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INTERIOR MOOSE STUDIES

by
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Volume I
Project Progress Report
Federal Aid in Wildlife Restoration
Projects W-17-4 and W-17-5, Jobs 1.3R, 1.4R and 1.8R

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JOB PROGRESS REPORT (RESEARCH)

State:	Alaska		
Cooperator:	John W. Coady		
Project Nos:	W-17-4 & W-17-5	Project Title:	Big Game Investigations
Job No:	1.3R	Job Title:	Evaluation of Moose Range and Habitat Utilization in Interior Alaska
Job No.:	1.4R	Job Title:	Evaluation of Moose Browse and Rumen Fermentation in Interior Alaska
Period Covered:	July 1, 1971 to June 30, 1973		

SUMMARY

This report describes major activities undertaken between February 1971 and June 1973. A vegetation type map of the Tanana Flats was completed in spring 1972. The vegetation, browse selection by moose and hares, and soil conditions in different habitats in the Tanana Flats and in the Elliott Creek burn on the Little Chena Drainage were described during summer 1972. Gross trends in moose food habits were examined by identifying the botanical composition of over 100 rumen content samples collected during four seasons near Fairbanks. Estimates of seasonal energy requirements and rates of rumen fermentation and food consumption by moose were obtained between May 1972 and April 1973 by measuring volatile fatty acid (VFA) production, total weight and water content, and chemical composition of rumen contents, and by extensively reviewing the literature. Nutritional status of moose and quality of moose range may be reflected by rates of rumen fermentation.

CONTENTS

OBJECTIVES

The objectives of this study are: 1) to construct a vegetation type map of the Tanana Flats; 2) to characterize botanical composition and soil conditions of major vegetation types in the Tanana Flats, and evaluate browse preference by both moose (*Alces alces*) and hares (*Lepus americanus*) in each habitat type; 3) to analyze the botanical composition of moose rumen contents collected near Fairbanks during different seasons; 4) to analyze the chemical composition of moose rumen contents collected during different seasons for components which reflect the relative digestability of the forage; and 5) to estimate the seasonal energy requirements and measure factors associated with rumen fermentation rates in moose which reflect nutritional status of the animal and quality of the food resource.

BACKGROUND

See Job 1.8R of this report.

PROCEDURES

Vegetation Type Map

A vegetation type map of the Tanana Flats was prepared from black and white aerial photographs (scale 1":1320') taken during the summers of 1968, 1969 and 1970. Identification of taxonomic units was based on stereoscopic examination of photographs and on field observation. Map units delineated on photographs were transferred using a light table to USGS topographic maps printed on photographic drafting film. Blue-line copies of the finished type map were printed from the film.

Several qualifications regarding the type map should be noted. Shapes of map units may differ from their appearance in the field since distinct boundaries between vegetation types seldom exist in nature. Aerial photographs were taken during relatively wet (June) and dry (August) months over three years, and therefore water levels in ponds and sloughs may differ from their present condition. In particular, 1968 photographs may indicate above normal water levels due to previous flooding in 1967. Aberrations in photographs may slightly distort true shapes of particular map units, although positions relative to surrounding units are correct.

In a project of this magnitude, using black and white photographs, errors in photo interpretation are unavoidable. Some taxonomic units have undoubtedly been incorrectly identified, especially when the interpreter was required to classify certain mixed vegetation stands based on dominant species. However, these errors are believed to represent only a small fraction of all map units and should not significantly affect the usefulness of the map.

Five major taxonomic units were identified:

Herbaceous Bog: designated by number "1" (blue), and consisting of marshes, shallow ponds and their aquatic margins, and shallow streams where movement of water is slow enough to support emergent vegetation.

Heath Bog: designated by number "2" (white), and consisting primarily of low shrubs and widely scattered trees. Scattered patches of shrub birch (*Betula glandulosa*), paper birch (*Betula papyrifera*), willow, spruce, and tamarack (*Larix laricina*) also occur.

Tall Shrub: designated by number "3" (yellow), and consisting primarily of willow and alder.

Deciduous Tree: designated by number "4" (red), and consisting primarily of paper birch, quaking aspen (*Populus tremuloides*), and cottonwood (*Populus balsamifera*).

Conifer Tree: designated by number "5" (green), and consisting primarily of black spruce (*Picea mariana*), white spruce (*P. glauca*) and tamarack.

Two burns were outlined on the map. One burn of approximately 200 km^2 on the east side of the Flats and south of Salchaket Slough occurred in 1957. The second burn of approximately 25 km^2 near the Blair Lakes occurred during summer 1969. A solid line indicates known boundaries, while a dotted line indicates approximate boundaries of the burns.

Unclassified area is designated by "uc" and consists primarily of deep lakes and steep rocky slopes.

Botanical Composition and Soil Conditions

Site characteristics and plant associations in six heath bog, six tall shrub, two deciduous tree and three conifer tree habitats on the Tanana Flats, and in two tall shrub and one heath bog habitats in the Elliott Creek burn in the upper Little Chena River drainage were described using a sampling scheme developed by Ohmann and Ream (1971). The scheme includes determining the approximate age of the stand by counting annual growth rings of the largest trees, recording species, size, and density of trees and shrubs, and determining the species and percent coverage of low growing plants. Depth to permafrost, moisture content, and mineral composition of the soil in each stand was also recorded.

Utilization of browse species by moose and hares in three heath bog, five tall shrub, and one deciduous tree stand in the Tanana Flats was evaluated using range survey techniques similar to those described by Cole (1963). Sixty to 200 individual plants of each major browse species in a stand were sampled using closest plant sampling techniques, and data were recorded on Alaska Department of Fish and Game Browse Survey forms (Fig. 1). A numerical index of one to three was used to indicate age class, where one indicates seedlings less than four and one-half feet (137 cm) high, two indicates saplings greater than four and one-half feet (137 cm) high but less than two inches (5 cm) in diameter at breast height (dbh), and three indicates trees greater than two inches (5 cm) dbh. Canopy range is the height range above ground from the first lateral branch to the top of the plant. Browse range for moose and for hares is the height range above ground of browsing by each species during the previous year. A numerical index of 0 to 4 was used to indicate browse class for moose and for hares, where 0 indicates no browsing during the previous year, and 1, 2, and 3 indicate 1-33 percent, 34-66 percent, and 67-100 percent, respectively, of the lateral branches within the browse range for moose and hares browsed during the previous year. A numerical index of 0 to 3 was used to indicate barking by hares, where 0 indicates no barking, and 1, 2, and 3 indicate a subjective evaluation of light, moderate, and severe (or girdled) barking, respectively.

Botanical Composition of Rumen Contents

In this preliminary study, no attempt was made to standardize the quantity of material collected from individual moose stomachs. A one-quart subsample was randomly collected from each sample and analyzed. This was done without knowing whether the one-quart subsample was representative of the gallons of material normally in a moose stomach.

The one-quart subsamples were emptied into a gang of sieves and washed with fresh water. Material retained by a 6.35 mm mesh sieve was separated by plant parts (twigs, fruit, leaves, etc.) to species where possible. This mesh sieve was used without determining its effectiveness in retaining food items. Food items that could not be readily identified to species were grouped into general categories of foods (e.g., leaves, twigs, fruits). All data were coded and recorded for direct automatic data processing, using summary programs developed by Cushwa et al. (1973). Frequency of occurrence, the number of samples each food item occurred

Figure 1. Alaska Department of Fish and Game browse survey form. (See text for description of figure.)

Stand ____________ Area ______________________________ Date ____________

Veg Type ______________________________________ Observer ____________

Remarks ____

Sp	Age Cl	Canopy Range	Moose Browse Range	Moose Browse Class	Hares Browse Range	Hares Browse Class	Barking

in, was calculated and reported. Neither volume nor importance value were reported because of the large number of factors which influence volume calculations over which an investigator has no control.

Chemical Composition of Moose Rumen Contents, Energy Requirements and Rumen Fermentation in Moose

Procedures have been described in two previous publications (Coady and Gasaway, 1972; Gasaway and Coady, 1973), and will not be reported here.

FINDINGS AND CONCLUSIONS

Vegetation Type Map

Approximately seven man-months of labor, $1,000 in materials, and 20 hours of air charter were devoted to this project. The type map was completed in April 1972 and is located in the Fairbanks Game Division office.

Botanical Composition and Soil Composition

The regional vegetation of northern boreal forests in Alaska, referred to by the Russian term "taiga," consists primarily of low, open-growing spruce forests, occasional stands of well developed spruce and hardwoods, and frequent tracts of treeless or sparsely timbered bogs. On south facing slopes and well drained sites the forest consists of white spruce and hardwood stands of quaking aspen and paper birch, while on cool, north facing slopes and poorly drained lowlands climax vegetation is generally black spruce, tamarack and bogs.

Extensive lowlands, locally referred to as "flats" or "muskeg," cover broad alluvial plains throughout interior Alaska, from the south slope of the Brooks Range to the southern coastal forests, and from the Alaska-Canada border nearly to the Bering and Chukchi seas (Wahrhaftig, 1965; Johnson and Hartman, 1969). Approximately 30 percent of this area is forested, while the remaining land consists of bogs, shrub thickets, and alpine tundra (Viereck, in press). Surface vegetation patterns are closely related to topography, drainage, presence or absence of permafrost and past forest fire history.

Surface features in lowland areas frequently include extensive flood plains with little relief, meander scars and oxbow lakes, terraces, and alluvial outwash deposits (Black, 1958; Wahrhaftig, 1965). Loess, sand, and outwash of Quaternary age, organic deposits formed in bogs, and recently deposited alluvium frequently overlay a micaceous schist bedrock (Dutro and Payne, 1957; Viereck, in press). Forest soils are generally shallow with poorly developed profiles. Piedmont streams, many of glacial origin, change from braided to tightly meandering tributaries as they enter lower elevations.

Permafrost, or permantly frozen ground, is a widespread phenomenon throughout much of the Alaskan taiga. Between the Alaska Range and the Brooks Range permafrost occurs in all areas except for south facing slopes and recently deposited alluvium, while south of the Alaska Range permafrost is sporadic in occurrence, and is found only in bogs and on north facing slopes (Viereck, in press). An important influence of permafrost on vegetation patterns results from the frozen impervious substrate which prevents lateral movement and downward percolation of soil water (Benninghoff, 1952). Thus, permafrost results in saturated soils or standing water throughout much of the taiga.

Regional distributions of vegetation types and permafrost in lowland areas are inextricably interrelated. Insulation provided by black spruce and bog vegetation prevents melting of permafrost during summer months, while permafrost governs climax vegetation during the course of succession (Benninghoff, 1952; Drury, 1956). Disjunct stands of shrubs and deciduous trees scattered throughout Alaskan lowlands are frequently the result of burning of climax vegetation, which results in lowering of permafrost tables, and formation of a substrate temporarily favorable to subclimax vegetation (Viereck, pers. comm.).

