although variable from area to area, and apparently from year to year), limited areas of other habitats were heavily used. Grazed sites found during the June, 1977 survey were generally located around the peripheries of salt licks (both natural and artificial), along stream courses, and on flat saturated areas which provided support sufficient to bear the weight of a horse. They were similar in that moribund material was lacking and forage (primarily Carex spp.) growth was open to sparse and therefore presumably highly accessible. Stubble height varied downward from one dm to grubbed. Although the total extent of grazed areas was small (less than 5% of non-forested habitat), destruction of forage through grazing and trampling reached severe levels on some sites. Damage was particularly evident on wet sites lacking a moss base, such as in hummocky areas or on flat, hard tables adjacent to streams. Prior observations indicated that many of these areas are used year after year, and that some of the damage is exacerbated by cattle later in the season, particularly due to trampling along access routes to water.

As yet there is little quantitative information available on the impact of horses on vegetation in preferred habitats in other areas, or on effects of multi-species grazing on range condition. Observations reported to date indicate a great deal of variation from area to area, depending on stocking level and range type. Horses on Sable Island, for example, maintained the vegetation in an arrested succession of marram grass (Ammophila breviliqulata), but posed little threat to the stability of the sand dune complex characterizing the island (Welsh 1973). Free-ranging horses studied in southern New Mexico did not appear to be destroying the range plants or causing range deterioration (Hansen 1976), and although wild horses, cattle and mule deer were present for all or part of the year in each of three vegetation zones studied in Colorado combined [illegible] was not excessive (Hubbard and Hansen 1976). In some a[illegible] of the western United States, however, the feral horse population has reportedly grown beyond carrying capacity, and destruction of elk and bighorn sheep range have been cited (Anon. 1976). In northeastern California and northwestern Nevada a downward trend in vegetation cover and some local erosion have been attributed to combined use by feral horses, burros, deer, antelope and cattle (Reavely 1974).

7.8 General Discussion

As noted above, a primarily descriptive approach was adopted in this study toward determination of spatial, habitat use and dietary relationships of feral horses with coexisting herbivores. It is recognized that when viewed superficially indications of spatial overlap may be taken as evidence either for or against competition (Sale 1974, Hudson et al. 1976). As well, similar patterns of habitat use and similar food habits do not necessarily imply competitive relationships, as such overlap may be functionally synergistic, at least in some grazing systems (Bell 1971). Clearly, a purely descriptive approach based on only one or two parameters may lead to ambiguity and difficulties in interpretation. The likelihood of serious misinterpretation is remote, however, when the use of food and space, range condition and the behaviour and physical condition of the animals are considered together rather than in isolation (Wilkinson et al. 1976). In the present study, evidence of competition was sought from the condition of the range and from behavioural interactions, interpreted in light of knowledge of spatial and dietary relationships.

Association and coincidence indices calculated from plot data revealed the basic spatial relationships between feral horses and other ungulates. Perhaps the most interesting finding was the high frequency of occurrence of multi-season horse pellet groups as compared to those of other species. This may indicate a broad niche and 'non-specialist' strategy of habitat occupation by horses, although it has been shown that their seasonal distribution was decidedly non-random. Diagrammatic representation of spatial relations showed that, on a multi-season basis, horses overlapped almost completely onto the areas used by all other species. However, consideration of seasonal distribution indicated that much of this overlap was non-contemporaneous.

C8 values provided a measure of "the tendency of two species to occur together more (or less) often than expected by chance" (Hurlbert 1969). In plant communities this coefficient is little influenced by competition unless it is severe, since the calculation is based on presence-absence data and one species must be completely eliminated from the plot or quadrat before C8 is affected (Hurlbert 1969). The extent to which this holds in highly mobile large herbivore communities is unknown, but certainly presence/absence data obtained from large plots (as used in this study) would be expected to be less influenced by competition than would abundance data. Significant lack of association between two species, as measured by G8, may therefore reflect differing ecological distributions of species pairs. Evidence for different habitat preferences based on presence-absence data may be a further indication of spatial separation. Thus, from spatial and habitat relationships, there appeared to be significant ecological separation of feral horses and deer, and feral horses and moose, during winter. Conversely, feral horses and elk were significantly positively associated during this period, and preferred some of the same habitats. Non-significant C8 values, as occurred in the remainder of spatial relationships, are indicat[illegible] neither of association nor separation.

Strongly expressed competitive interference, in which case one species might be actively prevented from using an area by another, would alter the interpretation of spatial separation. Behavioural observations provided little evidence for competition through interference in this grazing system, however, the only observed incident involving a small herd of horses apparently blocking the access of four cow elk to a salk lick in mid-June. Cattle, mule deer, elk and moose were observed feeding in proximity to feral horses without interaction.

Exploitation, or depletion of the food resource by one species, also would be expected to affect and be affected by spatial relationships. Since their diet consisted almost entirely of herbaceous material feral horses would not be expected to exploit the food resource of browsing herbivores, at least not under conditions similar to those prevailing at the time of the study, however. Dietary similarities and spatial overlap indicated the potential for forage competition between feral horses and elk and feral horses and cattle, but grazing relationships were complex. The ability of elk to subsist on a browse diet (see Kufeld 1973) makes the importance of potential competition with feral horses for food difficult to determine. Spring grazing by horses did not deplete ranges preferred later in the season by cattle, but common use areas (primarily dry grasslands, with cattle being the major users) were overgrazed by autumn. The use of these ranges by several species in spring illustrated a feedback effect of previous grazing resulting in increased availability of succulent forage early in the next growing season. Conversely, large areas of meadow habitat of apparently similar species composition were ungrazed throughout the year.

Detailed studies of multi-species grazing assemblages have shown that selection of different plant parts by two or more herbivores having superficially similar food habits may be a mechanism of ecological separation (Bell 1971). In the present study, there was some evidence that during winter deer and elk fed on plant stubble remaining in craters made by horses, but this was related more to snow cover than to selection of plant parts <u>per se</u>. Differential use of the same plant was not otherwise considered important in grazing relationships, with the possible exception of the 'feedback' effect described above.

Heavy grazing is generally recognized as being deleterious to range productivity, particularly if it occurs during critical parts of the growing period (Heady 1975, Stoddart et al. 1975). Grazing by elk and/or horses has altered species composition in contiguous mountain grasslands (Stringer 1972). Although the present study [illegible] too short to attempt documentation of changes [illegible] productivity or species composition, [illegible] and invading species were certainly present and in [illegible]es abundant in dry grassland habitat, indicating histo[illegible] change. Whether this was du[illegible]imarily to grazing by horses or by cattle (or more likely both) is unknown. Also, the stability of the grazing pattern (ie. the period over which certain areas are heavily grazed, while others remain ungrazed) co[illegible] not be determined from the information available. This would be expected to be strongly affected by factors such as location of artificial salt licks, alterations in cattle distribution through increased management, and removal of litter by fire,

SUMMARY

1. Domestic horses were first brought into Alberta in the early 1700s. Feral horse populations deriving from subsequent introductions were added to by escaped or unmanaged domestic horses until fairly recently.
2. Attempts at management of feral horse populations began in the mid-1950s. Over 2000 horses were removed under permit from the Forest Reserve between 1962 and 1972.
3. As of early 1977 there were an estimated 900 feral horses in Alberta with a centre of abundance in the central foothills area. In addition there were approximately 900 free-ranging horses owned by natives, Metis, guides or outfitters.
4. Information on social organization, food habits, habitat utilization and relationships with other ungulates was obtained during a study of a feral horse population in the foothills west of Sundre, Alberta, during June 1975 to June 1977.
5. A total of 206 horses were identified on the 200 km² study area during 1976, the period of most intensive study.
6. The horses were organized into permanent harem groups dominated by a mature stallion and consisting of a variable number of adult mares and immature animals. Mean group size was 7.7 during June, 1976. Excess stallions formed bachelor groups.
7. Both harem and bachelor groups remained within home

ranges of less than 15 km² throughout 1976. Home ranges appeared to remain stable from year to year.

8. Home ranges of different groups overlapped considerably and there was no evidence of territoriality.

9. Spatial relationships among herds were maintained by displays and interactions between dominant stallions and involved a minimum of fighting. Scent-marking with urine and feces also appeared to play a role in spatial relationships.

10. Dominant stallions played a major role in keeping their harems intact, although there also may have been some intragroup bonding. Permanent changes in harem group structure involved primarily immature animals of both sexes.

11. Solitary, bachelor males posed the greatest threat to harem stability. Attempts by bachelors to begin their own harems often were unsuccessful.

12. All but one of 37 foals observed during 1976 were born between early April and late June. This was also the period during which stallions tended mares.

13. The population of 206 horses described during 1976 was comprised of 52.9% adults, 12.1% two year olds, 17.0% yearlings and 18.0% foals.

14. The horses were well-adapted to feeding during the period of snow cover, digging craters to uncover forage plants and utilizing areas of reduced snow depth.

15. About three-quarters of daylight hours were spent

foraging during both winter (January-March) and spring (April-June). Feeding time appeared to decrease during summer.

16. Quantities of soil were ingested at both natural mineral licks and cattle salt licks throughout the year, with a peak in spring.

17. Grasses, sedges and rushes together constituted the bulk of the diet throughout the year, never occurring at a level of less than 83% during any one month. Hairy wild rye (<u>Elymus innovatus</u>) constituted on average over 25% of the monthly diet. Forbs did not exceed a level of 3% during any one month. Pine and spruce needles found in the feces were considered to be accidentally ingested as litter during the period of snow cover.

18. Diet quality was highly variable seasonally, with a peak in June and a low in January.

19. Habitats in the study area were classified into 17 categories on the basis of plant species composition and structure. Food plants occurred in greater variety and abundance in meadow and shrubland as compared to forested habitat types.

20. Some use was made of nearly all habitats, although quantitative analyses suggested preferential use of meadow and shrubland as compared to forested habitats on a year-long basis.

21. Both forested and non-forested habitats were important during winter. With the onset of greenup in spring

there was a distinct shift to meadow and shrubland habitats. Forested habitats increased in importance again during summer, and fall-early winter.

22. Habitat utilization appeared to be affected primarily by forage availability, with other factors being of secondary importance.

23. On a year-long basis horses and deer shared an estimated 48%, horses and moose 45% and horses and elk 12% of their combined range. Figures for winter distribution were 20%, 21% and 12%. Horses were more ubiquitous in their distribution on both a multi-season basis and during winter than any other ungulate.

24. Horse pellet groups representing year-round deposition were found on 91% of plots also containing cattle pellet groups. However, horses used in spring only 39% of areas used by cattle in summer. During summer horses used only 2% of plots concurrently used by cattle.

25. Horse and elk diets were 51% identical during winter and 28% identical during spring. Major shared forages were _Festuca spp_. and _Elymus innovatus_.

26. Horse diets in spring were 64% identical to those chosen by cattle in summer. Horse summer and cattle summer diets were 67% identical. _Festuca spp_. and _Carex spp_. were major shared forages.

27. A range survey carried out during mid-October, 1976 showed that 75% of meadow and shrubland habitat was used at a 'safe' or lower level as a result of combined

cattle and horse grazing. Most of the remaining 25% received 'heavy' utilization; i.e. between 66 and 80% of available herbage had been removed. Dry grassland areas received the heaviest use.

28. Examination of a traditional cattle range in early June, 1977, showed that forage utilization by feral horses was 'none' to 'very light' (<35%) over 95% of the area.

29. Spring grazing by feral horses was concentrated around salt licks, along stream courses and on flat saturated areas. An estimated 5% of non-forested habitat showed evidence of spring grazing by horses. Destruction of forage through grazing and trampling reached severe levels on a limited number of sites; this damage was exacerbated during subsequent grazing and trampling by cattle.

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Appendix 1: Habitat Classification

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4. Three-dimensional ordination of 73 non-forested stands.

Field Methodology

Field methodology utilized in gathering data for development of a habitat classification is summarized in section 6.21. In summary, 152 stands of vegetation were sampled; data records consisted of canopy cover values of all vascular plant species and of mosses and lichens within 15 m diameter circular plots. A preliminary habitat classification was used in the field and later tested and refined by numerical analysis of the original data.

Data Analysis

Cluster analysis and principal components analysis techniques were applied to the data using the CLUSTAN IC cluster analysis package (Wishart 1975). Principal Components Analysis as implemented in this program was limited to 80 variables (in this case species). Although cluster analysis could accept up to 200 species, use of this number on the large stand population (152) would have been prohibitively expensive. For these reasons the population was subsetted and the number of variables was reduced.

As a first step in the analysis five stands representing cut-over sites were removed from the population and their species composition was tabulated by hand. The remaining population was divided into 73 stands representing herbaceous and scrub communities and 74 stands representing forest and open woodland communities. The number of species used for the analysis was then reduced to 59 for the herbaceous / scrub group and 53 for the forest / woodland group (Table 1). Species were chosen on the basis of high constancy within previously delineated communities (MacKenzie - Grieve 1970) or within tentative habitat types (1975 vegetation plot data) to represent the herbaceous, dwarf shrub, shrub, tree sapling[1] and tree strata. Similar criteria for reducing variables used in vegetation analysis have been reported by Franklin et al. (1970) and Ohmann et al. (1973).

Separate but parallel analyses were run on the two data sets. Prior to analysis the species - coverage values were converted to cover-abundance indices using a modified Braun-Blanquet scale (Table 2). These were used as real numbers (ie. 5.0, 4.0 etc.) in the calculation of squared Euclidean distance between each possible pair of stands for input into distance matrices. Hierarchical cluster analyses were then performed using Ward's method of the least increase in the error sum of squares and dendrograms were plotted (Figures 1,2). Examination of the dendrograms indicated the levels at which the number of groups produced made the most sense on an intuitive basis. This was determined by working down from the top of each dendrogram and successively examining photographic slides of stands assigned to the subgroups. This also provided a visual check against gross

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[1] less than 2 cm dbh.

Table 1. Plant Species Used in Numerical Analysis of Herbaceous/Scrub Stands (1) and Forest/Woodland Stands (2).

Trees
- Abies lasiocarpa[2]
- Picea glauca[2]
- P. mariana[2]
- Pinus contorta[2]
- Populus balsamifera[2]
- P. tremuloides[2]

Seedlings
- Abies lasiocarpa[2]
- Picea glauca[1,2]
- P. mariana[1,2]
- Pinus contorta[1,2]
- Populus balsamifera[1]
- P. tremuloides[1]

Shrubs
- Alnus crispa[2]
- Betula glandulosa[1]
- Eleagnus commutata[1]
- Juniperus communis[2]
- Potentilla fruticosa[1]
- Ribes hirtellum / lacustre / oxycanthoides[2]
- Rosa acicularis[1,2]
- Rubus strigosus[2]
- Salix spp.[1]
- Shepherdia canadensis[2]

Dwarf shrubs
- Arctostaphylos uva-ursi[2]
- Cornus canedensis[2]
- Ledum groenlandicum[2]
- Linnaea borealis[2]
- Rubus acaulis[1]
- Rubus pubescens[2]
- Vaccinium caespitosum[2]
- V. membranaceum[2]
- V. vitis-idaea[2]

Forbs
- Achillea millefolium[1,2]
- Agoseris glauca[1,2]
- Anetennaria neglecta[2]
- A. nitida / parviflora[2]
- Arnica cordifolia[2]
- Aster ciliolatus / laevis[1,2]
- A. conspicuus[2]
- A. junciformus[1]
- A. sibiricus[1]
- Campanula rotundifolia[1]

Castilleja miniata[2]
Cerastium arvense[1]
Delphinium glaucum[2]
Dodecatheon conjugens[1]
Dryas drummondii[1]
Epilobium angustifolium[1,2]
Fragaria virginiana[2]
Galium boreale[1,2]
Gentianella amarella[1]
Geranium richardsonii[2]
Geum macrophyllum[1]
G.rivale[1]
G.triflorum[1]
Heracleum lanatum[2]
Lathyrus ochroleucus[1,2]
Mertensia paniculata[1,2]
Mitella nuda[1,2]
Parnassia palustris[1]
Pedicularis groenlandica[1]
Penstemon procerus[1]
Petasites palmatus[1,2]
P.sagittatus[1]
Polemonium caeruleum[1]
Polygonum viviparum[1]
Potentilla diversifolia / gracilis[1]
Pyrola asarifolia[2]
Pyrola secunda[2]
Rumex alpestris[1]
Smilacina stellata[2]
Stellaria longifolia / longipes[1]
Stenanthium occidentale[2]
Streptopus amplexifolius[2]
Thalictrum venulosum[1]
Valeriana septentrionalis[1]
Vicia americana[1,2]
Viola rugulosa[2]
Zizia aptera[1]
Zygadenus elegans[2]

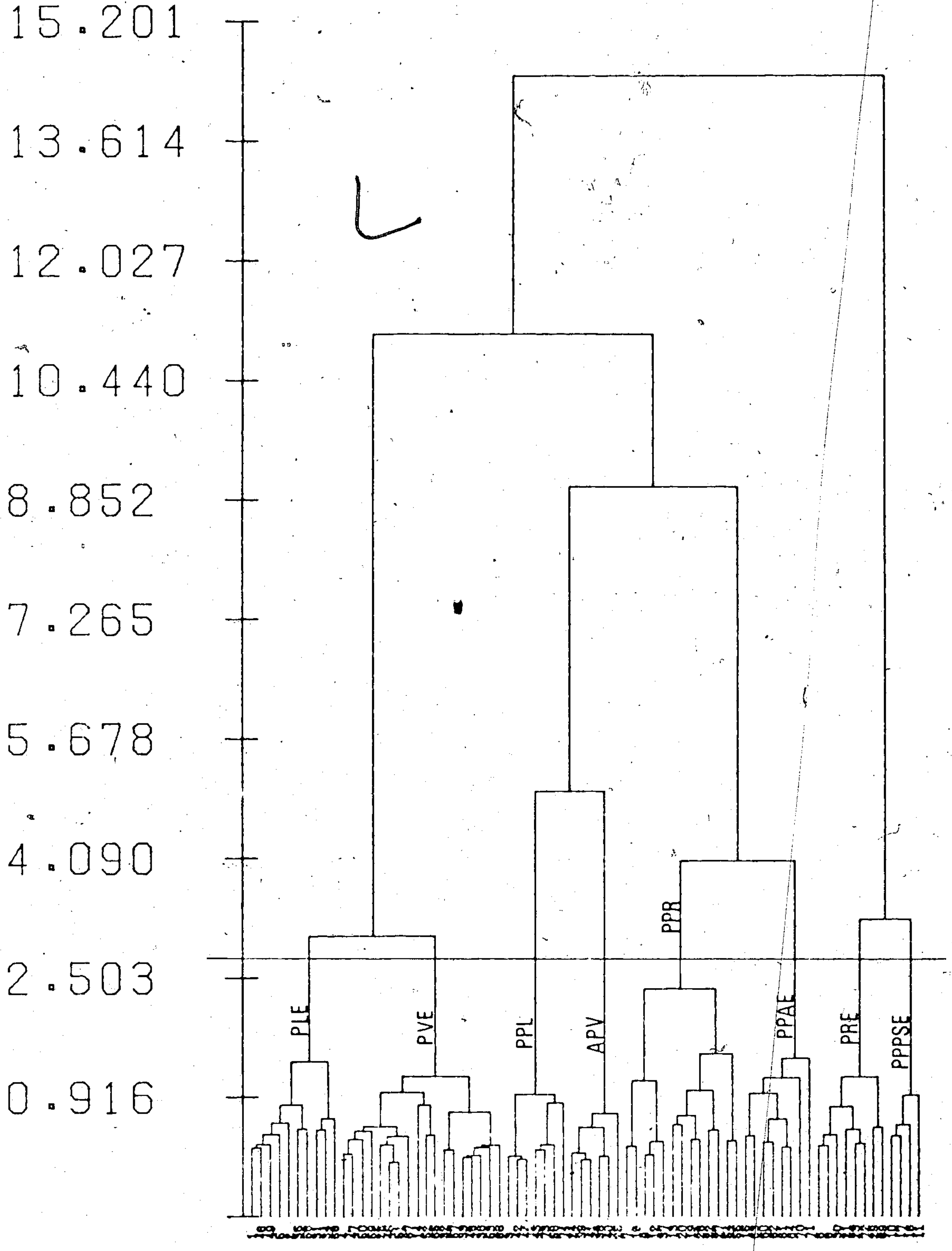
Grasses and Grass-likes

Agropyron subsecundum[1]
A.trachycaulum[1]
Bromus ciliatus / pumpellianus[1]
Calamagrostis canadensis[1,2]
C.inexspansa[1,2]
Carex spp.[1]
Danthonia intermedia[1]
Deschampsia caespitosa[1]
Elymus innovatus[1,2]
Festuca rubra[1]
F.saximontana[1]
F.scabrella[1]
Juncus balticus[1]
Koeleria cristata[1]
Poa pratensis[1]
Scirpus caespitosus[1]

Table 2. Conversion of Percent Cover Values to Cover-Abundance Values for Numerical Analysis of Vegetation Data.

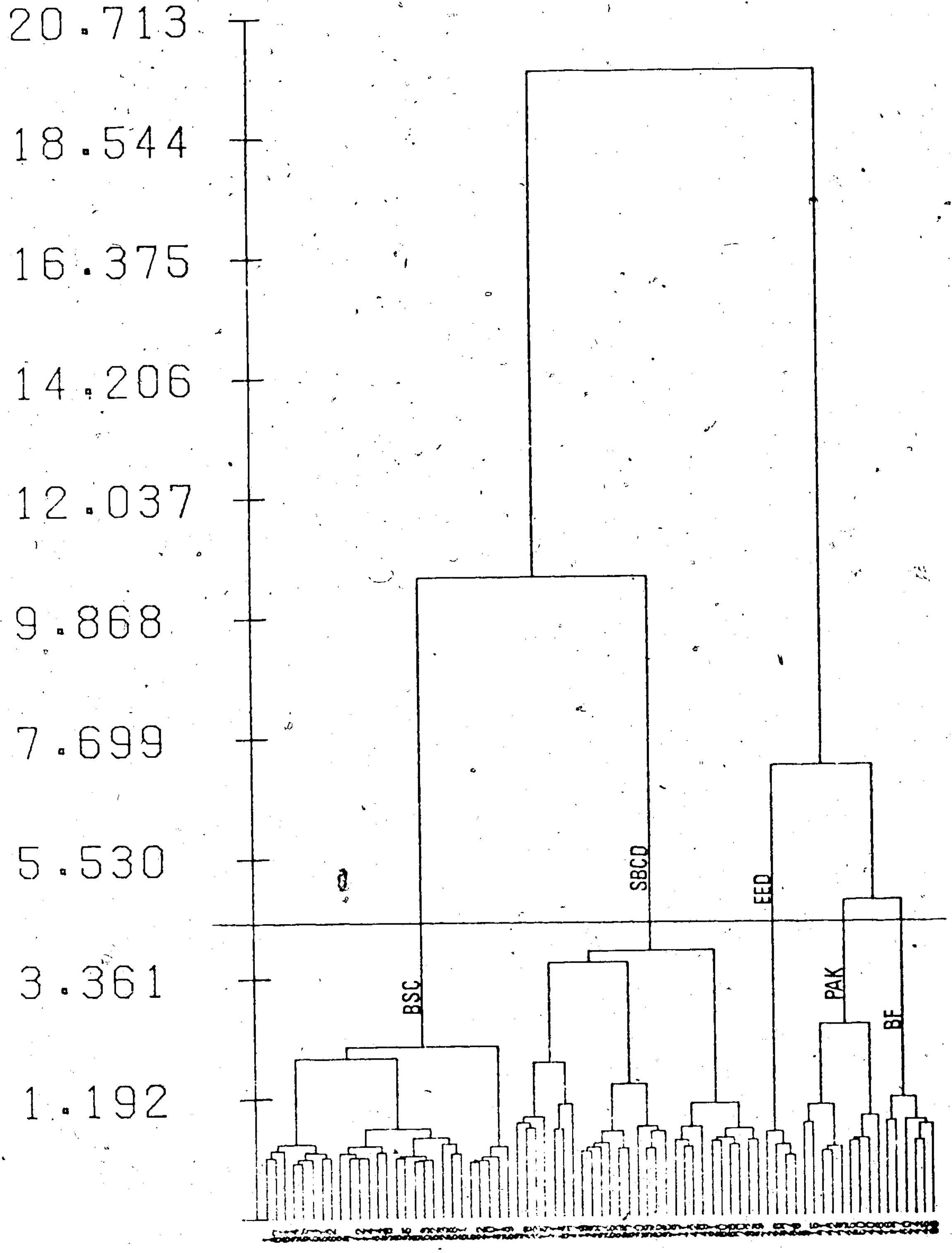
Class	Modified Daubenmire (1959) percent cover scale used to record field data		Modified Braun-Blanquet (1932) cover-abundance scale used for data analysis	
	Percent coverage		Equivalent cover-abundance	
	Range	Value (midpoint)	Description	Value
1	outside of plot	OP	rare, outside of plot	0.1
2	0-1	1	common, cover less than 1%	0.5
3	1-5	3	abundant, cover 1-5%	1.0
4	5-25	12	abundant, cover 5-25%	2.0
5	25-50	38	abundant, cover 25-50%	3.0
6	50-75	62	abundant, cover 50-75%	4.0
7	75-95	85	abundant, cover 75-95%	5.0
8	95-100	98	abundant, cover 95-100%	6.0

Figure 1. Dendrogram showing classification of 74 forested stands into clusters based on Ward's method. The horizontal line indicates the level at which vegetation associations were best defined. Abbreviations refer to association names given in Table 3.