Geologically and vegetatively the flats of interior Alaska consist of treeless or nearly treeless bogs and more or less forested areas surrounding or occurring within the bogs. Drury (1956) and Viereck (1970a, 1970b) have discussed lowland forest succession and origin of bogs along braided or meandering streams in interior Alaska. Freshly deposited alluvium is first colonized by willow (*Salix* spp.) or alder (*Alnus* spp.), and later by balsam poplar (*Populus balsamifera*). An understory of low shrubs and horsetails (*Equisetum* spp.) along with white spruce seedlings may develop beneath the poplars. As white spruce matures an organic ground layer of mosses, herbs, and low shrubs develops, resulting in permafrost formation and a substrate more favorable to black than to white spruce after 200 to 300 years.

Local disturbance of the insulating organic layer in black spruce forests may result in shallow thawing of the permafrost, water accumulation, and bog formation (Benninghoff, 1952; Drury, 1956). Development and expansion of bogs are frequently indicated by angular growth of trees due to soil instability. The resulting vegetation over extensive lowland areas becomes an intricate mosaic of black spruce forests, bogs, shrub and hardwood sub-climax communities, as well as numerous intermediate stages.

Floristics of northern lowlands have been studied by several workers including Ritchie (1959) and Larsen (1965) in subarctic Canada, Hanson (1951, 1953) in western Alaska, Drury (1956) in the upper Kuskokwim River region of Alaska, and Johnson and Vogel (1966) in the Yukon Flats of Alaska. In addition, Anderson (1959), Hultén (1968), and Viereck and Little (1972) have described the circumpolar distribution of trees, shrubs, and herbs found in Alaska.

Recent alluvial deposits on lowland floodplains throughout interior Alaska are generally colonized first by horsetails (*Equisetum arvense*), grasses (*Calamagrostis canadensis*), willows (*Salix alaxensis*, *S.*

arbusculoides, S. bebbiana), and alders (*Alnus tenuifolia*). As balsam poplar and later, white spruce or mixed white spruce-paper birch become established, herbs such as wintergreen (*Pyrola* spp.) and fireweed (*Epilobium angustifolium*), and low shrubs such as roses (*Rosa acicularis*), currants (*Ribes triste*), and high bush cranberry (*Viburnum edule*) appear. Accompanying the replacement of white spruce and paper birch by black spruce is a gradual increase in the sphagnum moss cover (*Sphagnum capillaceum, S. girgensobnii, S. fuscus*, and *S. rubellum*) and growth of a dense shrub layer of bog blueberry (*Vaccinium uliginosum*), Labrador tea (*Ledum groenlandicum, L. decumbens*) and birch (*B. glandulosa, B. nana*). A dense ground cover of sphagnum and low shrubs, along with willows (*S. pulchra, S. bebbiana*), and widely spaced paper birch, black spruce, or tamarack may replace stands of black spruce. The recurring process of bog formation and subsequent reforestation has been described in detail by Drury (1956).

All stages of bog development, from open water to black spruce forest are found in Alaskan lowlands. Sphagnum mosses, sedges (*Carex* spp. and *Eriophorum* spp.) and pond lilies (*Nuphar polysepalum* and *Nymphaea tetragona*) are common in open water, while other sedges (*C. aquatilis*) and horsetails (*E. fluviatile, E. palustre*) are found along margins of ponds and shallow flowing water. Bog shrubs, such as bog rosemary (*Andromeda polifolia*), Labrador tea, bog blueberry (*Vaccinium uliginosum*), swamp cranberry (*Oxycoccus microcarpus*), leather-leaf (*Chamaedaphne calyculata*), cloudberry (*Rubus chamaemorus*), dwarf birch (*Betula nana*) and shrub birch along with sphagnum mosses are common on moist ground.

The vegetation of the Tanana Flats, a 1300 square-mile alluvial lowland lying immediately south of Fairbanks, Alaska, has been recently studied (Coady and Simpson, in prep.). The area is bounded on the south by the rugged Alaska Range, on the north and east by the glacial Tanana River, and on the west by the glacial Wood River, and is part of the much larger Tanana-Kuskokwim physiographic province described by Wahrhaftig (1965).

Surface deposits from glacial streams flowing into the Tanana Flats on the south form a belt of broad coalescing fans that grade from coarse sand and gravel near the mountains to fine sand and silt at lower elevations. Material manteling the eastern and northern portion of the Flats has been deposited by the Tanana River (Andreasen, et al., 1964). Except for scattered low hills of granite, ultramafic rocks, and possibly Precambrian schist, the Flats are an area of little relief (Andreasen, et al., 1964). The entire region is underlain by permafrost (Black, 1958; Wahrhaftig, 1965), and drainage is poor, resulting in numerous small, shallow ponds, extensive bogs, and meander scars.

Herbaceous bogs occur primarily in the northern portion of the Flats and cover approximately 7 percent of the area. Vegetation is dominated by emergent species, and live trees and shrubs are totally absent (Table 1). Stagnant or slowly flowing water depths vary seasonally, although they range from several inches to several feet after spring run-off. Bog bottoms consist of a meter or more of dead and

Table 1. Floristics of herbaceous bog community; Tanana Flats, Interior Alaska.

Trees	Tall Shrubs	Low Shrubs	Herbaceous
None	None	None	*Potentilla palustris*
			Gramina spp.
			Eriophorum spp.
			Equisetum hiemale var. *californicum*
			Equisetum fluviatile
			Equisetum palustre
			Iris setosa subsp. *interior*
			Ranunculus Gmelini subsp. *Purshii*
			Ranunculus sp.
			Sanguisorba officinalis
			Petasites frigidus
			Petasites sagittatus
			Valeriana capitata
			Caltha palustris subsp. *arctica*
			Cardamine sp.
			Rumex sp.
			Carex spp.
			Potentilla spp.
			Utricularia vulgaris subsp. *macrorhiza*
			Typha latifolia
			Nymphae tetragona
			Chrysoplenium tetrandrum
			Hippuris vulgaris
			Utricularia minor

decaying vegetation, and permafrost depths are presumably well below the upper surface of organic material.

Heath bogs are widespread throughout the Flats, occupying approximately 40 percent of the land. Dominant vegetation consists of mosses and shrubs, although scattered trees and various herbs rooting on precipituous sedge hummocks are common (Table 2). Both mineral soil and permafrost tables occur within a meter of the surface, although seasonal thaw may extend to greater depths in some areas. Soil moisture is high and shallow standing water is common in many areas.

Tall shrub communities occur throughout approximately 10 percent of the Flats but are most frequent along rivers, streams, and sloughs and along margins of ponds and meander scars. Recent wildfire burns may also support tall shrub communities. Vegetation ranges from pure to mixed stands of willow and alder with a dense understory of mosses, herbs, and low shrubs in poorly drained sites (Table 3). Exposed mineral soil, low moisture content, and absence of permafrost are common on recent alluvial deposits, while a thick organic layer, impeded drainage, and high permafrost tables are found in other areas.

Discontinuous pure or mixed stands of paper birch, quaking aspen, or balsam poplar occur throughout approximately 8 percent of the Flats, particularly on slightly elevated land and on coarse river alluvium. Understory vegetation ranges from a dense herbaceous cover in cottonwood stands to mixed herbs and low shrubs in aspen and birch stands. Scattered willows and alders are common among cottonwood communities (Table 4). Well drained mineral soil lies close to the surface and permafrost tables are deep or nonexistent.

Scattered conifer stands in the western portion and extensive low, dense black spruce and occasional tamarack forests in the southern area cover approximately 35 percent of the Flats. Mature white spruce forests with a ground vegetation of low shrubs and mosses are common near streams, while black spruce forests underlain by a dense mat of moss, herbs, and low shrubs grow in poorly drained areas (Table 5). Soil organic layer, moisture content, and permafrost tables range from low in young white spruce stands to high in black spruce and tamarack stands.

Moose Use

The seasonal importance to moose of local flatlands south of the Brooks Range is diverse. Lowland areas, by virtue of their abundant herbaceous vegetation, are generally important summer ranges for moose of all sex and age groups. Furthermore, seclusion provided by numerous dense stands of tall shrubs and trees frequently creates favorable calving areas for large numbers of moose (Bishop, 1969).

On the Tanana Flats moose commonly feed in herbaceous bogs from spring thaw to late summer. However, greatest use of this habitat appears to be during early to midsummer. During late summer moose may feed more frequently on herbaceous and woody browse in heath bog and tall shrub communities.

Table 2. Floristics of heath bog community; Tanana Flats, Interior Alaska.

Trees	Tall Shrubs	Low Shrubs	Herbaceous
Betula papyrifera subsp. *humilis*	*Salix bebbiana*	*Salix brachyocarpa* subsp. *niphoclada*	*Rubus chamaemorus*
Picea glauca	*Salix glauca*	*Salix myrtillifolia*	*Potentilla palustris*
Picea mariana	*Salix arbusculoides*	*Betula nana*	*Eriophorum* spp.
Larix laricina var. *alaskensis*	*Salix planifolia* subsp. *pulchra*	*Ledum palustre* subsp. *decumbens*	*Gramina* spp.
	Betula papyrifera x *glandulosa*	*Ledum palustre* subsp. *groenlandicum*	*Rubus arcticus*
		Vaccinium uliginosum subsp. *alpinum*	*Stellaria* spp.
		Vaccinium vitis-idaea subsp. *minus*	*Epilobium angustifolium* subsp. *angustifolium*
		Andromeda polifolia	*Cornus canadensis*
		Myrica gale var. *tomentosa*	*Pyrola* spp.
		Potentilla fruticosa	*Equisetum pratense*
		Chamaedaphne calyculata	*Equisetum variegatum*
		Linnaea borealis	*Equisetum arvense*
		Arctostaphylos uva-ursi	*Equisetum scirpoides*
		Arctostaphylos rubra	*Equisetum fluviatile*
		Rosa acicularis	*Pedicularis labradorica*
		Oxycoccus microcarpus	*Saussurea* sp.
			Mertensia paniculata var. *paniculata*
			Mertensia sp.
			Solidago sp.
			Lupinus arcticus
			Iris setosa subsp. *interior*
			Sanguisorba officinalis
			Petasites frigidus
			Trientalis europea subsp. *arctica*
			Ranunculus sp.
			Spiranthes Romanzoffiana

Table 3. Floristics of tall shrub community; Tanana Flats, Interior Alaska.

Trees	Tall Shrubs	Low Shrubs	Herbaceous
Populus balsamifera subsp. balsamifera	Salix arbusculoides	Rosa acicularis	Gramina spp.
Picea glauca	Salix bebbiana	Potentilla fruiticosa	Carex spp.
Picea mariana	Salix monticola	Ledum palustre subsp. groenlandicum	Equisetum arvense
Betula papyrifera subsp. humilis	Salix glauca	Vaccinium uliginosum subsp. alpinum	Equisetum palustre
	Salix lanata subsp. richardsonii	Vaccinium vitis-idaea subsp. minus	Equisetum pratense
	Salix lasiandra	Arctostaphylos rubra	Equisetum fluviatile
	Salix hastata	Arctostaphylos uva-ursi	Equisetum scirpoides
	Salix planifolia subsp. pulchra	Ribes hudsonianum	Potentilla spp.
	Salix novae-angliae	Ribes triste	Achillea siberica
	Alnus crispa subsp. crispa	Rubus idaeus subsp. melanolasius	Rubus arcticus
	Alnus incana subsp. tenuifolia	Viburnum edule	Stellaria spp.
	Betula papyrifera x glandulosa	Linnaea borealis	Pyrola secunda
		Myrica gale var. tomentosa	Pyrola spp.
		Oxycoccus microcarpus	Epilobium angustifolium subsp. angustifolium
			Cornus canadensis
			Erigeron sp.
			Trientalis europaea subsp. arctica
			Petasites saggitatus
			Petasites frigidus
			Moneses uniflora
			Aster sp.
			Galium boreale
			Galium trifidum subsp. trifidum
			Fragaria virginiana subsp. glauca
			Mertensia paniculata var. paniculata
			Rubus chamaemorus
			Parnassia palustris subsp. neogaea

Table 4. Floristics of deciduous tree community; Tanana Flats, Interior Alaska.

Trees	Tall Shrubs	Low Shrubs	Herbaceous
Populus balsamifera subsp. *balsamifera*	*Alnus crispa* subsp. *crispa*	*Rosa acicularis*	*Stellaria spp*.
Populus tremuloides	*Alnus incana* subsp. *tenuifolia*	*Ribes triste*	*Pyrola secunda*
Betula papyrifera subsp. *humilis*	*Salix alexensis*	*Ribes* sp.	*Epilobium angustifolium*
Picea glauca	*Salix interior*	*Rubus idaeus* subsp. *melanolasius*	*Gramina* spp.
Picea mariana	*Salix lanata* subsp. *richardsonii*		*Equisetum silvaticum*
	Salix novae-angliae		*Equisetum palustre*
	Salix planifolia subsp. *pulchra*		*Equisetum arvense*
			Equisetum pratense
			Polygonum alpinum
			Mertensia paniculata var. *paniculata*
			Trientalis europea subsp. *arctica*
			Thalictrum sparsiflorum
			Galium boreale
			Artemsia sp.

Table 5. Floristics of conifer tree community; Tanana Flats, Interior Alaska.

Trees	Tall Shrubs	Low Shrubs	Herbaceous
Picea glauca	*Alnus crispa* subsp. *crispa*	*Viburnum edule*	*Equisetum arvense*
Picea mariana	*Alnus incana* subsp. *tenuifolia*	*Rosa acicularis*	*Equisetum pratense*
Larix laricina var. *alaskensis*	*Salix alexensis*	*Ribes hudsonianum*	*Equisetum fluviatile*
Betula papyrifera subsp. *humilis*	*Salix bebbiana*	*Ribes* sp.	*Equisetum palustris*
Populus balsamifera subsp. *balsamifera*	*Salix glauca*	*Rubus idaeus* subsp. *melanolasius*	*Equisetum scirpoides*
	Salix arbusculoides	*Empetrum hermaphroditum* subsp. *nigrum*	*Cornus canadensis*
		Arctostaphylos uva-ursi	*Cornus stolonifera*
		Vaccinium vitis-idaea subsp. *minus*	*Gramina* spp.
		Linnaea borealis	*Trientalis europea* subsp. *arctica*
			Stellaria spp.
			Mertensia paniculata
			Rubus arcticus
			Pyrola spp.
			Geocaulon lividum
			Potentilla spp.
			Epilobium angustifolium subsp. *angustifolium*
			Goodyera repens
			Galium sp.
			Thalictrum sparsiflorum
			Galium trifidum subsp. *trifidum*
			Cypripedium guttatum subsp. *guttatum*
			Platanthera obtusata
			Listera borealis

Use of different lowland areas by moose during fall and winter depends largely upon the availability of adequate quality winter browse. Following the 600 square-mile 1947 burn on the Kenai Peninsula lowlands, white birch regrowth created major winter range for large numbers of moose. Spencer and Chatelain (1953) discussed other lowland areas in Alaska which have become important winter moose range following fires.

Generally, the Tanana Flats do not seem to be good winter moose range, and large scale emigration of animals during fall and early winter supports this conclusion. While several species of willows are widely scattered throughout portions of the Flats, they are often old and extremely decadent. Apparently, changes in local edaphic factors, such as soil temperature, moisture, and organic content, due to the dynamic nature of bog formation, frequently create substrates unfavorable to continued growth of tall shrub and other sub-climax communities. However, vigorous growth of shrubs occurs on well drained recent deposits along some streams, and these areas may support large numbers of moose during winter.

The effects of fire in creating winter moose browse on the Tanana Flats have been variable. Although much of the Flats has burned within the past 50-100 years, early seral stages have frequently not developed or have been of short duration and consequently of minor importance to moose. However, a 75 square-mile burn in 1957 on the east side of the Flats has resulted in exposure of mineral soil and considerable reduction in permafrost levels in many areas. Consequently, much of the area is well drained and supports moderately dense, mixed stands of willow (*Salix glauca, S. arbusculoides, S. bebbiana*), poplar (*Populus tremuloides, P. balsamifera*), and paper birch. For the past several years the area has supported a sizable number of moose during winter. Other recent burns of considerably smaller size have provided limited winter browse to a few animals.

A more complete description of the vegetation of the Tanana Flats will be presented in a future publication (Coady and Simpson, in prep.).

Data from the moose and hare browse study have not been fully summarized, and therefore, no quantitative results are available. However, observations leave little doubt that deciduous shrubs and trees preferred by moose are also used extensively by hares. These species include willows (*Salix* spp.), paper birch, quaking aspen and cottonwood. The portion of the plant browsed by the two animals differs, of course, depending largely on snow depths. The only conifer trees occurring in interior Alaska, tamarack, black spruce and white spruce, are used extensively by hares and rarely by moose.

Botanical Analysis of Moose Rumen Contents

During the winter of 1970-71 (September through May) the Fairbanks weather station recorded the heaviest total snowfall (307 cm) since it began keeping records during the winter of 1933-34. Maximum snow depths on the ground exceeded 101 cm in January. Examination of 44 samples of moose stomach contents collected during this period revealed a diet primarily of deciduous woody plants (Table 6). Of the identified food items, twigs of willow, birch, aspen, and alder, respectively, were most frequently eaten. Other foods, ranked by frequency, included fruit (catkins, seeds, or flower parts), dry aspen leaves, spruce twigs, willow fruit, and dry leaves. A small quantity of unidentified herbaceous material was found in one sample.

During the winter of 1971-72, total snowfall was 229 cm in January. Examination of 10 samples collected during this time indicated that the diet again consisted primarily of deciduous woody materials (Table 7). Of the identified food items, willow twigs, birch twigs, birch fruit, alder, aspen, and cottonwood twigs, alder fruit, followed by dry birch leaves, green spruce needles, willow fruit and dry leaves, were the most frequently eaten foods. One sample contained a small quantity of unidentified sedges. The record snowfall during the winter of 1970-71, when 140 cm more snow than fell during 1971-72, did not influence the frequency of occurrence of major food items found in stomach contents of moose. It is also interesting to note that during periods of greater than normal snowfall, when moose died from malnutrition, only one of the 44 samples contained spruce. It therefore appears that spruce does not constitute a major portion of the moose's winter diet near Fairbanks, Alaska. It also appears that spruce is not used as an emergency food by moose.

During the spring of 1971, 15 samples of moose stomach contents were collected near Fairbanks. Analysis of these samples revealed that hardened twigs of willow and birch were most frequently eaten (Table 8). Other foods, in descending order, were fruit and dry willow leaves, hardened aspen twigs, green willow leaves, hardened alder twigs, sedges, hardened *Vaccinium* twigs, and succulent willow twigs.

Six samples collected during spring 1972 were analyzed. Hardened willow and birch twigs were found in all samples, and birch fruit and hardened alder twigs occurred in half the samples (Table 9).

Seven samples were collected during the fall of 1971. Hardened twigs of willow and birch were followed in descending order by birch fruit, dry and green willow leaves, hardened aspen twigs, green birch leaves, hardened alder twigs, and *Equisetum* (Table 10).

During the fall of 1972, 15 samples from the Fairbanks area contained hardened willow and birch twigs, dry leaves of willow and birch, hardened twigs of cottonwood and alder, and *Equisetum* (Table 11).

Ten samples were collected during the summer of 1972. All samples contained green willow leaves, while succulent willow twigs and *Equisetum* were found in nine samples. Six samples contained green shrub birch leaves, five grass, and four hardened birch twigs (Table 12).

A more complete analysis and discussion of the data has been recently completed (Cushwa and Coady, 1973), and will not be presented here.

Table 6. Moose stomach contents analysis from Game Management Unit 20A and 20B during winter 1970-71. Sample size = 44.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Dry leaves	2.3
	Hardened twigs	56.8
Birch	Hardened twigs	70.5
Spruce sp.	Hardened twigs	2.3
Tall Shrubs		
Willow sp.	Fruit	2.3
	Dry leaves	2.3
	Hardened twigs	86.4
Alder	Fruit	4.6
	Hardened twigs	25.0
Unidentified		
	Hardened stems	93.2
	Dry leaves	31.8
	Green leaves	2.3
	Dead stems / bark	34.1
Herbaceous		
Unidentified		
	Dry stems and leaves	2.3

[1] Relative frequency of occurrence.

Table 7. Moose stomach contents analysis from Game Management Unit 20A and 20B during winter 1970-71. Sample size = 10.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Hardened twigs	20.0
Birch	Fruit	70.0
	Dry leaves	10.0
	Hardened twigs	90.0
Cottonwood	Hardened twigs	20.0
Spruce sp.	Green needles	10.0
Tall Shrubs		
Willow sp.	Fruit	10.0
	Dry leaves	10.0
	Hardened twigs	10.0
Unidentified		
	Hardened twigs	100.0
	Dry deciduous leaves	40.0
	Green deciduous leaves	5.0
	Dead twigs / bark	10.0
Herbaceous		
Unidentified		
	Sedge	10.0

[1] Relative frequency of occurrence.