CLOSED FOREST AND WOODLAND VEGETATION TYPES

Figure 2. Dendrogram showing classification of 73 non-forested stands into clusters based on Ward's method. The horizontal line indicates the level at which vegetation associations were best defined. Abbreviations refer to association names given in Table 3.



SCRUB AND HERBACEOUS VEGETATION TYPES

misclassifications. There are no statistical tests to determine the 'optimum' number of subgroups, the level at which these are designated depending largely on the purpose of the classification (West 1966).

Levels designating five and eight subgroups were chosen for the herbaceous / scrub and forest / woodland dendrograms respectively. Cluster circles representing the subgroups were plotted on a three-dimensional ordination of the plots produced by the principal components analyses (Figures 3, 4). These diagrams illustrate the relationships of the clusters and the individual plots to others in the population. The part-optimum classifications derived by Ward's method were optimized using an iterative relocation procedure (RELOCATE, Wishart 1975), and the resulting classifications were contrasted with the initial ones through comparison of the three-dimensional cluster circle diagrams (Figures 3, 4). Since the clusters produced by this procedure resulted in only slight modifications of the originals, the dendrograms produced by Ward's method were accepted as working classifications.

Each of the 13 vegetation associations derived via cluster analysis was named according to the dominant species in the various strata. After the consideration of structural characteristics 11 of the associations met the criterion of ready recognition as unique habitats (based on physiognomy <u>and</u> floristics); one of the remaining associations was split

Figure 3. Three-dimensional ordination of 74 forested stands. Circles corresponding to the clusters shown in Figure 1 are superimposed. Numbers correspond to the cluster to which each stand has been assigned on the ordination diagram.

3a. Cluster circle positioning derived from procedure HIERARCHY.

3b. Cluster circle positioning derived from procedure RELOCATE.

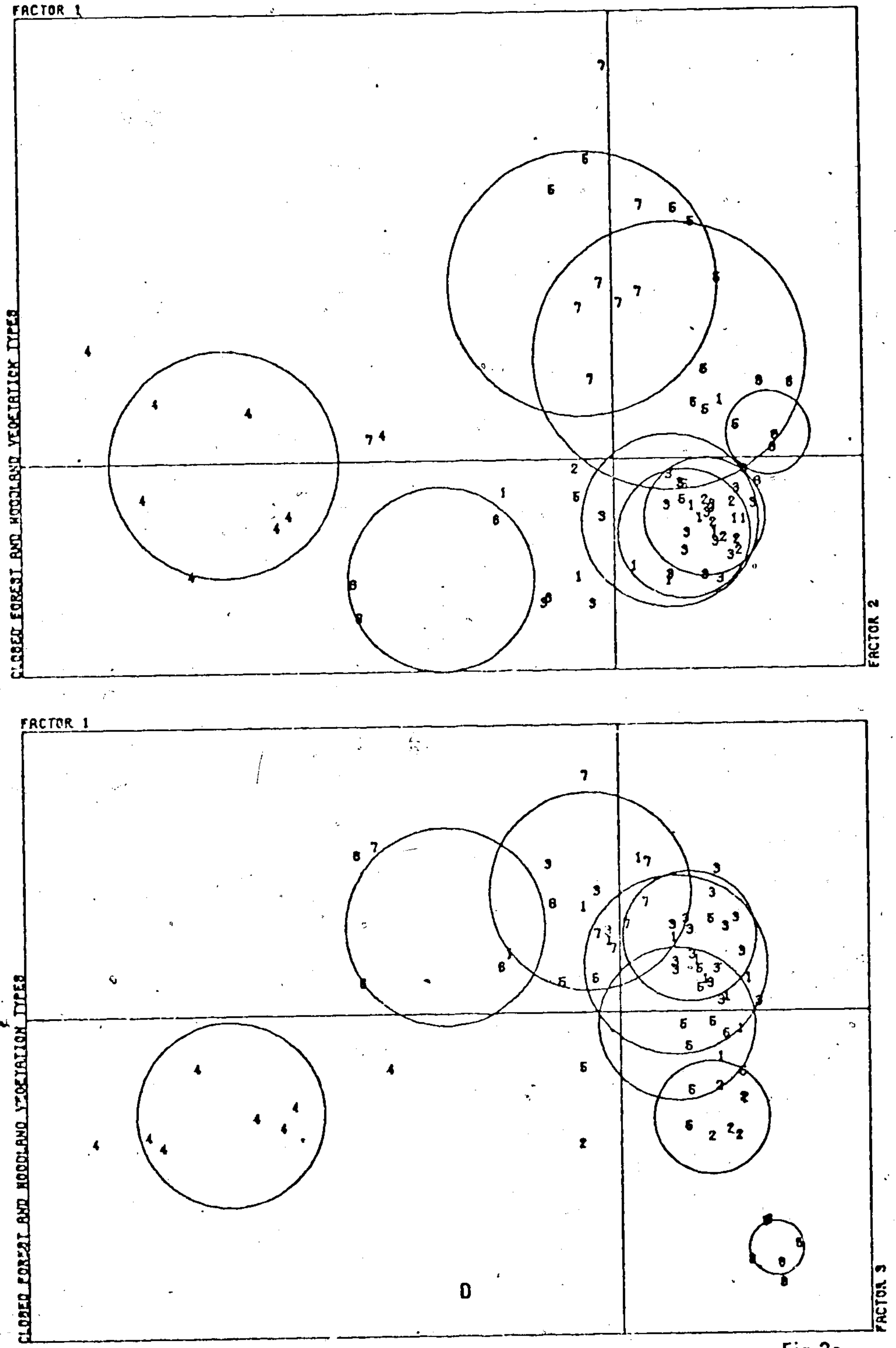

FACTOR 1
CLOSED FOREST AND WOODLAND VEGETATION TYPES
FACTOR 2
FACTOR 1
CLOSED FOREST AND WOODLAND VEGETATION TYPES
FACTOR 3
D

Fig 3a

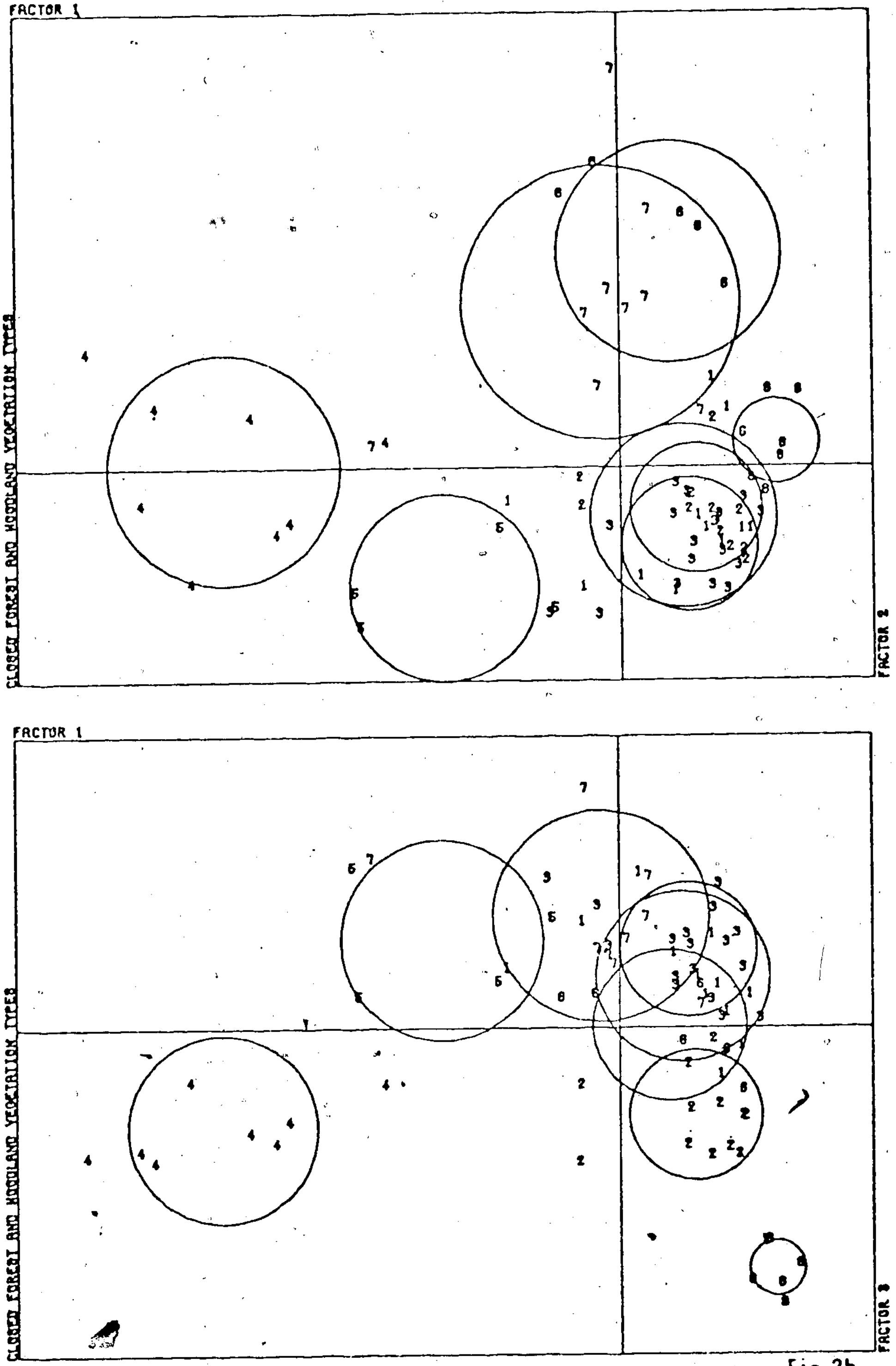

FACTOR 1
CLOSED FOREST AND WOODLAND VEGETATION TYPES
FACTOR 2
FACTOR 1
CLOSED FOREST AND WOODLAND VEGETATION TYPES
FACTOR 3

Fig. 3b

Figure 4. Three-dimensional ordination of 73 non-forested stands. Circles corresponding to the clusters shown in Figure 2 are superimposed. Numbers correspond to the cluster to which each stand has been assigned on the ordination diagram.

4a. Cluster circle positioning derived from procedure HIERARCHY.

4b. Cluster circle positioning derived from procedure RELOCATE.

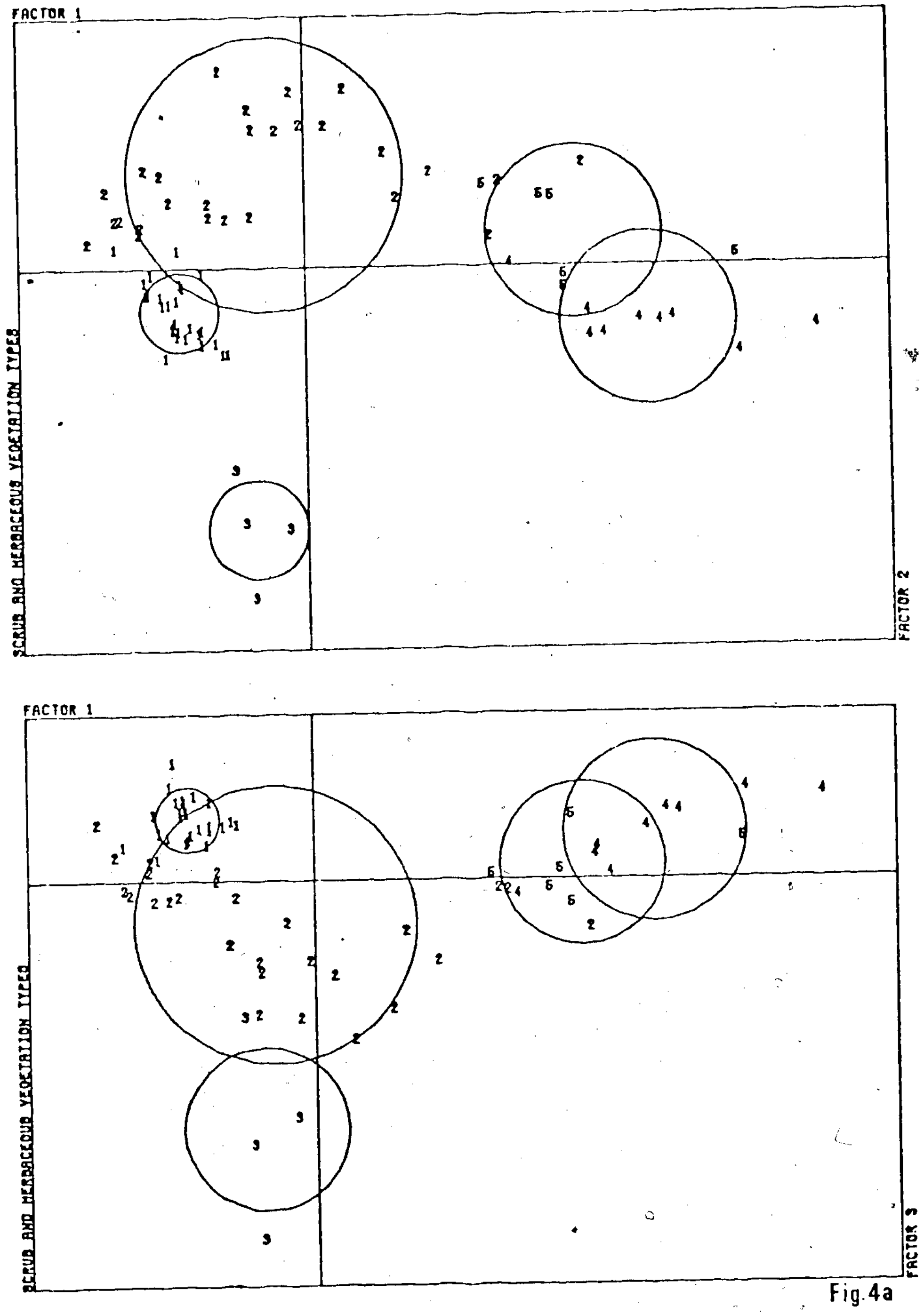

FACTOR 1
SCRUB AND HERBACEOUS VEGETATION TYPES
FACTOR 2
FACTOR 1
SCRUB AND HERBACEOUS VEGETATION TYPES
FACTOR 3

Fig.4a

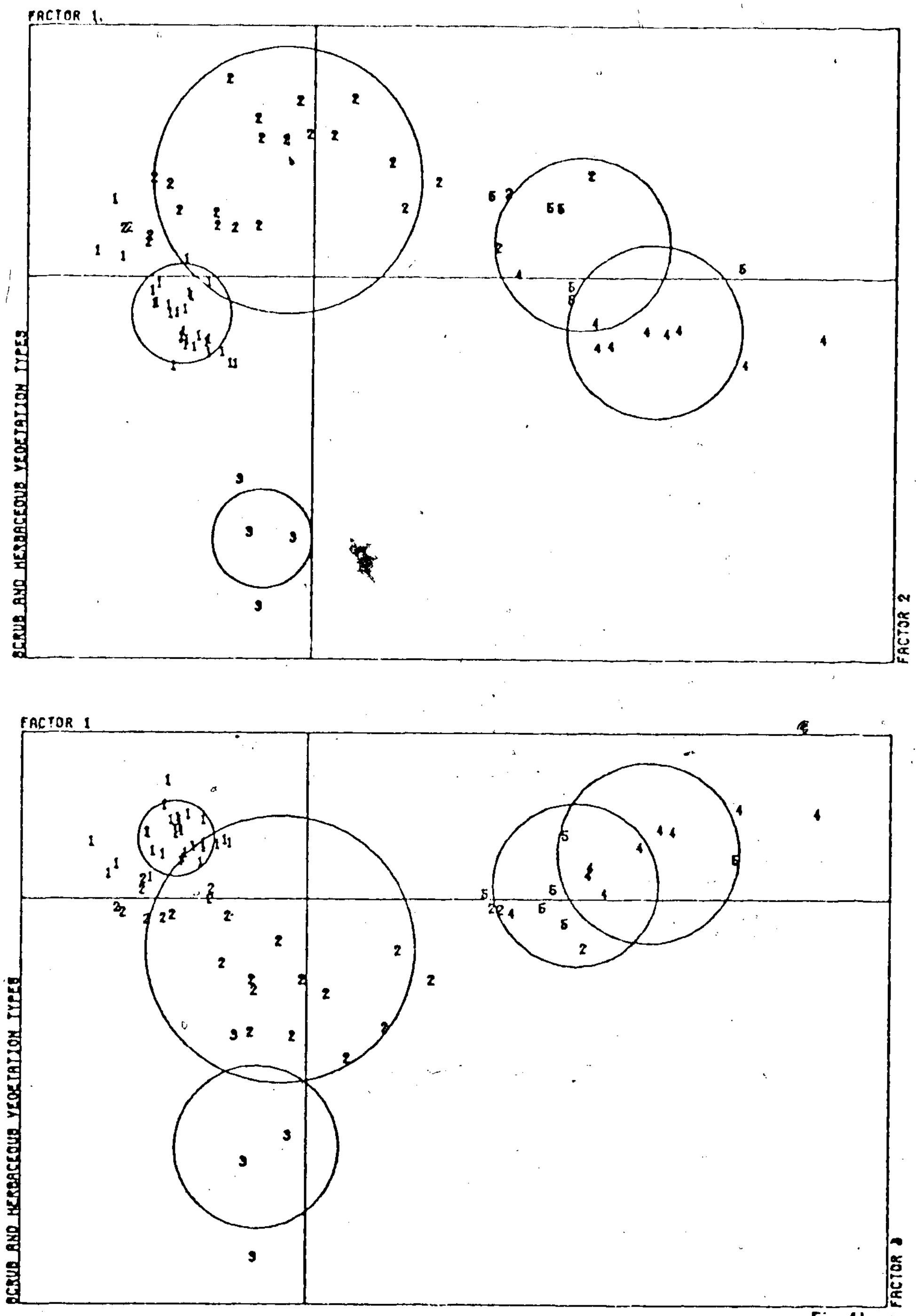

FACTOR 1
SCRUB AND HERBACEOUS VEGETATION TYPES
FACTOR 2
FACTOR 1
SCRUB AND HERBACEOUS VEGETATION TYPES
FACTOR 3

Fig.4b

into two habitats on the basis of shrub height, the other on the basis of shrub density. A disturbed habitat type (represented by five cut-over stands) and a forested watercourse habitat type (not represented in the vegetation samples) were added to the classification, and each of the 17 habitats was given a descriptive name based on the dominant species, physiognomy or both (Table 3).

Habitat Descriptions

Dwarf birch meadow. A habitat type characterized by complete moss cover, a dense growth of *Carex spp.* and an open scrub layer has developed on the flat, wet meadows found on the eastern half of the study area. The majority of sampled stands were classed as wet-saturated (free water produced by pressure on the moss layer) although in some stands the moss was merely damp and in others it formed a floating or quaking mat. Typical stands had flat to hummocky microtopography, often with standing water present in small pools between the hummocks. Shrubs were low and only rarely exceeded 5 dm in height. Species with high mean cover-abundance values were *Carex spp.* (5.4), *Betula glandusosa* (2.6), *Salix spp.* (2.1) and *Deschampsia caespitosa* (1.1). *Scirpus caespitosus* and *Eriophorum viridi - carinatum* were found in several stands and were unique to this habitat, although their cover was low. Mean number of species per stand was relatively low for a meadow community (Table 3).

Table 3. Habitat Types Derived from Cluster Analysis and Subjective Classification.

Habitat Type	No. stands sampled	Mean number[1] of species ±1s.d.	Parent Vegetation Association from Cluster Analysis Name	Abbre-viation
Dwarf birch meadow	24	17.6±4.69	Betula/Salix-Carex	BSC
Sedge meadow	3	4.7±1.53	Betula/Salix-Carex	BSC
Mixed shrub meadow	19	25.8±3.53	Salix/Betula-Carex/Deschampsia	SBCD
Willow thicket	8	30.4±7.29	Salix/Betula-Carex/Deschampsia	SBCD
Dry grassland	9	36.7±7.65	Potentilla-Agropyron/Koeleria	PAK
Dwarf birch thicket	6	34.5±5.39	Betula-Festuca	BF
Silverberry thicket	4	26.2±2.63	Eleagnus-Elymus/Dryas	EED
Mesic pine woods	10	25.8±9.15	Pinus-Ledum-Elymus	PLE
Dry pine woods	18	23.4±4.30	Pinus-Vaccinium-Elymus	PVE
Black spruce woods	7	15.6±5.16	Picea mariana/Pinus-Ledum	PPL
White spruce woods	13	20.5±7.70	Picea glauca/Pinus-Rosa	PPR
Poplar woods	8	26.1±3.91	Populus-Rosa-Elymus	PRE
Mixed woods	4	36.2±4.64	Pinus/Populus/Picea-Shepherdia-Elymus	PPPSE
Alder thicket	8	27.9±5.91	Pinus/Populus-Alnus-Elymus	PPAE
Alpine fir woods	6	16.8±3.31	Abies/Picea-Vaccinium	APV
Disturbed sites	5	24.0±6.32	not included in analysis	-
Forested watercourse	-	-	not sampled	-

---

[1] Includes mosses and lichens each as single species group. Species occurring in tree and seedling layer counted twice.

Sedge meadow. Examination of the *Betula*/*Salix*-*Carex* group produced by cluster analysis indicated that member stands represented two distinctive habitats - dwarf birch meadows and sedge meadows - related in terms of spatial proximity and high *Carex* spp. cover but differing in terms of species diversity and shrub cover. Sedge meadows were readily recognized by a complete lack of shrubs and very low species diversity (Table 3); *Carex* spp. (c.a. 5.3) and moss (c.a. 5.2) formed a more or less complete cover. Two of the three sampled stands were dominated by *Carex aquatilus*, one by *C. rostrata*. *Menyanthes trifoliata* was the only other species found at more than one site. All stands were wet at the time of sampling or showed evidence of previous flooding. This type was found as pure stands in small meadows or as patches within the more widespread dwarf birch meadow type.

Mixed shrub meadow. This habitat was developed on meadow locations where drainage was improved by slight sloping of the terrain, although soil moisture conditions were highly variable even within the same stand. Mixed shrub meadows had both structural and floristic similarities to dwarf birch meadows, but the generally drier conditions were reflected in an increase in species diversity (Table 3), a predominance of willows over dwarf birch, a decrease in sedge cover, and an increase in grass cover and diversity. These two habitats often occurred together and merged imperceptibly. Microtopography in mixed shrub meadows was generally very hummocky, with shrub heights in the order of 5 dm and not generally exceeding one meter. Species with high cover-abundance values were *Carex spp.* (3.8), *Deschampsia caespitosa* (2.9), *Salix spp.* (2.7), *Betula glandulosa* (1.8), *Geum rivale* (1.7), *Juncus balticus* (1.5), *Festuca rubra* (1.1) and *Petasites sagittatus* (1.0). This was a widespread habitat found in association with both rolling and gently sloping meadows.

Willow thicket. A distinctive tall willow habitat was included with mixed shrub meadow stands within the *Salix* / *Betula* - *Carex* / *Deschampsia* cluster (Figure 2) due to floristic similarities, but was clearly separable on the basis of shrub height. Willow thickets were particularly well developed on flat benches adjacent to streams where the soil was hard and dry, but also occurred in patches within mixed shrub meadows and dry grasslands, sharing species with both. The characteristic feature of this habitat was the presence of a dense, relatively tall (8-15 dm) shrub layer dominated by Salixes. Species with high cover-abundance values were *Salix spp.* (4.5), *Carex spp.* (2.2), *Geum rivale* (2.0), *Deschampsia caespitosa* (2.0), *Agropyron trachycaulum* (1.9), *Juncus balticus* (1.8), *Aster ciliolatus* / *laevis* (1.8), *Betula glandulosa* (1.5), *Achillea millefolium* (1.1), *Rubus acaulis* (1.1), *Epilobium angustifolium* (1.1), *Festuca rubra* (1.1), *Mertensia paniculata* (1.1), and *Bromus sp.* (1.0).