Table 8. Moose stomach contents analysis from Game Management Unit 20A during spring 1971. Sample size = 15.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Succulent twigs	6.7
	Hardened twigs	20.0
Birch	Hardened twigs	80.0
Spruce sp.	Hardened twigs	6.7
Tall Shrubs		
Willow sp.	Fruit	26.7
	Green leaves	20.0
	Dry leaves	26.7
	Succulent twigs	13.3
	Hardened twigs	86.7
Alder	Fruit	6.7
	Hardened twigs	13.3
Shrub birch	Hardened twigs	6.7
Low Shrubs		
Vaccinium sp.	Green leaves	6.7
	Hardened twigs	13.3
Unidentified	Hardened stems	100.0
	Dry deciduous leaves	13.3
	Dead stems / bark	33.3
Herbaceous		
Unidentified	Grass	6.7
	Mushrooms	6.7
	Sedges	13.3

[1] Relative frequency of occurrence.

Table 9. Moose stomach contents analysis from Game Management Unit 20A during spring 1972. Sample size = 6.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Hardened twigs	16.7
Birch	Fruit	50.0
	Hardened twigs	100.0
Cottonwood	Hardened twigs	16.7
Tall Shrubs		
Willow sp.	Hardened twigs	100.0
Alder	Fruit	16.7
	Dry leaves	16.7
	Hardened twigs	50.0
Unidentified		
	Hardened twigs	100.0
	Green deciduous leaves	16.7

[1] Relative frequency of occurrence.

Table 10. Moose stomach contents analysis from Game Management Unit 20A and 20B during fall 1971. Sample size = 7.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Hardened twigs	28.6
Birch	Fruit	42.9
	Green leaves	28.6
	Dry leaves	14.3
	Hardened twigs	71.4
Tall Shrubs		
Willow sp.	Green leaves	42.9
	Dry leaves	42.9
	Hardened twigs	85.7
Alder	Hardened twigs	28.6
Shrub birch	Dry leaves	14.3
	Hardened twigs	14.3
Low Shrubs		
Vaccinium sp.	Green leaves	14.3
Unidentified		
	Hardened stems	100.0
	Dry leaves	14.3
	Green leaves	28.6
Herbaceous		
Identified		
Equisetum		28.6
Unidentified	Dry stems and leaves	14.3
	Sedges	14.3
	Fruit	14.3
	Grass	14.3

[1] Relative frequency of occurrence.

Table 11. Moose stomach contents analysis from Game Management Unit 20A and 20B during fall 1972. Sample size = 15.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Dry leaves	13.3
	Hardened twigs	6.7
Birch	Green leaves	6.7
	Dry leaves	20.0
	Hardened twigs	66.7
Cottonwood	Green leaves	6.7
	Hardened twigs	20.0
Spruce sp.	Dry needles	6.7
Larch	Hardened twigs	6.7
Tall Shrubs		
Willow sp.	Green leaves	6.7
	Dry leaves	40.0
	Hardened twigs	86.7
Shrub birch	Dry leaves	13.3
Alder	Fruit	6.7
	Green leaves	6.7
	Dry leaves	6.7
	Hardened twigs	20.0
Low Shrubs		
Vaccinium vitis-idaea	Green leaves	6.7
Ledum	Green leaves	6.7
Arctostaphylos	Dry leaves	6.7
Unidentified		
	Hardened twigs	86.7
	Dry deciduous leaves	20.0
	Green deciduous leaves	53.3
Herbaceous		
Identified		
Equisetum		20.0
Unidentified		
	Grass	6.7
	Mushrooms	13.3

[1] Relative frequency of occurrence.

Table 12. Moose stomach contents analysis from Game Management Unit 20A during summer 1972. Sample size = 10.

Food Item	Plant Part	Frequency[1]
Woody		
Identified		
Trees		
Aspen	Green leaves	10.0
Birch	Succulent twigs	10.0
	Hardened twigs	40.0
Tall Shrubs		
Willow sp.	Green leaves	100.0
	Succulent twigs	90.0
Shrub birch	Green leaves	60.0
	Dry leaves	10.0
	Succulent twigs	10.0
Alder	Green leaves	10.0
	Dry leaves	10.0
	Succulent twigs	10.0
Salix pulchra	Green leaves	
Unidentified	Succulent twigs	20.0
	Green deciduous leaves	20.0
	Dead twigs / bark	10.0
Herbaceous		
Identified		
Equisetum		90.0
Unidentified		
	Grass	50.0

[1] Relative frequency of occurrence.

Chemical Composition of Moose Rumen Contents and Energy Requirements and Rumen Fermentation in Moose

Findings have been reported in two previous publications (Coady and Gasaway, 1972; Gasaway and Coady, 1973), and will not be presented again at this time. However, an abstract of the most recent publication (Gasaway and Coady, 1973) is given below:

A review of seasonal energy requirements and utilization of food by moose, with reference to other wild and domestic species, is presented. Energy requirements are difficult to estimate because no metabolic studies have been conducted with moose and comparative data from other wild and domestic species differ widely. It is assumed that basal metabolic rate (BMR) conforms to the empirical relationship of weight to metabolic rate, where BMR = $70^{.75}$, and maintenance demands approximate 1.7 times BMR. Energy requirements of female moose begin to increase significantly in March due to pregnancy and reach a peak of three to four times BMR in June, due to lactation and lipogenesis.

Major seasonal differences in rumen contents and estimates of food consumption by moose are described. Rumen fill in cow moose was greatest during early winter, lowest during late spring, and intermediate during summer. Percent dry matter was lowest during summer and highest during winter. Washed rumen contents were higher in crude protein and lower in acid detergent fiber and lignin during summer than during winter, reflecting the superior quality of summer forage. Estimates of food intake by moose vary greatly in the literature, although there is considerable evidence indicating that a greater quantity of food is consumed during summer than during winter. Dry matter consumed by adult females was estimated to be three to four times greater during summer than during winter. Increased rumen fill and decreased food intake during winter apparently result from slow passage of low quality food which restricts additional food intake, and from voluntary reduction of forage consumption.

Volatile fatty acids (VFA) produced by rumen microbes by fermentation of dietary carbohydrates and proteins constitute approximately 57 percent of the digestible energy of ruminants. VFA production, which is directly related to food quality, was determined seasonally on free-ranging moose in interior Alaska using the "zero time rate" method. Production rates varied from a mean low of 18 eq VFA/ml rumen liquor/hr during winter to 60 eq VFA/ml rumen liquor/hr during summer.

Moose undergo a large seasonal change in body weight which corresponds closely to seasonal rates of VFA energy production. Metabolizable energy (ME), calculated from estimated VFA production, increased from 7,300 kcal/day in females during winter to 20,900 kcal/day in lactating moose during summer. It was estimated that approximately 6,000 kcal/day of ME was required for BMR. During winter an estimated average of 3,900 kcal/day was obtained from catabolism of fat and protein reserves to meet the energy requirements not provided by forage, while during summer 7,600 kcal/day of fat and protein were deposited.

A review of effects of malnutrition on rumen function shows that a decrease in food quantity or quality depresses microbial populations and rates of fermentation.

The value and practical application of using various parameters of rumen function to evaluate nutritional status of ruminants and quality of the habitat are discussed.

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LITERATURE CITED

Anderson, J. P. 1959. Flora of Alaska and adjacent parts of Canada. Iowa State Univ. Press, Ames. 543 pp.

Andreasen, G. E., C. Wahrhaftig, and I. Zietz. 1964. Aeromagnetic reconnaissance of the east-central Tanana lowland, Alaska. USGS, Washington. 3 pp.

Benninghoff, W. S. 1952. Interaction of vegetation and soil frost phenomena. Arctic 5:34-44.

Bishop, R. H. 1969. Preliminary review of changes in sex and age ratios of moose and their relation to snow conditions on the Tanana Flats, Alaska. Paper presented at 6th Annu. N. Am. Moose Committee Meeting, Feb. 3-5, Kamloops, B. C. 14 pp. Xerox.

Black, R. F. 1958. Lowlands and plains of interior and western Alaska in H. Williams, ed. Landscapes of Alaska. Univ. Calif. Press, Berkeley. pp. 76-81.

Coady, J. W. and W. C. Gasaway. 1972. Rumen function and energy production of moose in interior Alaska. In R. B. Addison ed. Proceedings of the 8th North American Moose Conference and Workshop. Queen's Printer for Ontario. pp. 80-104.

Cole, G. F. 1963. Range survey guide. Grand Teton Natl. Hist. Assoc. Moose, Wy. 22 pp.

Cushwa, C. T. and J. W. Coady. 1973. Moose food habits in Alaska, a preliminary study using stomach contents analysis. MS 21 pp. Xerox.

___________., S. A. Liscinsky, R. F. Harlow and M. J. Puglisi. 1973. Rumen analysis in white-tailed deer management - development, use, and evaluation of a procedure. MS 40 pp.

Drury, W. H., Jr. 1956. Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska. Contrib. Gray Herb. No. 178, Harvard Univ. 130 pp.

Dutro, J. T. and T. G. Payne. 1957. Geological map of Alaska. USGS, Scale 1:2,500,000.

Gasaway, W. C. and J. W. Coady. 1973. Review of energy requirements and rumen fermentation in moose and other ruminants. Int. Symp. on Moose Ecology, Quebec City. March 1973. 37 pp.

Hanson, H. C. 1951. Characteristics of some grassland, marsh, and other plant communities in western Alaska. Ecol. Monogr. 21(4): 317-378.

___________. 1953. Vegetation types in northwestern Alaska and comparisons with communities in other arctic regions. Ecology 34(1):111-140.

Hultén, E. 1968. Flora of Alaska and neighboring territories. Stanford Univ. Press. 1,008 pp.

Johnson, P. L. and T. C. Vogel. 1966. Vegetation of the Yukon Flats region, Alaska. CRREL Research Report 209. Hanover, N. H. 53 pp.

Johnson, P. R. and C. W. Hartman. 1969. Environmental atlas of Alaska. Inst. of Arctic Env. Eng. and Inst. of Water Res. Univ. Alaska, College. 111 pp.

Larsen, J. A. 1965. The vegetation of the Ennadai Lake area, N.W.T.: Studies in subarctic and arctic bioclimatology. Ecol. Monogr. 35(1):37-59.

Ohmann, L. F. and R. R. Ream. 1971. Wilderness ecology: virgin plant communities of the Boundary Waters Canoe area. USDA Forest Serv. Res. Paper NC-63.

Ritchie, J. C. 1959. The vegetation of northern Manitoba. AINA Tech. Paper 3. 56 pp.

Spencer, D. H. and E. F. Chatelain. 1953. Progress in the management of the moose in southcentral Alaska. Trans. 18th N. Am. Wildl. Conf. pp. 539-552.

Viereck, L. A. 1970a. Forest succession and soil development adjacent to the Chena River in interior Alaska. Arctic and Alpine Res. 2(1):1-26.

____________. 1970b. Soil temperatures in river bottom stands in interior Alaska. In Ecology of the subarctic regions, Proc. Helsinki Symp. (Ecol. and Conser. No. 1). Paris, UNESCO. 364 pp.