Dry grassland. A xeric grassland habitat was found throughout the area on warm south and southwest facing slopes and on dry flats. It was associated both with gently rolling meadows, where it occurred within the more extensive mixed shrub meadow type, and with steep slopes (up to 50%) where it occurred in association with poplar woods. Development was extensive on raised dry flats, such as occurred at Deer Creek. Shrub cover tended to be sparse or absent on flat areas, *Potentilla fruticosa* being the characteristic species on these sites. On steep slopes shrub cover tended to be much more extensive although low in height (<5 dm), characteristic shrubs being *Rosa sp.*, *Amelanchier alnifolia*, *P. fruticosa* and *Symphoricarpos sp.*. *Artemesia campestris*, *A. ludoviciana*, *A. frigida*, *Gaillardia aristata*, *Helictotrichon hookeri* , *Orthocarpus luteus* and *Sisyrinchium montanum* were found only within this habitat. Species with high cover-abundance values were *Agropyron subsecundum* (2.4), *Koeleria cristata* (2.2), *Potentilla fruticosa* (2.1), *Danthonia intermedia* (1.8), *Potentilla diversifolia* (1.7), *Festuca scabrella* (1.6), *Geum triflorum* (1.3), *Galium boreale* (1.3), *Achillea millefolium* (1.3), *Thalictrum venulosum* (1.2), *Aster ciliolatus / laevis* (1.1) and *Vicia americana* (1.0). Much of this habitat appeared to have been altered by heavy grazing.

Dwarf birch thicket. Dwarf birch thickets were characterized by a dense, relatively tall (to 15 dm) growth of *Betula* glandulosa. Dry, shrub covered slopes (5-30%, variable aspect) of rolling meadows were generally assignable to this habitat, as were Betula covered areas of dry flats. This habitat graded into mixed shrub meadow habitat in rolling topography, but tended to occur more on the dry tops and sides of knolls, whereas the latter was characteristic of the more mesic lower slopes and swales. The dwarf birch thicket type was closely related floristically to dry grassland and had a comparable species diversity (Table 3). Species with high cover-abundance values were Betula glandulosa (4.0), Festuca scabrella (4.0), Aster ciliolatus (2.2), Salix spp. (1.4), Achillea millefolium (1.3), Epilobium angustifolium (1.3), Danthonia intermedia (1.3), Potentilla fruticosa (1.3), Thalictrum venulosum (1.2), Galium boreale (1.0), Zizia aptera (1.0) and Festuca saximontana (1.0).

Silver-berry thicket. A unique habitat dominated by Eleagnus commutata was found along the Red Deer River on sand and gravel flats. This type was subject to periodic flooding and in places contained accumulations of driftwood. Individuals of Picea glauca and Populus balsamifera were scattered throughout but did not attain heights of over 8 m - they were best represented in the sapling layer. Eleagnus commutata (height 10-15 dm) and Dryas drummondii were unique to this habitat. Species with high cover-abundance values were Eleagnus commutata (4.2), Elymus innovatus (2.0), Dryas drummondii (2.0), Picea glauca saplings (2.0), Festuca rubra (1.8), Bromus sp. (1.4), Aster sibiricus (1.2) and Agropyron trachycaulum (1.2).

Mesic pine woods. This type occurred on flat to moderate slopes (0-20%) of NE to SE aspect. The tree overstory was characterized by mature Pinus contorta with occasional tree-sized Populus tremuloides, Picea glauca and Picea mariana, although the latter two normally occurred in the intermediate and sapling layers. A tree layer of moderate density, a sparse shrub understory, a well-developed dwarf shrub layer and light to moderate deadfall were characteristic. Species with high cover-abundance values were Pinus contorta (3.2) and Picea mariana (1.1) in the tree layer, Rosa acicularis (1.3) in the shrub layer, Vaccinium vitis-idaea (3.5), Ledum groenlandicum (3.1), Linnaea borealis (2.0), Cornus canadensis (1.9), and Vaccinium caespitosum (1.2) in the dwarf shrub layer, and Elymus innovatus (3.6) in the herb layer. The mesic pine woods type corresponded to the pine-feather moss faciation described for moist and shaded sites of lodgepole pine forest by Moss (1955).

Dry pine woods. Developed on flat to moderate (0-30%) slopes varying in aspect from 180-360° (but tending more to westerly and southwesterly exposures) this habitat was closely related to the mesic pine woods type but tended to be more xeric. The two were very similar in terms of height, dbh and density of the tree layers (Table 4). Pinus contorta clearly dominated the canopy, other species occurring only rarely; Picea glauca, however, was the primary understory tree. The understory appeared open due to the lack of a well-developed shrub layer, and deadfall was light to moderate. Species with high cover-abundance values were Pinus contorta (3.6) in the tree layer, Rosa acicularis (1.0) in the shrub layer, Vaccinium vitis - idaea (3.6), Linnaea borealis (2.7), Arctostaphylos uva-ursi (1.5), Vaccinium caespitosum (1.2) and Cornus canadensis (1.0) in the dwarf shrub layer, and Elymus innovatus (2.9) in the herb layer. This type corresponded to the pine-heath faciation described by Moss (1955) for the drier and more open parts of lodgepole pine stands.

Black spruce woods. Black spruce woods occurred on flat to moderate slopes (0-20%) of west to northerly aspect. Black spruce, pine and white spruce occurred in combination in the tree layer, black spruce generally dominating and sometimes forming pure stands. Trees were relatively short and mean density was high in both the canopy and intermediate layers (Table 4). Shading and aspect resulted in a mesic habitat of low species diversity (Table 3) and sparse shrub and herbaceous layer development over a continuous moss carpet. A wet phase with pools of standing water occurred along the edge of some flat meadows. Species with high cover-abundance

Table 4. Major Structural Features of Forest/Woodland Habitat Types.

Habitat	Tree growth form	Canopy Mean height (m)	Canopy Mean dbh (cm)	Canopy Mean density (no./ha)	Intermediate[1] Mean density (no./ha)
Mesic pine woods	Conifer	14	20.1	1200	741
Dry pine woods	Conifer	14	19.4	1296	708
Black spruce woods	Conifer	12	18.6	2241	2159
White spruce woods	Conifer	15	25.6	1189	836
Poplar woods	Deciduous	14	23.5	770	672
Mixed woods	Conifer Deciduous	13 14	24.8 21.8	215 158	283 354
Alder thicket	Conifer	15	30.0	515	241
Alpine fir woods	Conifer	18	28.1	690	1000

[1] Greater than 2 cm dbh but below canopy height.

values were Picea mariana (3.0), Pinus contorta (1.7), Vaccinium vitis-idaea (1.8) and Linnaea borealis (1.0).

White spruce woods. This type occurred on flat to steep slopes (0-40%) of predominantly northwest to easterly exposure. Picea glauca and Pinus contorta co-dominated the overstory layer in the majority of stands, although one or the other were sometimes more abundant at individual sites. Canopy height was usually in the 15 m range, similar to other coniferous habitat types (Table 4). The shrub layer was only moderately developed, while the dwarf shrub / herbaceous layer was highly variable, ranging from nearly absent (moss carpet) to dense. Deadfall was moderate to heavy. Species with high cover-abundance values were Pinus contorta (2.6), Picea glauca (2.5), Rosa acicularis (1.5), Alnus crispa (1.2), Cornus canadensis (1.6), Linnaea borealis (1.5), Vaccinium vitis-idaea (1.0), Elymus innovatus (2.9) and Arnica cordifolia (1.3).

Poplar woods. Poplar woods were developed on dry, moderate to steep (10-50%) south and west-facing slopes. The tree overstory was dominated by Populus tremuloides and scattered individuals of Populus balsamifera, although the latter was more common in the intermediate and sapling layers. Tree density was low in comparison to pine dominated habitats (Table 4) but canopy cover was similar due to the wide-crowned deciduous growth form. Well-developed sapling, low shrub and herbaceous layers were characteristic. Species with high cover-abundance values were *Populus tremuloides* (2.9) in the tree layer, *P. tremuloides* (1.6) and *P. balsamifera* (1.0) in the sapling layer, *Rosa acicularis* (2.2) in the shrub layer, and *Elymus innovatus* (5.2), *Fragaria virginiana* (2.0), *Lathyrus ochroleucus* (1.8), *Geranium richardsonii* (1.6), *Aster ciliolatus / laevis* (1.3), Vicia americana (1.2) and *Heracleum lanatum* (1.1) in the herb layer.

Mixed woods. This type occurred on flat to slight slopes (0-10%) and was characterized by a mixed *Pinus contorta* - *Populus tremuloides* - *Picea glauca* tree layer. The canopy was open and the overstory trees generally well-spaced, although not particularly large (Table 4). The understory was moderately well-developed as was the sapling / shrub stratum which reached up to 15 dm in height. Mean species diversity was the highest of any of the wooded habitats (Table 3). Species with high cover-abundance values were *Pinus contorta* (2.2), *Populus tremuloides* (2.0), *Picea glauca* (1.2), *Populus tremuloides* saplings (2.0), *P. balsamifera* saplings (1.0), *Shepherdia canadensis* (2.3), *Rosa acicularis* (1.8), *Arctostaphylos uva-ursi* (2.5), *Linnaea borealis* (1.4), *Elymus innovatus* (4.2), *Lathyrus ochroleucus* (2.2), *Fragaria virginiana* (1.2) and *Aster ciliolatus / laevis* (1.1).

Alder thicket. Although the alder thicket habitat type had a well-developed tree canopy, the defining feature was a relatively dense *Alnus crispa* shrub understory. *Pinus contorta* dominated the overstory, although in 50% of the stands *Populus tremuloides* or *Populus balsamifera* were also present. Occasional tree-sized individuals of *Picea glauca* were also found but this species was more abundant in the intermediate and sapling layers. This was generally an open canopy habitat with well-spaced trees in both the overstory and intermediate layers (Table 4). The characteristic alder understory generally attained a cover of greater than 50% and often reached heights of over 25 dm. Deadfall was light. Species with high cover-abundance values were *Pinus contorta* (2.8) and *Populus tremuloides* (1.0) in the tree layer, *Alnus crispa* (4.0), *Rosa acicularis* (1.9) and *Rubus strigosus* (1.1) in the shrub layer, *Linnaea borealis* (1.9), *Cornus canadensis* (1.3) and *Rubus pubescens* (1.0) in the dwarf shrub layer, and *Elymus innovatus* (3.6), *Aster conspicuus* (1.9), *Epilobium angustifolium* (1.6), *Calamagrostis inexpansa* (1.5), *Arnica cordifolia* (1.4) and *Fragaria virginiana* (1.3) in the herb layer. This was a widespread habitat occurring on slight to moderate slopes with south and western exposures.

Alpine fir woods. Alpine fir woods occurred only at the highest elevations in the study area, on slight to steep (5-50%) slopes with northeastern and eastern exposures.

Deadfall was moderate to dense and in extreme cases formed a barrier to movement through the stand. Abies lasiocarpa was the major tree in the overstory layer although Picea glauca was co-dominant in some stands. P.glauca/engelmannii hybrids occurred at the highest elevations. The canopy was the highest of any of the forest habitats at a mean of over 18 m, and the large size of the trees was also reflected by the dbh (Table 4). This was a shaded, species-poor habitat with poorly developed shrub and herbaceous layers. Species with high cover-abundance values were Abies lasiocarpa (3.2) and Picea glauca (2.3) in the tree layer and Vaccinium membranaceum (2.5), fir saplings (2.0), Linnaea borealis (1.7), Cornus canadensis (1.5) and white spruce saplings (1.1) in the sapling and dwarf shrub layers.

Disturbed sites. Road building, seismic exploration, well-site preparation and logging have disturbed a small proportion of the vegetation throughout the study area. These were all considered as disturbed sites for purposes of the present habitat classification, although there were obvious differences in successional stage and potential for regeneration of vegetative cover which resulted in highly variable species composition. In addition, some of the more recently disturbed areas were reseeded to tame grasses.

Only logged sites (5 stands) were sampled during the vegetation survey. Plant cover on these sites was a mix of original understory species and invaders, with the following species having high cover-abundance values: *Elymus innovatus* (3.2), *Calamagrostis inexpansa* (2.0), *Epilobium angustifolium* (2.0), *Rosa acicularis* (1.8), *Cornus canadensis* (1.8), *Arnica cordifolia* (1.3) and *Poa pratensis* (1.2).

Forested watercourse. This was a highly variable and rather limited habitat located in wooded ravines and swales and was not sampled during the vegetation analysis. However, 16 pellet group macroplots were subsequently located in this type, and it was important and unique enough to warrant separate description. Tree cover consisted primarily of *Picea glauca* with various admixtures of *Populus balsamifera*, *P. tremuloides*, and tree-sized *Salix sp.*. At some locations tall willow (up to 4 m) formed the primary cover. The shrub understory consisted usually of *Populus spp.* saplings, *Salix spp.* and *Rosa acicularis*, with a combined cover of less than 50%. In damp, shaded situations, such as occurred along small, spring-fed streams in steep topography, the herbaceous layer was poorly developed and consisted largely of *Equisetum spp.* on a damp moss ground cover. In drier situations, as along swales and shallow ravines, tree cover tended to be more open and a well-developed herb layer often was present.