____________. (in press). Wildfire in the taiga of Alaska. J. Quant. Res. 75 pp.

Viereck, L. A. and E. L. Little, Jr. 1972. Alaska trees and shrubs. U.S. Dept. Agr. Handbook 410. 265 pp.

Wahrhaftig, C. 1965. Physiographic divisions of Alaska. Geol. Surv. Prof. Paper 482. U. S. Gov. Printing Office, Wash. 52 pp.

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JOB PROGRESS REPORT (RESEARCH)

State:	Alaska		
Cooperator:	John W. Coady		
Project Nos:	W-17-4 & W-17-5	Project Title:	Big Game Investigations
Job No:	1.8R	Job Title:	Snow Characteristics in Relation to Moose Distribution in Interior Alaska

Period Covered: July 1, 1971 to June 30, 1973

SUMMARY

This report describes major activities undertaken between February 1971 and June 1973. This research project was initiated in February 1971 during a winter of record snowfall in interior Alaska. Substantial winter mortality of moose permitted collecting numerous data on sex and age, body weights and measurements, reproductive status of females, and bone marrow fat content of moose in the Interior. Collection of these data has continued to the present as opportunity has permitted. Both NRC instruments and the Swiss Rammsonde Penetrometer have been used since November 1972 to monitor physical characteristics of the snow cover at various sites in Game Management Units 20A and 20B. Frequent aerial surveys and ground track counts have been conducted near snow study sites to relate moose movement and distribution to snow conditions. Although rarely used in biological studies, the ease, accuracy, and properties of the snow measured by the Rammsonde appear to make the instrument useful for assessing severity of snow conditions for large ungulates. A limited radio telemetry program initiated in November 1972 provided additional information regarding moose movement in response to snow conditions and habitat use, and indicated that telemetry may be a useful tool for studying certain aspects of moose behavior in interior Alaska.

CONTENTS

BACKGROUND

Moose (*Alces alces*) are Holarctic in distribution (Rausch, 1963), occurring in several Eurasian countries, Canada, the conterminous United States, and Alaska. Four Eurasian races (Heptner et al., 1961) and four North American races (Hall and Kelson, 1959) of moose are recognized. The Alaskan moose (*A. a. gigas*) is of pre-Wisconsin age, remains having been found in Illinoian beds in the "Cripple Creek sump" near Fairbanks (Péwé and Hopkins, 1967).

Moose are expanding their range throughout North America (Kelsall, 1972; Kelsall and Telfer, 1973). In Alaska, moose are widespread within the boreal forest zone (Alaska Dept. of Fish and Game, 1973), although many reports suggest they are more common beyond tree line in several areas than in previous years (Rausch, 1951; Bee and Hall, 1956; Lutz, 1960; Pruitt, 1966; Chesemore, 1968; and LeResche et al., 1973). Northward dispersal of moose may be due in part to an increase in riparian climax vegetation resulting from gradual Holarctic warming trends during the last half century (Leopold and Darling, 1953). This apparent expansion may also result from recent increased human activity in northern regions, thereby increasing opportunity for sighting animals (Kelsall, 1972).

Moose play an important economic and cultural role in Alaska. Between 1963 and 1972 an average of 7500 moose per year were reported killed by hunters. In 1971 alone, over 8800 moose were reported killed, 1070 of which were from the Fairbanks region (Game Management Unit 20). Thousands of recreationists photograph and observe moose each year. The extensive distribution, large numbers, and relatively visible nature of the species has made moose a symbol of Alaskan wildlife.

Since statehood in 1959 the Alaska Department of Fish and Game has actively engaged in collecting information in interior Alaska relating to moose biology. Major emphasis has been placed on extensive aerial surveys during fall to document changes in productivity, to assess the effect of hunting on bull-cow ratios, to determine survival of moose to

1.5 years of age, and to document changes in relative abundance and distribution of moose. Annual aerial surveys have been conducted in selected areas during spring to assess survival of moose to 1 year of age, and to monitor changes in relative abundance and distribution of moose. Harvest statistics and basic life history information have also been collected. In spring 1966 a moose calf tagging program was initiated on the Tanana Flats south of Fairbanks to help determine distribution, movement, and population identity of moose calving in the area. Between 1966 and 1969 over 800 moose calves were tagged, and locations of tagged moose continue to be recorded as sightings are made.

Major contributions to moose studies in interior Alaska have been made by Robert A. Rausch (Rausch, 1967, 1971; Rausch and Bishop, 1968) and Richard Bishop (Bishop, 1969, 1970; Bishop and Rausch, 1973). Together these individuals conducted and directed many early studies of moose in interior Alaska. Their work has provided the background for and continues to provide guidance in developing current moose studies.

In February 1971, a winter of record snowfall in interior Alaska, a moose research program was initiated at Fairbanks to further identify and quantify major control factors affecting moose populations. Basic emphasis of the program centers around effects of certain relationships between snow and range conditions on the production, survival, and distribution of moose in interior Alaska. Information obtained from this project will hopefully contribute to efficient management of moose in interior Alaska, where growth of human populations and increased demands on wildlife and land resources are expected.

OBJECTIVES

The objectives of this study are 1) to obtain certain data pertaining to production, survival, and general condition of moose in interior Alaska; 2) to evaluate the morphological adaptation to snow of various sex and age class moose; 3) to monitor distribution, survival, and productivity of moose in relation to characteristics of the snow cover in interior Alaska; 4) to test different instruments and techniques for evaluating the severity of winter conditions to moose; and 5) to determine the influence of snow and habitat on the seasonal movement and distribution patterns of radio-collared moose breeding in the Little Chena drainage, and to test the feasibility of using biotelemetry to study movements of moose in interior Alaska.

The following data were collected:

1) Body weights and measurements of pre- and post-natal moose;

2) Chest height and foot load of post-natal moose;

3) Reproductive status of females over 1 year of age;

4) Percent femur marrow fat;

5) Sex and age of moose dying from both malnutrition and unnatural causes;

6) Snow depth, hardness, density, temperature, and Rammsonde hardness at various sites in relation to distribution and abundance of moose;

7) Visual search time, location, habitat selection and activity of radio-collared moose.

PROCEDURES

Production, Survival and Physical Condition of Moose

Moose dying from natural (malnutrition, predation) and unnatural (highway and railroad collisions, shooting) causes between February 1, 1971 and June 1, 1973 within 100 miles of Fairbanks were examined. Moose killed on highways were retrieved with a truck, while specimens from animals killed on the railroad were collected with a rail-car. Snow machines, fixed-wing aircraft, and helicopters were used to collect animals or specimens in remote areas. Private individuals also collected numerous specimens.

Post-natal body weights were measured with a commercial truck scale in Fairbanks or with a spring scale suspended under a helicopter. Fetal body weights were measured with a hand-held spring scale.

The following measurements were obtained when possible:

1) Heart girth: measured immediately behind front legs;

2) Total length: measured along contour of body from hairless portion of nose to base of tail;

3) Total height: measured along contour of body from tip of hoof to top of shoulder or scapula;

4) Chest height: measured from tip of hoof to brisket or sternum, with leg in "normal" position relative to body;

5) Hind leg: measured from tip of hind hoof to hock or tuber calcis;

6) Knee: measured from tip of front hoof to middle of knee or carpus;

7) Foot load: determined by measuring area of four feet and dividing total area by body weight, according to the procedure described by Kelsall and Telfer (1971).

Only heart girth and body contour length were measured on pre-natal animals.

Reproductive tracts of females over 1 year old were examined for pregnancy. Ovaries were collected and preserved in formalin.

Incisors were collected from animals over 1 year old, and the age determined by examining cementum growth layers.

Percent fat in femur or tibia marrow was determined by drying marrow from fresh or frozen bones at 65°C to constant weight according to a method developed by Neiland (1970). Although marrow is composed of water, fat, and non-fat residue, the non-fat residue is small (2-6 percent of total weight), and the dried marrow is assumed to consist entirely of fat.

Unless otherwise stated, 0.05 was the probability level at which the null hypothesis was rejected.

Snow Measurements

Methods of measuring properties of a snow cover have been described by several authors (Klein et al., 1950; Benson, 1962; Keeler, 1969; Test Lab, 1970; and others). Two similar sets of instruments, a National Research Council of Canada (NRC) kit and a USA Cold Regions Research and Engineering Laboratory (USACRREL) kit have been used to measure temperature, density, and hardness of a snow cover. However, modified snow study kits have also been used (Richens and Madden, 1973). These measurements are generally obtained in "pit" studies, in which a trench is dug in the snow to ground level. Thickness, temperature, density, hardness, and sometimes crystal type and size of major strata are recorded. Snow samples or measurements are generally taken in a horizontal plane, although vertical as well as horizontal hardness measurements should be made (Pruitt, 1971a). The International Workshop on *Rangifer* Winter Ecology (Pruitt, 1971a) has recommended measuring the thinnest distinct strata which a given instrument size will allow.

Depth of snow cover is probably the most common and important measurement obtained in studying snow ecology of moose. In addition to ease of measurement, snow depth provides a measure of the thickness of the medium through which an animal must move if not supported by the snow. Depth of snow or thickness of strata can be measured with any conveniently calibrated probe. In addition, in interior Alaska 5 cm diameter stakes, clearly calibrated at 30.5 cm (12 in) intervals, have been permanently located in remote or inaccessible areas to measure snow depth from fixed wing aircraft. Depth can consistently be estimated within 3 to 5 cm of the actual snow depth, although this method has the disadvantages of limiting measurements to the number of stakes at a study site, and limiting study sites to relatively open areas where the aircraft may be flown near ground level. Snow depths relative to anatomical features of moose also provide a useful and reasonably accurate estimate of snow depth from the air.

Snow temperatures of each substrate or at intervals on the pit wall, beginning at ground level or in the subnivian space and ending within 2 cm of the surface, may be measured. However, the International

Workshop on *Rangifer* Winter Ecology (Pruitt, 1971a) has questioned the significance of measuring snow temperature in *Rangifer* research, and has recommended limiting measurements to ground level and air temperatures. While a relationship between snow temperature and moose behavior has been alluded to by Des Meules (1964), the ease and speed of temperature measurement in pit studies and its possible significance to moose behavior probably merit its continued measurement. Measurements may be made with either an alcohol or bimetallic thermometer.

Density, determined by weighing a known volume of snow, is probably the most widely used index of snow type, and under certain snow conditions it may be correlated with hardness (Keeler and Weeks, 1967; Bilello et al., 1970). Increased density presumably causes increased drag on legs or the body of ungulates during movement, and thereby inhibits locomotion. Several snow cutters for obtaining snow density samples are available. The NRC kit employs two 250 ml snow cutters, one for soft and one for hard snow, while the USACRREL kit uses 500 ml sampling tubes. Swedish workers use a Swedish Army density "box" which reportedly gives reliable results because of its large 1,000 cm^3 volume (Pruitt, 1971a). In interior Alaska a 650 cm^3 plastic cylinder has been used with satisfactory results.

Snow hardness reflects the degree of bonding between crystals and in most types of snow increases as density increases and/or snow temperature decreases (Gold, 1956). In addition to snow depth, hardness is probably the most critical parameter of a snow cover to ungulates since it reflects the force which must be exerted to move legs or body through the snow, and the ability of the snow to partially or fully support the animal. NRC and USACRREL snow hardness gauges are similar, and consist of a spring-loaded push rod with provision for mounting discs of different areas on one end and a calibrated gauge on the other end. The disc is pressed against a snow surface and the maximum stress associated with the initial collapse of the snow structure is noted on the gauge. By using a high and low range gauge and different sized discs, hardnesses of 0 to 100,000 g/cm^2 can be measured. Useful modifications to the instrument developed in Sweden and now used by Pruitt (per. comm.) include a ratchet which retains the calibrated gauge at the extended position reached at the instant of snow collapse, thereby providing more accurate measurements.

Snow hardness may also be measured with a cone penetrometer, commonly referred to as a Swiss Rammsonde. The instrument and its use have been described by several workers (Bader et al., 1939; Benson, 1962; Keeler, 1969; Test Lab., 1970; and others). Basically, it consists of a hollow steel shaft with a 60° conical tip 4 cm in diameter and 3.5 cm high. A solid rod mounted on top of the steel shaft guides a hammer which is dropped from a measured height. The height of the drop, weight of the entire instrument, and depth of penetration may be related to the resistance of snow to penetration by the cone using the following formula: $R = \frac{Whn}{x} + W + Q$, where R = ram hardness number or resistance

to penetration, W = weight (kg) of penetrometer. The equation ignores friction between the cone and snow and elasticity in th e penetrometer.

However, error is small, especially for snow of relatively low hardness (Keeler, 1969; Benson, per. comm.).

The ram hardness number, R, indicates the resistance (kg) of a layer of snow to penetration by the cone of the penetrometer. In practice it may be useful to determine the ram hardness value for the total snow depth. To do this an integrated ram hardness number, R_i (kg-cm), is calculated by multiplying each depth increment (cm) times its ram hardness number, R (kg), and summing the values from the snow surface to ground level or to any given depth. The integration indicates the work done by the penetrometer as it moves through the snow to a given depth.

The Rammsonde can be used in several ways. It can rapidly distinguish different strata and provide a ram hardness profile or an integrated ram hardness value of the total snow cover without digging a pit. Rammsonde measurements are less subject to operator error than are NRC or USACRREL snow hardness values (Benson, 1962). Limitations to this procedure include lack of resolution at low snow hardness. However, a modified 120° cone, 10 cm in diameter, has been satisfactorily used by Abele (1968) in soft snow. The hardness number obtained with the large cone is divided by a factor of 10 to obtain the approximate ram hardness value of the standard cone (Test Lab, 1970).

Rammsonde hardness numbers can be correlated with other derived snow measurements under most temperature and snow conditions, and with the support capacity of snow. Bull (1956) and Keeler (1969) have correlated ram hardness values with snow densities, while Abele (1963) has related ram values to compression strength or hardness. Abele et al. (1965, 1968), Wuori (1962, 1963) and others have related ram hardness to vehicle support capacity of snow roads and runways.

While the Rammsonde penetrometer has been used extensively to study mechanical properties of a snow pack, it has been used rarely in biological applications. Other than Lent and Knutson (1971) working with musk-oxen (*Ovibos moschatus*), Coady (this report) working with moose, and some investigators in Canada and Scandinavia working with reindeer (*Rangifer* sp.) (c.f. Pruitt, 1971b), the instrument has not been widely used in studies of ungulate snow ecology. Additional measurements and experience are certainly required to evaluate the usefulness of the Rammsonde penetrometer in biological studies. Ease, speed, and consistency of identifying stratigraphic horizons and measuring hardness of a snow cover may make the Rammsonde a potentially valuable instrument for assessing the resistance to movement through or the support capacity of snow.

Both NRC and Rammsonde snow measurements were recorded at each station on a data form (Fig. 1). Site characteristics, weather, general snow conditions, presence or absence of moose in the vicinity, and if moose are present, the depth of foot penetration into the snow were recorded. NRC measurements consisted of weight of snow, hardness, temperature, and crystal type (optional) in each snow layer on the pit wall. Rammsonde measurements were obtained by noting weight of hammer,

Fig. 1. Alaska Department of Fish and Game data form used to record National Research Council (NRC) of Canada and Swiss Rammsonde Penetrometer snow measurements.

ALASKA DEPARTMENT OF FISH AND GAME SNOW SURVEY

Station ____________________

Altitude ____________ **Exposure** ____________

Vegetation ____________________

Date ____________ Time ____________ Observer ____________

Air Temp ____________ Weather ____________

Snow Depth ____________ Snow Surface ____________

Moose Present ____________ Track Depth ____________

NRC Measurements

Depth	Gross Wt	Density	Hardness	Temp	Crystals	Remarks

Rammsonde Measurements

Wt	Ht	Penetration (1)	(2)	(3)	(4)	(5)	Resistance (1)	(2)	(3)	(4)	(5)

height of hammer drip, and total depth of Rammsonde penetration after each hammer drop (recorded in a vertical column). Rammsonde measurements were repeated five times at each station. The resistances for each increment of Rammsonde penetration and for each trial were calculated at a later date.

Trends in snow severity for moose in interior Alaska were examined by plotting weather bureau records of snow depth on the ground in Fairbanks versus month throughout the winter, and measuring the area under the curve with a planimeter. A similar procedure could be used to evaluate temperature severity. While weather bureau measurements may not indicate actual conditions on winter moose range, they probably reflect relative differences between years and long-term trends.

Depth, temperature, density, hardness (NRC hardness gauge, and Rammsonde hardness of the snow cover) and relative abundance of moose were monitored at weekly to monthly intervals in different habitats in the Chatanika drainage, the Chena drainage, the Tanana Flats, and the north side of the Alaska Range foothills. The major study area is located near 40 mile Steese Highway (Chatanika drainage), where relationships between altitudinal moose movements and snow conditions were monitored during the winters of 1971-72 and 1972-73. The seven day total (counted daily) of fresh moose tracks crossing a one-half mile long transect in the Chatanika River valley was recorded between November and May. The valley is located at 245 m elevation, and represents typical winter riparian moose habitat. The number of moose counted during frequent intensive aerial surveys in a 75 km^2 drainage above the valley transect was also recorded. The upland site ranges from 550 to 670 m elevation and consists of mixed conifer and deciduous trees and shrubs which characteristically support modest numbers of moose during summer and fall in interior Alaska. Snow measurements were obtained in shrub communities in the upland site, and in shrub, deciduous tree, conifer tree, and grass communities in the valley site.

Radio Telemetry

Six adult female moose were radio collared in the 15-year-old Elliott Creek burn along the upper Little Chena River (elevation 300-700 m) during November 1972. Collaring procedures and transmitter specifications are on file at the Alaska Department of Fish and Game office in Fairbanks, and will not be reported here. Collared animals were located from the air at two- to ten-day intervals, and the location of individual moose was plotted on one inch to one mile USGS maps or on four inch to one mile vegetation type maps. Habitat selection (herbaceous bog, heath bog, shrub, deciduous tree, conifer tree), activity (bedded, standing), and time spent visually searching for the animal after her location was determined electronically were recorded on data forms (Fig. 2). Snow depth in the Elliott Creek burn was monitored from the air using permanently located calibrated stakes. Monthly aerial moose surveys were conducted in the Elliott Creek burn between November and March.

Fig. 2. Alaska Department of Fish and Game data form used to record observations of radio collared moose in GMU 20A and 20B.

RADIO-COLLARED MOOSE OBSERVATIONS

Area	Snow
Date	
Pilot/Observer	
Temp	
Weather	
Wind	

Animal	1	2	3	4	5	6
Detect Signal?						
Locate?						
Visually						
Time of Day						
Visual Search Time						
Habitat						
Activity						
Grouping						

FINDINGS AND CONCLUSIONS

Production, Survival and Physical Condition of Moose

Weights and Measurements: Weights and measurements were obtained from 22 moose fetuses collected in interior Alaska (Table 1). Date of death is recorded to the nearest day or month, when known. Five fetuses, ranging in weight from 13.6 to 17.2 and averaging 15.2 kg, were collected on the Tanana Flats on May 24, 1971. Calving was underway at this time, and therefore the above weights are considered to represent the approximate birth weight of moose calves in the area.

Growth rates for moose fetuses have been recorded by Edwards and Ritcey (1958) in British Columbia, by Rausch (1959) in Alaska, and by Markgren (1969) in Sweden. Growth rate of fetuses reported in Table 1, based on total contour length and date of death, when known, agree closely with that reported by Rausch.

Birth weights of 6 to 16 kg have been reported for moose in the USSR (Knorre, 1961), of 11.2 kg for moose in Michigan (Verme, 1970), and of 11.3 to 15.9 kg for moose in Alaska (Rausch, 1959). Markgren (1966) measured weights of 11.5 and 13.5 kg for two 4-day-old moose in Sweden. The average weight of 15.2 kg reported in this study for near-term moose fetuses agrees most closely with the findings of Rausch, and is somewhat greater than the weights recorded by other investigators.

Knorre (1961) found an average birth weight of 12.8 kg for single and 10.3 kg for twin calves. Individual weights of the one set of twins near term in this study were similar to weights of the three single calves (Table 1).

Weights and measurements were obtained from approximately 25 moose calves under 1 year of age (Table 2). Based on limited data presented in this report, birth weight (see Table 1) increased over 2.5 times by four weeks, over 4.5 times by six weeks, and by approximately 10 times by 6 to 12 months of age.

The extremely rapid growth rate of moose calves has been noted by many workers. Rausch (1959) also reported that moose calves in Alaska increase their birth weight by a factor of 10 after six months. Verme (1970) found that calves in Michigan tripled their birth weight by four weeks and weighed 159 kg by six months of age. In Alberta Blood et al. (1967) found average weights of 197 and 174 kg for male and female calves, respectively, after six months. Weights of moose calves have also been reported by Denniston (1956), Dodds (1959), Knorre (1961), Peek (1962), and Markgren (1966). Earlier studies have been summarized by Peterson (1955).

Weights and measurements from approximately 55 moose older than 1 year were obtained during winter and spring (Table 3), summer (Table 4), and fall (Table 5). During each period maximum body weight and skeletal measurements were reached after approximately three years of life (Figs. 3-7). These age specific data suggest that moose, at least females, in

Table 1. Weights and measurements of moose fetuses from interior Alaska (GMU 20A and 20B).