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Table 1. Parameters Recorded Within 15 m Diameter Plots for Quantitative Assessment of Habitat Utilization.

Variables Period of utilization	Winter	All Seasons
Period of survey	Jan-Mar	July-August
Indicators of animal use		
Number of pellet groups		
horse	x^1	x
cow	-	x
deer	x	pres/abs
elk	x	"
moose	x	"
Number of tracks		
horse	x	-
deer	x	-
elk	x	-
moose	x	-
Number of feeding craters		
horse	x	-
elk	x	-
Browse utilization (% by shrub species)	x	x
Grazing index (% of plants grazed, stubble height)	-	x
Physical parameters		
Location (to nearest 50 m)	x	x
Slope (%)	x	x
Aspect (o)	x	x
Topography (subjective classification)	x	x
Soil moisture (rating)	-	x
Snow cover (%)	x	-
Snow depth (cm)	x	-
Snow hardness (cm compaction)	x	-
Distance to nearest road or seismic line (m)	x	x
Distance to nearest meadow edge (m)	x	x
Vegetation		
Vegetation (cover) type	x	x
Canopy cover (%)		
conifers	x	x
deciduous trees	x	x
shrubs	x	x
Cover (%) and density (rating)		
forbs	-	x
grasses	-	x
sedges	-	x
Mean height		
conifer canopy (m)	x	x
deciduous canopy (m)	x	x
dominant shrubs (m)	x	x
forb leaf layer (dm)	-	x
grass leaf layer (dm)	-	x
sedge leaf layer (dm)	-	x
Major species		
tree layer	x	x
shrub layer	x	x
forb layer	-	x
grass layer	-	x
sedge layer	-	x
Rank order of forbs, grasses and sedges in total herbage biomass	-	x
Deadfall rating (amount of fallen timber on plot, scale 0-5)	x	x
Diversity index (number of major cover types within 100 m radius)	x	x

[1] x = recorded during survey

Table 2. Distribution of Winter Feeding Craters, Tracks, Pellet Groups and Total Horse Sign by Habitat Type, January - March, 1976.

Habitat Type	Number of plots in habitat type[1]		No. plots with feeding craters	No. plots with tracks	No. plots with pellet groups	No. plots with craters, tracks and/or pellet groups		X^2
						Obs.	Exp.	
Dwarf birch meadow	26	(5.3)	4(7.7)	9(6.5)	10(9.2)	12(6.5)	10	0.40
Sedge meadow	2	(0.4)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1	1.00
Mixed shrub meadow	42	(8.5)	9(17.3)	16(11.6)	17(15.6)	21(11.4)	16	1.56
Willow thicket	13	(2.6)	5(9.6)	5(3.6)	3(2.7)	7(3.8)	5	0.80
Dry grassland	37	(7.5)	2(3.8)	4(2.9)	16(14.7)	18(9.7)	14	1.14
Dwarf birch thicket	16	(3.2)	2(3.8)	7(5.1)	4(3.7)	8(4.3)	6	0.67
Silverberry thicket	1	(0.2)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	0	0.00
Mesic pine woods	6	(1.2)	1(1.9)	1(0.7)	1(0.9)	1(0.5)	2	0.50
Dry pine woods	71	(14.4)	1(1.9)	8(5.8)	6(5.5)	11(6.0)	27	9.48
Black spruce woods	15	(3.0)	2(3.8)	7(5.0)	2(1.8)	7(3.8)	6	0.17
White spruce woods	35	(7.1)	0(0.0)	2(1.4)	3(2.7)	4(2.2)	13	6.23
Poplar woods	21	(4.3)	6(11.5)	7(5.1)	10(9.2)	14(7.6)	8	4.50
Mixed woods	63	[illegible]	6(11.5)	24(17.4)	15(13.8)	26(14.0)	24	0.17
Alder thicket	132	(26.8)	12(23.1)	42(30.4)	21(19.3)	50(27.0)	50	0.00
Alpine fir woods	2	(0.4)	0(0.0)	0(0.0)	0(0.0)	0(0.0)	1	1.00
Disturbed	2	(0.4)	0(0.0)	1(0.7)	0(0.0)	1(0.5)	1	0.00
Forested watercourse	9	(1.8)	2(3.8)	5(3.6)	1(0.9)	5(2.7)	3	1.33
	493	99.8	52	138	109	185		28.95*

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[1] Percent of total in parentheses. Expected number of plots = proportion of plots in habitat type x total number of plots with sign. Habitats contributing 10% or more to total X^2 value are underlined.

*Probability of obtaining a greater X^2 value <.05.

Table 3. Distribution of Winter Sign (Tracks, Pellet Groups or Feeding Craters) of Horses in Relation to Environmental Variables, with Confidence Intervals on Observed Distribution.

	Proportion of plots p_{io}	No. plots with sign	Expected no. plots	X^2	Proportion observed $\bar{p}_i$	Confidence interval
Conifer cover						
none	.280	73	51.80	8.68	.395	$.311 \le p_1 \le .479$
1-5%	.030	6	5.55	0.04	.032	$.002 \le p_2 \le .062$
6-25	.156	32	28.86	0.34	.173	$.108 \le p_3 \le .238$
26-50	.288	47	53.28	0.74	.254	$.180 \le p_4 \le .328$
51-75	.245	27	43.32	6.15	.146	$.086 \le p_5 \le .206$
	.999	185	184.82	15.94***	1.000	
Conifer height						
absent or < 1m	.280	73	51.80	8.68	.395	$.311 \le p_1 \le .479$
1-5m	.028	5	5.18	0.01	.027	$np \le 5$
6-10	.085	18	15.72	0.33	.097	$.046 \le p_3 \le .148$
11-15	.515	73	95.27	5.20	.395	$.311 \le p_4 \le .479$
16-20	.091	16	16.84	0.04	.086	$.038 \le p_5 \le .134$
	.999	185	184.82	14.26**	1.000	
Deciduous cover						
none	.734	124	135.79	1.02	.670	
0-5%	.069	12	12.76	0.04	.065	
6-25	.150	35	27.75	1.89	.189	
26-50	.036	11	6.66	2.83	.059	
51-75	.010	3	1.85	0.71	.016	
	.999	185	184.82	6.51	.999	
Deciduous height						
absent or < 1m	.734	125	135.79	0.86	.676	
1-5 m	.006	0	1.11	1.11	.000	
6-10	.087	24	16.10	3.88	.130	
11+	.172	36	31.82	0.55	.194	
	.999	185	184.82	6.40	1.000	

Major trees						
no trees	.227	55	42.00	4.02	.297	$.215 \leq p_1 \leq .379$
black spruce	.038	8	7.03	0.13	.043	$.007 \leq p_2 \leq .079$
white spruce	.034	10	6.29	2.19	.054	$.013 \leq p_3 \leq .095$
pine	.337	45	62.34	4.82	.243	$.166 \leq p_4 \leq .320$
poplar	.051	16	9.44	4.56	.086	$.036 \leq p_5 \leq .136$
mixed conifer	.106	8	19.61	6.87	.043	$.007 \leq p_6 \leq .079$
mixed con./dec.	.207	43	38.30	0.58	.232	$.201 \leq p_7 \leq .263$
	1.000	185	185.00	23.18***	.998	
Shrub cover						
no shrubs	.026	3	4.81	0.68	.016	$np \leq 5$
1-5%	.205	22	37.92	6.68	.119	$.062 \leq p_2 \leq .176$
6-25	.339	65	62.72	0.08	.351	$.267 \leq p_3 \leq .435$
26-50	.294	69	54.39	3.92	.373	$.288 \leq p_4 \leq .458$
51-75	.112	22	20.72	0.08	.119	$.062 \leq p_5 \leq .176$
76-95	.024	4	4.44	0.04	.022	$np \leq 5$
	1.000	185	185.00	11.49*	1.000	
Shrub height						
absent	.026	3	4.81	0.68	.016	
1-5 dm	.235	41	43.48	0.14	.222	
6-10	.278	54	51.43	0.13	.292	
11-15	.183	33	33.86	0.02	.178	
16-20	.120	15	22.20	2.34	.081	
21+	.158	39	29.23	3.26	.221	
	1.000	185	185.00	6.57	1.000	
Major shrub						
no shrubs	.026	3	4.81	0.68	.016	$np \leq 5$
willow	.140	35	25.90	3.20	.189	$.119 \leq p_2 \leq .259$
dwarf birch	.160	37	29.60	1.85	.200	$.128 \leq p_3 \leq .272$
Shepherdia	.154	14	28.49	7.37	.076	$.028 \leq p_4 \leq .124$
poplar regen.	.150	38	27.75	3.79	.205	$.132 \leq p_5 \leq .278$
alder	.290	50	53.65	0.25	.270	$.190 \leq p_6 \leq .350$
rose	.079	8	14.62	3.00	.043	$.009 \leq p_7 \leq .081$
	.999	185	184.82	20.13***	.999	

Deadfall						
none-very light	.552	128	102.12	6.56	.692	$.611 \leq p_1 \leq .773$
light	.183	31	33.86	0.24	.168	$.102 \leq p_2 \leq .234$
moderate	.128	16	23.68	2.49	.086	$.037 \leq p_3 \leq .135$
heavy	.077	5	14.24	6.00	.027	$np \leq 5$
very heavy	.020	3	3.70	0.13	.016	$np \leq 5$
missing data	.041	2	7.58	4.11	.011	$np \leq 5$
	1.001	185	185.18	19.53***	1.000	
Topography						
flat	.166	31	30.71	0.00	.168	
rolling	.462	74	85.47	1.54	.400	
steep	.371	80	68.64	1.88	.432	
	.999	185	184.82	3.42	1.000	
Slope						
0-10%	.686	120	126.91	0.38	.649	
11-20	.138	26	25.53	0.01	.140	
21-30	.118	28	21.83	1.74	.151	
30+	.059	11	10.92	0.00	.059	
	1.001	185	185.18	2.13	.999	
Aspect						
north	.057	4	10.54	4.06	.022	$np \leq 5$
NE	.075	5	13.86	5.66	.027	$np \leq 5$
east	.136	20	25.16	1.06	.108	$.050 \leq p_3 \leq .166$
SE	.099	15	18.32	0.60	.081	$.030 \leq p_4 \leq .132$
south	.156	43	28.86	6.93	.232	$.153 \leq p_5 \leq .311$
SW	.089	17	16.46	0.02	.092	$.038 \leq p_6 \leq .146$
west	.061	12	11.28	0.04	.065	$.019 \leq p_7 \leq .111$
NW	.049	6	9.06	1.03	.032	$.000 < p_8 \leq .065$
no slope	.278	63	51.43	2.60	.340	$.252 \leq p_9 \leq .428$
	1.000	185	185.00	22.01***	.999	
Diversity index						
1	.286	36	52.91	5.40	.195	$.133 \leq p_1 \leq .257$
2	.566	113	104.71	0.66	.611	$.535 \leq p_2 \leq .687$
3	.148	36	27.38	2.71	.195	$.133 \leq p_3 \leq .257$
	1.000	185	185.00	8.77*	1.001	
Snow cover						
<50%	.067	25	12.39	12.83	.135	$.079 \leq p_1 \leq .191$
51-75	.036	12	6.66	4.28	.065	$.025 \leq p_2 \leq .105$
76-95	.136	36	25.16	4.67	.195	$.130 \leq p_3 \leq .260$
96-100	.761	112	140.78	5.88	.605	$.525 \leq p_4 \leq .685$
	1.000	185	185.00	27.67***	1.000	

Snow depth						
no snow	.034	11	6.29	3.53	.059	$.017 < p_1 \leq .101$
1-10 cm	.101	34	18.68	12.56	.184	$.114 \leq p_2 \leq .254$
11-20	.245	41	43.32	0.12	.222	$.147 \leq p_3 \leq .297$
21-30	.282	48	52.17	0.33	.259	$.180 \leq p_4 \leq .338$
31-40	.245	40	43.32	0.25	.216	$.142 < p_5 \leq .290$
41-50	.077	11	14.24	0.74	.059	$.017 \leq p_6 \leq .101$
50+	.014	0	2.59	2.59	.000	$np \leq 5$
	.998	185	184.63	20.13***	.999	

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[1] Based on presence/absence of sign in plots examined January - March, 1976. Confidence intervals were calculated on observed distribution when this differed ($P < .05$) from that expected on the basis of occurrence of environmental variable categories within the plot sample ($n=493$ for each variable). If observed $\bar{p}i$ was within calculated confidence intervals (i.e. $pi \neq pi_o$, when $np>5$) sign was considered to be associated with the variable category more ($pi>pi_o$) or less ($pi<pi_o$) frequently then expected by chance ($\alpha = .10$).