Sex	Wt (kg)	Total Contour Length (cm)	Heart Girth (cm)	Date of Death	Age of Cow
F	0.64	33.0	20.3	12/70	4
M	3.86	66.0	38.1	3/12/71	11
F	2.28	52.7	31.1	-	2
F	1.81	45.7	-	-	14
M	2.94	63.5	34.3	3/71	14
F	0.79	29.8	18.4	-	10
M	1.02	49.5	30.5	-	11
F	4.08	62.2	33.7	3/71	13
F (twin)	1.36	41.9	26.7	-	-
F (twin)	1.13	40.6	27.2	-	-
F (twin)	0.57	33.7	18.4	-	13
F (twin)	0.91	33.7	19.1	-	-
M	3.40	62.2	34.3	3/20/71	11
M	4.98	69.9	40.6	4/8/71	15
F	0.24	26.6	-	-	10
M	3.44	61.1	33.0	-	16
F	4.54	69.9	38.7	-	16
F	17.23	106.7	55.9	5/24/71	11
F	13.61	100.3	53.3	5/24/71	-
M	14.51	96.5	53.3	5/24/71	2
F (twin)	15.87	96.5	53.3	5/24/71	8
F (twin)	14.97	95.3	52.1	5/24/71	8

Table 2. Weights (kg) and measurements (cm) of moose calves from interior Alaska (GMU 20A and 20B).

Age and Measurement	No.	Mean	S. D.	S. E.	Range
4 weeks					
Weight	2	41.5			28.6-54.4
6 weeks					
Weight	1	70.0			
Heart girth	1	88			
Total length	1	128			
Shoulder height	1	86			
6-12 months					
Weight	23	157	25	5	113-238
Heart girth	17	143	15	4	127-186
Total length	22	204	11	2	173-213
Shoulder height	21	148	16	4	122-194
Chest height	21	84	8	2	66-95
Hind foot length	20	63	5	1	51-74

Table 3. Weights (kg) and measurements (cm) of male and female moose over 1 year of age during winter and spring in interior Alaska (GMU 20A and 20B).

Age and Measurement	No.	Mean	S. D.	S. E.	Range
1 year					
Weight	1	254			
Heart girth	1	203			
Total length	1	254			
Chest height	1	94			
Hind foot length	1	69			
2 years					
Weight	2	356			295-417
Heart girth	3	195	19	11	173-211
Total length	4	275	18	9	262-302
Total height	5	183	13	6	163-198
Chest height	5	101	4	2	97-105
Hind foot length	6	71	4	2	66-76
3 years					
Weight	1	279			
Total length	1	254			
Shoulder height	1	175			
Chest height	2	97			97-97
Hind foot length	2	71			71-71
4 years					
Weight	2	368			361-374
Heart girth	2	196			194-198
Total length	2	271			270-272
Total height	2	181			175-187
Chest height	2	103			101-104
Hind foot length	2	82			79-85
6 years					
Weight	1	385			
Heart girth	1	188			
Total length	1	254			
Shoulder height	1	183			
Chest height	2	93			91-94
Hind foot length	2	65			61-69

Table 3. Continued.

Age and Measurement	No.	Mean	S. D.	S. E.	Range
7-8 years					
Weight	2	368			361-374
Heart girth	2	192			192-192
Total length	2	277			274-280
Total height	1	177			
Chest height	1	108			
Hind foot length	1	77			
10-11 years					
Weight	5	351	69	34	266-435
Heart girth	3	177	4	2	173-180
Total length	2	281			269-292
Shoulder height	6	182	12	6	163-196
Chest height	5	102	5	2	97-109
Hind foot length	5	63	5	3	61-71
13 + years					
Weight	2	325			313-336
Heart girth	3	179	8	4	175-188
Total length	4	274	13	7	259-290
Shoulder height	5	179	11	5	165-193
Chest height	5	100	2	1	97-102
Hind foot length	12	68	4	1	61-74

Table 4. Weights (kg) and measurements (cm) of cow moose over 1 year of age during late June in interior Alaska (GMU 20A).

Age and Measurement	No.	Mean	Range
1 year			
Weight	1	227	
Heart girth	1	156	
Total length	1	203	
Shoulder height	1	151	
Chest height	1	92	
2 years			
Weight	3	395	381-408
Heart girth	3	177	174-182
Total length	3	265	242-278
Shoulder height	3	180	177-183
Chest height	3	112	106-118
3 years			
Weight	1	463	
Heart girth	1	204	
Total length	1	272	
Shoulder height	1	188	
Chest height	1	110	
4 years			
Weight	1	390	
Heart girth	1	172	
Total length	1	273	
Shoulder height	1	184	
Chest height	1	113	
6 years			
Weight	1	367	
Heart girth	1	186	
Total length	1	284	
Shoulder height	1	188	
Chest height	1	105	
10-11 years			
Weight	2	413	376-449
Heart girth	2	191	188-194
Total length	2	269	268-269
Shoulder height	2	182	174-190
Chest height	2	107	106-107

Table 5. Weights (kg) and measurements (cm) of male and female moose over 1 year of age during October in interior Alaska (GMU 20A and 20B).

Age and Measurement	No.	Mean	Range
3 years			
Weight	1	490	
Heart girth	2	216	202-230
Total length	2	295	276-314
Shoulder height	1	209	
Chest height	1	107	
Hind foot length	1	88	
4 years			
Weight	3	524	501-546
Heart girth	3	213	210-214
Total length	3	289	270-306
Shoulder height	3	188	183-192
Chest height	3	111	107-118
5 years			
Weight	1	512	
Heart girth	1	186	
Total length	1	304	
Shoulder height	1	192	
Chest height	1	106	
Hind foot length	1	79	
7 years			
Weight	1	458	
Heart girth	2	209	204-214
Total length	2	275	260-289
Shoulder height	1	172	
Chest height	1	108	
Hind foot length	1	82	
10-11 years			
Weight	1	517	
Heart girth	3	208	204-212
Total length	3	306	297-311
Shoulder height	1	180	
Chest height	1	106	
Hind foot length	2	86	83-89

Fig. 3. Hind foot and total body length of male and female moose obtained in GMU 20A and 20B during winter and spring, 1971 to 1973.

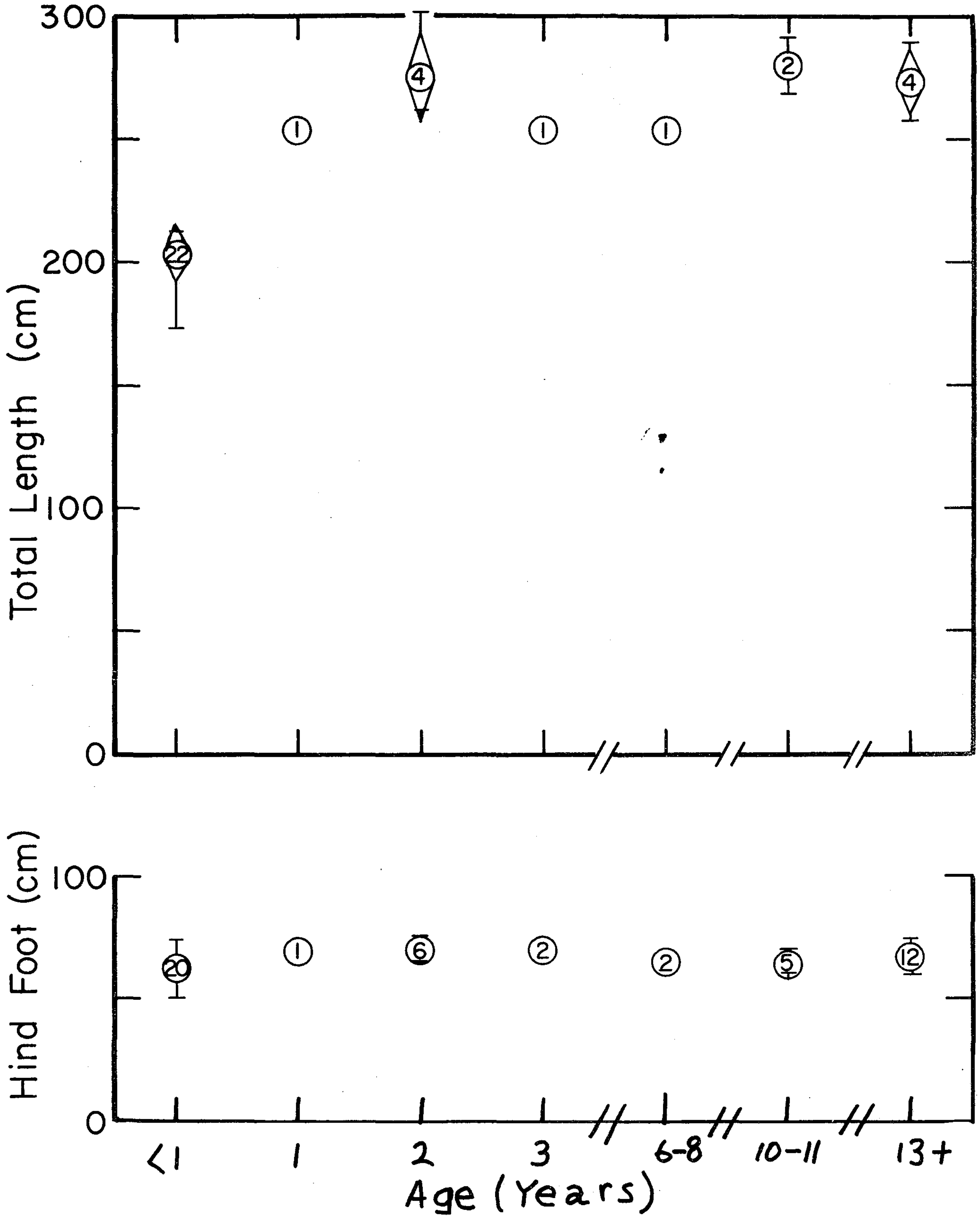


Fig. 4. Heart girth and total body weight of male and female moose obtained in GMU 20A and 20B during winter and spring, 1971 to 1973.