* probability of obtaining a greater X^2 value: $.05 \geq p \geq .01$.

** $.01 \geq p \geq .005$.

*** $p \leq .005$.

Table 4 . Distribution of Spring, Summer and Total Horse Pellet Groups by Habitat Type, July-August, 1976.

Habitat Type	No. of plots in habitat type		Spring No. plots with spring pellet groups Obs.	Exp.	X^2	Summer No. plots with summer pellet groups	Total No. plots with any age pellet groups Obs.	Exp.	X^2	Mean no. all age groups per plot
Dwarf birch meadow	12	(2.4)[1]	3(2.3)	3	0.00	0(0.0)	10(2.4)	10	0.00	8.4
Sedge meadow	0	-	-	-	-	-	-	-	-	-
Mixed shrub meadow	31	(6.3)	20(15.2)	8	18.00	5(17.8)	29(7.0)	26	0.35	8.8
Willow thicket	8	(1.6)	0(0.0)	2	2.00	1(3.6)	4(1.0)	7	1.28	2.8
Dry grassland	20	(4.1)	6(4.5)	5	0.20	0(0.0)	20(4.8)	17	0.53	4.4
Dwarf birch thicket	11	(2.2)	9(6.8)	3	12.00	3(10.7)	11(2.6)	9	0.44	8.9
Silverberry thicket	0	-	-	-	-	-	-	-	-	-
Mesic pine woods	0	-	-	-	-	-	-	-	-	-
Dry pine woods	100	(20.4)	30(22.7)	27	0.33	7(25.0)	80(19.2)	85	0.29	3.2
Black spruce woods	12	(2.4)	3(2.3)	3	0.00	1(3.6)	12(2.9)	10	0.40	6.5
White spruce woods	21	(4.3)	4(3.0)	6	0.67	5(17.8)	16(3.8)	18	0.22	3.2
Poplar woods	19	(3.9)	7(5.3)	5	0.80	1(3.6)	18(4.3)	16	0.25	4.9
Mixed woods	83	(16.9)	34(25.8)	22	6.54	1(3.6)	77(18.4)	70	0.70	4.2
Alder thicket	161	(32.9)	15(11.4)	43	18.23	3(10.7)	131(31.4)	137	0.26	3.2
Alpine fir woods	0	-	-	-	-	-	-	-	-	-
Disturbed	5	(1.0)	0(0.0)	1	1.00	0(0.0)	3(0.7)	4	0.25	4.0
Forested watercourse	7	(1.4)	1(0.8)	2	0.50	1(3.6)	6(1.4)	6	0.00	3.3
	490	99.8	132		60.27***	28	417		4.97	

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[1] Percent of total in parentheses. Expected number of plots = proportion of plots in habitat type x total number of plots with specific pellet groups. Where observed distribution differs significantly from expected, habitats contributing 10% or more to total X^2 are underlined.

*** Probability of obtaining a greater X^2 value <.005.

Table 5. Distribution of Spring-type Pellet Groups of Horses in Relation to Environmental Variables, with Confidence Intervals on Observed Distribution.[1]

	Proportion of plots pi_o	No. plots with sign	Expected no. plots	X^2	Proportion observed $\bar{p}i$	Confidence Interval
Conifer cover						
none	.169	38	22.31	11.03	.288	$.196 \leq p_1 \leq .380$
1-5%	.059	12	7.79	2.28	.091	$.033 \leq p_2 \leq .149$
6-25	.214	26	28.25	0.18	.197	$.116 \leq p_3 \leq .278$
26-50	.412	43	54.38	2.38	.326	$.231 \leq p_4 \leq .421$
51-75	.145	13	19.14	1.97	.098	$.038 \leq p_5 \leq .158$
	.999	132	131.87	17.64***	1.000	
Conifer stems						
none	.176	39	23.23	10.71	.295	$.196 \leq p_1 \leq .394$
1-10	.282	36	37.22	0.04	.273	$.176 \leq p_2 \leq .370$
11-20	.171	22	22.57	0.01	.167	$.086 \leq p_3 \leq .248$
21-30	.169	19	22.31	0.49	.144	$.068 \leq p_4 \leq .220$
31-40	.106	9	13.99	1.78	.068	$.013 \leq p_5 \leq .123$
41-50	.060	5	7.92	1.08	.038	$np \leq 5$
51-60	.016	1	2.11	0.58	.008	$np \leq 5$
60+	.020	1	2.64	1.02	.008	$np \leq 5$
	1.000	132	132.00	15.71*	1.001	
Conifer height						
absent or < 1m	.171	38	22.57	10.55	.288	$.196 \leq p_1 \leq .380$
1-5m	.035	5	4.62	0.03	.038	$np \leq 5$
5-10	.133	22	17.56	1.12	.167	$.091 \leq p_3 \leq .243$
11-15	.641	66	84.61	4.09	.500	$.399 \leq p_4 \leq .601$
16-20	.020	1	2.64	1.02	.008	$np \leq 5$
	1.000	132	132.00	16.81***	1.001	
Deciduous cover						
none	.671	83	88.57	0.35	.629	
0-5%	.094	12	12.41	0.01	.091	
6-25	.143	19	18.88	0.00	.144	
26-50	.063	11	8.32	0.86	.083	
51-75	.029	7	3.83	2.62	.053	
	1.000	132	132.00	3.84	1.000	

Deciduous stems						
none	.682	84	90.02	0.40	.636	
1-10	.229	28	30.23	0.16	.212	
11-20	.049	8	6.47	0.36	.061	
21-30	.022	6	2.90	3.31	.045	
31-40	.008	3	1.06	3.55	.023	
40+	.010	3	1.32	2.14	.023	
	1.000	132	132.00	9.92	1.000	
Deciduous height						
absent or < 1m	.671	83	88.57	0.35	.629	
1-5m	.010	0	1.32	1.32	.000	
6-10	.118	22	15.58	2.64	.167	
11+	.200	27	26.40	0.01	.204	
	0.999	132	131.87	4.32	1.000	
Major trees						
no trees	.114	28	15.05	11.14	.212	$.125 \leq p_1 \leq .299$
black spruce	.033	3	4.36	0.42	.023	$np \leq 5$
white spruce	.029	2	3.83	0.87	.015	$np \leq 5$
pine	.431	42	56.89	3.90	.318	$.219 \leq p_4 \leq .417$
poplar	.055	10	7.26	1.03	.076	$.020 \leq p_5 \leq .132$
mixed conifer	.065	8	8.58	0.04	.061	$.010 \leq p_6 \leq .112$
mixed con./dec.	.274	39	36.17	0.22	.295	$.198 \leq p_7 \leq .392$
	1.001	132	132.13	17.63**	1.000	
Shrub cover						
no shrubs	.008	1	1.06	0.00	.008	
1-5%	.147	17	19.40	0.30	.129	
6-25	.331	40	43.69	0.31	.303	
26-50	.335	59	44.22	4.94	.447	
51-75	.137	14	18.08	0.92	.106	
76-95	.043	1	5.68	3.86	.008	
	1.001	132	132.13	10.33	1.001	
Shrub height						
absent	.008	1	1.06	0.00	.008	$np < 5$
1-5 dm	.257	51	33.92	8.60	.386	$.285 \leq p_2 < .487$
6-10	.288	54	38.02	6.72	.409	$.307 \leq p_3 \leq .511$
11-15	.186	10	24.55	8.62	.076	$.021 \leq p_4 \leq .131$
16-20	.108	6	14.26	4.78	.045	$.002 \leq p_5 \leq .088$
21+	.153	10	20.20	5.15	.076	$.021 \leq p_6 \leq .131$
	1.000	132	132.00	33.88***	1.000	

Major shrub						
no shrubs	.009	1	1.06	0.00	.008	np ≤ 5
willow	.143	24	18.88	1.39	.182	$.100 \le p_2 \le .264$
dwarf birch	.063	19	8.32	13.71	.144	$.069 \le p_3 \le .219$
Shepherdia	.188	33	24.82	2.70	.250	$.158 \le p_4 \le .342$
poplar regen.	.076	9	10.03	0.10	.068	$.014 \le p_5 \le .122$
alder	.327	15	43.16	18.37	.114	$.046 \le p_6 \le .182$
rose	.196	31	25.87	1.02	.235	$.145 \le p_7 \le .325$
	1.001	132	132.13	37.29***	1.001	
Deadfall						
none-very light	.390	68	51.48	5.30	.515	$.414 \le p_1 \le .626$
light	.251	32	33.13	0.04	.242	$.155 \le p_2 \le .329$
moderate	.182	21	24.02	0.38	.159	$.085 \le p_3 \le .233$
heavy	.149	9	19.67	5.79	.068	$.017 \le p_4 \le .119$
very heavy	.029	2	3.83	0.87	.015	np ≤ 5
	1.001	132	132.13	12.38*	0.999	
Forb cover						
1-5%	.126	20	16.63	0.68	.152	$.079 \le p_1 \le .225$
6-25	.339	51	44.75	0.87	.386	$.287 \le p_2 \le .485$
26-50	.337	49	44.84	0.38	.371	$.273 \le p_3 \le .469$
41-75	.167	10	22.04	6.58	.076	$.022 \le p_4 \le .130$
76-95	.031	2	4.09	1.07	.015	np ≤ 5
	1.000	132	132.00	9.59*	1.000	
Sedge cover						
no sedges	.741	86	97.81	1.42	.652	
1-5%	.067	11	8.84	0.53	.083	
6-25	.078	12	10.30	0.28	.091	
26-50	.020	2	2.64	0.16	.015	
51-75	.014	3	1.85	0.71	.023	
76-95	.053	13	7.00	5.14	.098	
96-100	.026	5	3.43	0.72	.038	
	0.999	132	131.87	8.96	1.000	
Grass cover						
no grasses	.014	0	1.85	1.85	.000	
1-5%	.039	6	5.15	0.14	.045	
6-25	.082	6	10.82	2.15	.045	
26-50	.214	32	28.25	0.50	.242	
51-75	.374	47	49.37	0.11	.356	
76-95	.249	32	32.87	0.02	.242	
96-100	.029	9	3.83	6.98	.068	
	1.001	132	132.13	11.75	0.998	

Biomass						
mostly grass	.149	29	19.67	4.42	.220	$.139 \le p_1 \le .301$
mostly forbs	.400	30	52.80	9.84	.227	$.145 \le p_2 \le .309$
mostly sedge	.090	19	11.88	4.27	.144	$.076 \le p_3 \le .212$
mixed	.361	54	47.65	0.85	.409	$.313 \le p_4 \le .505$
	1.000	132	132.00	19.38***	1.000	
Topography						
flat	.114	22	15.05	3.21	.167	$.098 \le p_1 \le .236$
rolling	.471	89	62.17	11.58	.674	$.587 \le p_2 \le .761$
steep	.414	21	54.65	20.72	.159	$.091 \le p_3 \le .227$
	0.999	132	131.86	35.51***	1.000	
Slope						
0-10%	.629	107	83.01	6.93	.811	$.735 \le p_1 \le .887$
11-20	.210	11	27.72	10.08	.083	$.029 \le p_2 \le .137$
21-30	.122	10	16.10	2.31	.076	$.024 \le p_3 \le .128$
30+	.039	4	5.15	0.26	.030	$np \le 5$
	1.000	132	132.00	19.59***	1.000	
Aspect						
north	.055	11	7.26	1.93	.083	
NE	.086	11	11.35	0.01	.083	
east	.139	15	18.35	0.61	.114	
SE	.098	16	12.94	0.72	.121	
south	.133	18	17.56	0.01	.136	
SW	.108	17	14.26	0.53	.129	
west	.147	13	19.40	2.11	.098	
NW	.035	2	4.62	1.48	.015	
no slope	.200	29	26.40	0.26	.220	
	1.001	132	132.13	7.66	0.999	
Diversity index						
1	.318	36	41.98	0.85	.273	
2	.518	69	68.38	0.00	.523	
3	.151	25	19.93	1.29	.189	
4	.012	2	1.58	0.11	.015	
	0.999	132	131.87	2.25	1.000	
Soil moisture						
dry	.878	110	115.90	0.30	.833	$.760 \le p_1 \le .906$
damp	.071	15	9.37	3.38	.114	$.052 \le p_2 \le .176$
wet	.024	6	3.17	2.53	.045	$.005 \le p_3 \le .085$
saturated	.026	1	3.43	1.72	.008	$np \le 5$
	0.999	132	131.87	7.93*	1.000	

Major grass						
no grasses	.014	0	1.85	1.85	.000	$np \leq 5$
Elymus	.737	85	97.28	1.55	.644	$.544 \leq p_2 \leq .744$
Calamagrostis	.053	2	7.00	3.57	.015	$np \leq 5$
Deschampsia	.102	24	13.46	8.25	.182	$.102 \leq p_4 \leq .262$
Bromus	.041	4	5.41	0.37	.030	$0 \leq p_5 \leq .065$
Festuca	.053	17	7.00	14.28	.129	$.059 \leq p_6 \leq .199$
	1.000	132	132.00	29.88***	1.000	

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[1] Based on presence/absence of spring-type pellet g[illegible] examined July-August, 1976. Confidence intervals were calculated on observed distribution when this dif[illegible] (p[illegible]5) from that expected on the basis of occurrence of environmental variable categories within the plot sample (n = 49[illegible] each variable). If observed $\bar{p}i$ was within calculated confidence intervals (i.e. $\bar{p}i \neq pi_o$, when $np>5$) pellet groups were considered to be associated with the variable category more ($\bar{p}i>pi_o$) or less ($\bar{p}i<pi_o$) frequently than expected by chance ($\alpha = .10$).

* probability of obtaining a greater X^2 value: $.05 \geq p > .01$

** $.01 \geq p > .005$.

*** $p \leq .005$.

Table 6. Distribution of Deer, Moose and Elk Winter Sign by Habitat Type, January - March, 1976.

Habitat type	Number of plots in habitat type		Deer: No. plots with sign Obs.	Deer: Exp.	Deer: X^2	Moose: No. plots with sign Obs.	Moose: Exp.	Moose: X^2	Elk: No. plots with sign Obs.	Elk: Exp.	Elk: X^2
Dwarf birch meadow	26	(5.3)[1]	0(0.0)	7	7.00	9(7.1)	7	0.57	2(14.3)	1	1.00
Sedge meadow	2	(0.4)	0(0.0)	1	1.00	0(0.0)	1	1.00	0(0.0)	0	0.00
Mixed shrub meadow	42	(8.5)	3(2.4)	11	5.82	23(18.2)	11	13.09	0(0.0)	1	1.00
Willow thicket	13	(2.6)	1(0.8)	3	1.33	8(6.3)	3	8.33	0(0.0)	0	0.00
Dry grassland	37	(7.5)	1(0.8)	9	7.11	7(5.6)	9	0.44	7(50.0)	1	36.00
Dwarf birch thicket	16	(3.2)	1(0.8)	4	2.25	10(7.9)	4	9.00	0(0.0)	0	0.00
Silverberry thicket	1	(0.2)	0(0.0)	0	0.00	1(0.8)	0	1.00	0(0.0)	0	0.00
Mesic pine woods	6	(1.2)	3(2.4)	2	0.50	0(0.0)	2	2.00	0(0.0)	0	0.00
Dry pine woods	71	(14.4)	19(15.1)	18	0.06	24(19.0)	18	2.00	1(7.1)	2	0.50
Black spruce woods	15	(3.0)	2(1.6)	4	1.00	3(2.4)	4	0.25	0(0.0)	0	0.00
White spruce woods	35	(7.1)	23(18.2)	9	21.78	5(4.0)	9	1.78	0(0.0)	1	1.00
Poplar woods	21	(4.2)	4(3.2)	5	0.20	1(0.8)	5	3.20	2(14.3)	1	1.00
Mixed woods	63	(12.8)	20(15.9)	16	1.00	16(12.7)	16	0.00	2(14.3)	2	0.00
Alder thicket	132	(26.8)	45(35.7)	34	3.56	19(15.2)	34	6.62	0(0.0)	4	4.00
Alpine fir woods	2	(0.4)	2(1.6)	1	1.00	0(0.0)	1	1.00	0(0.0)	0	0.00
Disturbed	2	(0.4)	0(0.0)	1	1.00	0(0.0)	1	1.00	0(0.0)	0	0.00
Forested watercourse	9	(1.8)	2(1.6)	2	0.00	0(0.0)	2	2.00	0(0.0)	0	0.00
	493	99.8	126		54.61***	126		53.05***	14		44.50***

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[1] Percent of total in parentheses. Expected number of plots = proportion of plots in habitat type x total number of plots with specific sign. Where observed distribution differs significantly from expected habitats contributing 10% or more to total X^2 are underlined.

*** probability of obtaining a greater X^2 value <.005.

Table 7. Distribution of Deer, Moose, Elk and Cattle Pellet Groups by Habitat Type, July-August, 1976.

	Number of plots in habitat type		Deer			Moose			Elk			Cattle		
			No. plots with pellet groups		x^2	No. plots with pellet groups		x^2	No. plots with pellet groups		x^2	No. plots with pellet groups		x^2
			Obs.	Exp.		Obs.	Exp.		Obs.	Exp.		Obs.	Exp.	
Dwarf birch meadow	12	(2.4)[1]	0(0.0)	4	4.00	6(4.3)	3	3.00	0(0.0)	1	1.00	0(0.0)	2	2.00
Sedge meadow	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Mixed shrub meadow	31	(6.3)	0(0.0)	10	10.00	16(11.4)	9	5.44	0(0.0)	2	2.00	9(9.8)	6	1.50
Willow thicket	8	(1.6)	0(0.0)	3	3.00	2(1.4)	2	0.00	0(0.0)	0	0.00	8(8.7)	1	49.00
Dry grassland	20	(4.1)	3(1.9)	7	2.28	1(0.7)	6	4.17	3(10.7)	1	2.00	14(15.2)	4	25.00
Dwarf birch thicket	11	(2.2)	0(0.0)	3	3.00	8(5.7)	3	8.33	0(0.0)	1	1.00	11(12.0)	2	40.50
Silverberry thicket	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesic pine woods	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Dry pine woods	100	(20.4)	48(30.2)	32	8.00	38(27.1)	29	2.79	11(39.3)	6	4.17	14(15.2)	19	1.32
Black spruce woods	12	(2.4)	2(1.3)	4	1.00	2(1.4)	3	0.33	0(0.0)	1	1.00	2(2.2)	2	0.00
White spruce woods	21	(4.3)	8(5.0)	7	0.14	6(4.3)	6	0.00	1(3.6)	1	0.00	3(3.3)	4	0.25
Poplar woods	19	(3.9)	5(3.1)	6	0.17	0(0.0)	5	5.00	3(10.7)	1	4.00	6(6.5)	4	1.00
Mixed woods	83	(16.9)	30(18.9)	27	0.33	19(13.6)	24	1.04	5(17.9)	5	0.00	15(16.3)	16	0.06
Alder thicket	161	(32.9)	61(38.4)	52	0.17	37(26.4)	46	1.76	5(17.9)	9	1.78	5(5.4)	30	20.83
Alpine fir woods	0	-	-	-	-	-	-	-	-	-	-	-	-	-
Disturbed	5	(1.0)	0(0.0)	2	2.00	1(0.7)	1	0.00	0(0.0)	0	0.00	4(4.4)	1	9.00
Forested watercourse	7	(1.4)	2(1.3)	2	0.00	4(2.9)	2	2.00	0(0.0)	0	0.00	1(1.1)	1	0.00
	490	99.8	159		34.09***	140		33.86***	28		16.95	92		150.46***

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[1] Percent of total in parentheses. Expected number of plots = proportion of plots in habitat type x total number of plots with specific pellet groups. Where observed distribution differs significantly from expected, habitats contributing 10% or more to total X^2 are underlined.

*** probability of obtaining a greater X^2 value <.005.

Table 8. Association Values of Horses and Wild Ungulates.

	Horses and Deer	Horses and Moose	Horses and Elk
All Seasons[1]			
No. plots (n)	490	490	490
Plots with horse pellet groups	417	417	417
Plots with species 2 pellet groups	159	140	28
Plots with both	138	126	26
Plots with neither	52	59	71
Coincidence index	0.479	0.452	0.117
Association index			
Horses with species 2	0.868	0.900	0.928
Species 2 with horses	0.331	0.302	0.062
Coefficient of association C_8	0.110	0.326	0.519
X^2 value	0.53	3.71	1.41
Winter (Jan-Mar)[2]			
No. plots (n)	493	493	493
Plots with horse sign	185	185	185
Plots with species 2 sign	126	126	14
Plots with both	31	32	12
Plots with neither	213	214	306
Coincidence index	0.199	0.206	0.121
Association index			
Horses with species 2	0.246	0.254	0.857
Species 2 with horses	0.168	0.173	0.059
Coefficient of association C_8	-0.344	-0.323	0.771
X^2 value	12.05**	10.62**	14.29***

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[1] Based on presence/absence of pellet groups in macroplots examined July-August, 1976.

[2] Based on presence/absence of sign in macroplots examined January-March, 1976.

* Probability of obtaining a greater X^2 value: $.05 \geq p > .01$.

** $.01 \geq p > .005$.

*** $p \leq .005$.

Table 9. Association Values of Horses and Cattle.[1]

Relationship	Horse: all seasons Cattle:summer (4 mo.)	Horse:spring Cattle:summer	Horse:fresh feces Cattle:fresh feces
No. plots (n)	490	490	490
Plots with horse pellet groups	417	132	28
Plots with cattle pellet groups	92	92	41
Plots with both	84	36	1
Plots with neither	65	302	422
Coincidence index	0.330	0.321	0.029
Association index			
Horses with cattle	0.913	0.391	0.024
Cattle with horses	0.201	0.273	0.036
Coefficient of association C_8	0.414	0.167	-0.560
X^2 value	3.44	8.56*	0.89

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[1] Based on presence/absence of pellet groups in macroplots examined July-August, 1976.

*Probability of obtaining a greater X^2 value <.05.

Table 10. Degree of Grazing Utilization at Deer Creek Flats, 11 October, 1976 and 1 June, 1977.

	ha. of habitat in use class (October)[1]					ha. of habitat in use class (June)					
	None-very light	Light	Safe	Heavy	Severe	None-very light	Light	Safe	Heavy	Severe	Total habitat (ha)
Dwarf birch meadow	1.2	0	0	0	0	1.2	0	0	0	0	1.2
Mixed shrub meadow	0	0	0	0.2	0	0.2	0	0	0	0	0.2
Willow thicket	0	0	17.5	0	0	17.5	0	0	0	0	17.5
Dry grassland	0	2.3	5.0	28.9	0.8	35.8	1.2	0	0	0	37.0
Dwarf birch thicket	0	[illegible]	0	14.8	0	14.8	0	0	0	0	14.8
Total area (ha)	1.2	2.3	22.5	43.9	0.8	69.5	1.2	0	0	0	70.7
% of total	1.7	3.2	31.8	62.1	1.1	98.3	1.7	0	0	0	

[1] none - very light = 0-15% of herbage biomass removed; light = 16-35% removed; safe = 36-65% removed; heavy = 66-80% removed; severe = >80% removed, plants grubbed, trampling damage evident.

Table 11. Selected Formulae and Statistical Notations Used in Analyses of Food Habits and Habitat Utilization.

Formula or Notation	Location in Text	Explanation
R^2	Chapter 6	Generalized squared multiple regression coefficient indicating the proportion of variance explained by the Multiple Classification Analysis model.
Eta^2 (MCA)	Chapter 6	One-way analysis of variance coefficient indicating the bivariate relationship (explained variance) between the dependent variable and each predictor variable.
$Beta^2$(MCA)	Chapter 6	Experimental statistic indicating the predictive power (explained variance) of each independent variable while controlling for all others.
Association Index	Chapter 7	Calculated as A/B = h/b and B/A = h/a, where A and B are two different species, a = the number of samples (plots) in which species A occurs, b = the number of samples in which species B occurs, and h = the number of samples in which A and B occur together.
Coincidence Index	Chapter 7	Calculated as $\frac{2h}{a+b}$; symbols same as for association indices.
Coefficient of association (C_8)	Chapter 7	Calculated as $C_8 = \frac{ad-bc}{\|ad-bc\|}\sqrt{\frac{Obs\ X^2 - Min\ X^2}{Max\ X^2 - Min\ X^2}}$ where: Species B: present, absent Species A: present — a, b absent — c, d
Kulcyznski's similarity coefficient	Chapter 7	Calculated as $C = \frac{2w}{(a+b)} \times 100$, where w is the sum of the lowest percentage composition values of species common to two diets, and a and b are the total percentage values of all species in each diet. As used here a and b both = 100 ; thus the formula reduces to C = w.
Spearman's rho (r_8)	Chapter 7	Rank order correlation coefficient varying from -1.0 to +1.0, and based on ranking the data rather than the use of absolute values.