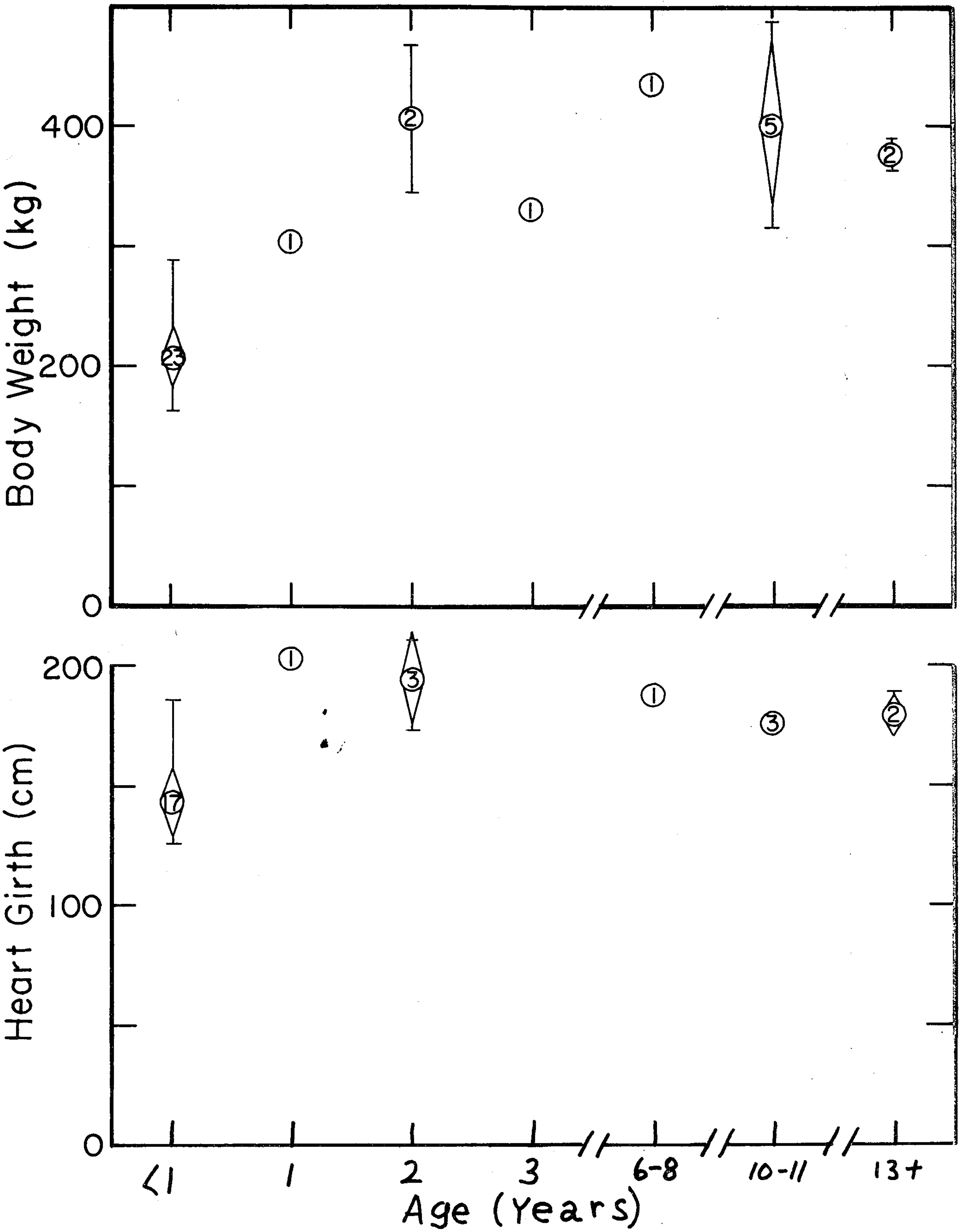


Fig. 5. Total body weight and body length of female moose obtained in GMU 20A during June, 1972.

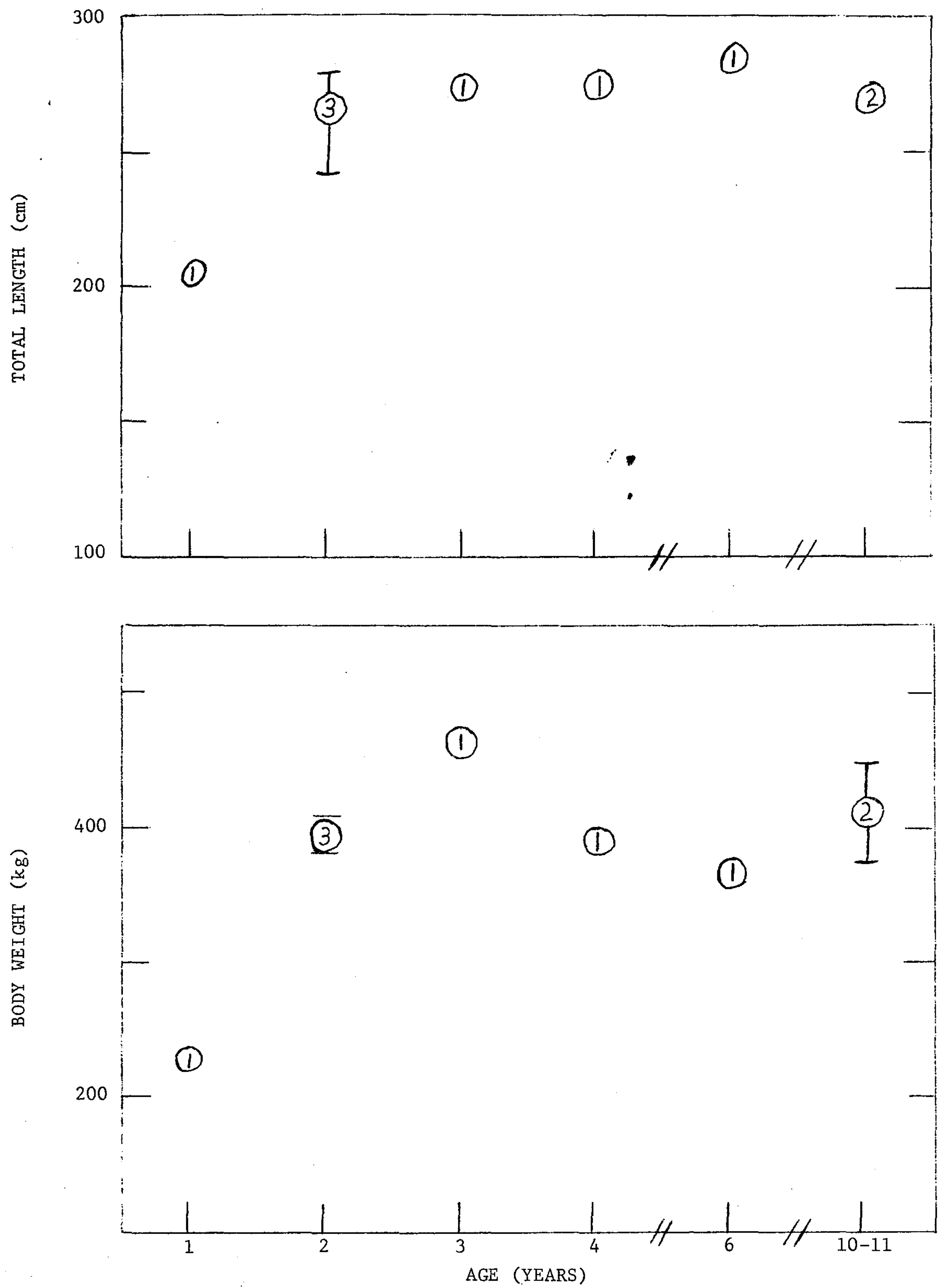


Fig. 6. Total body weight and body length of male and female moose obtained in GMU 20A and 20B during fall, 1971 and 1972.

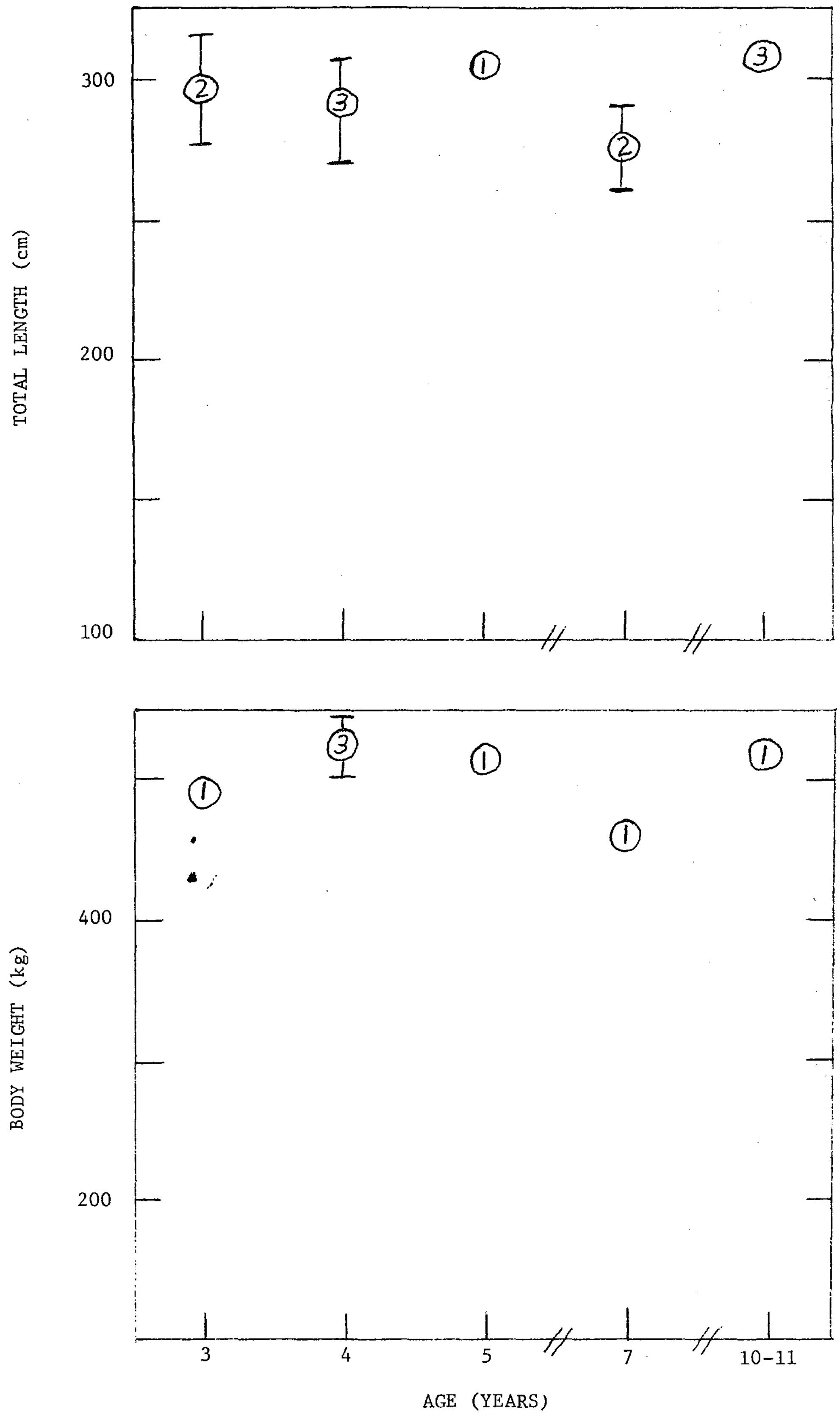
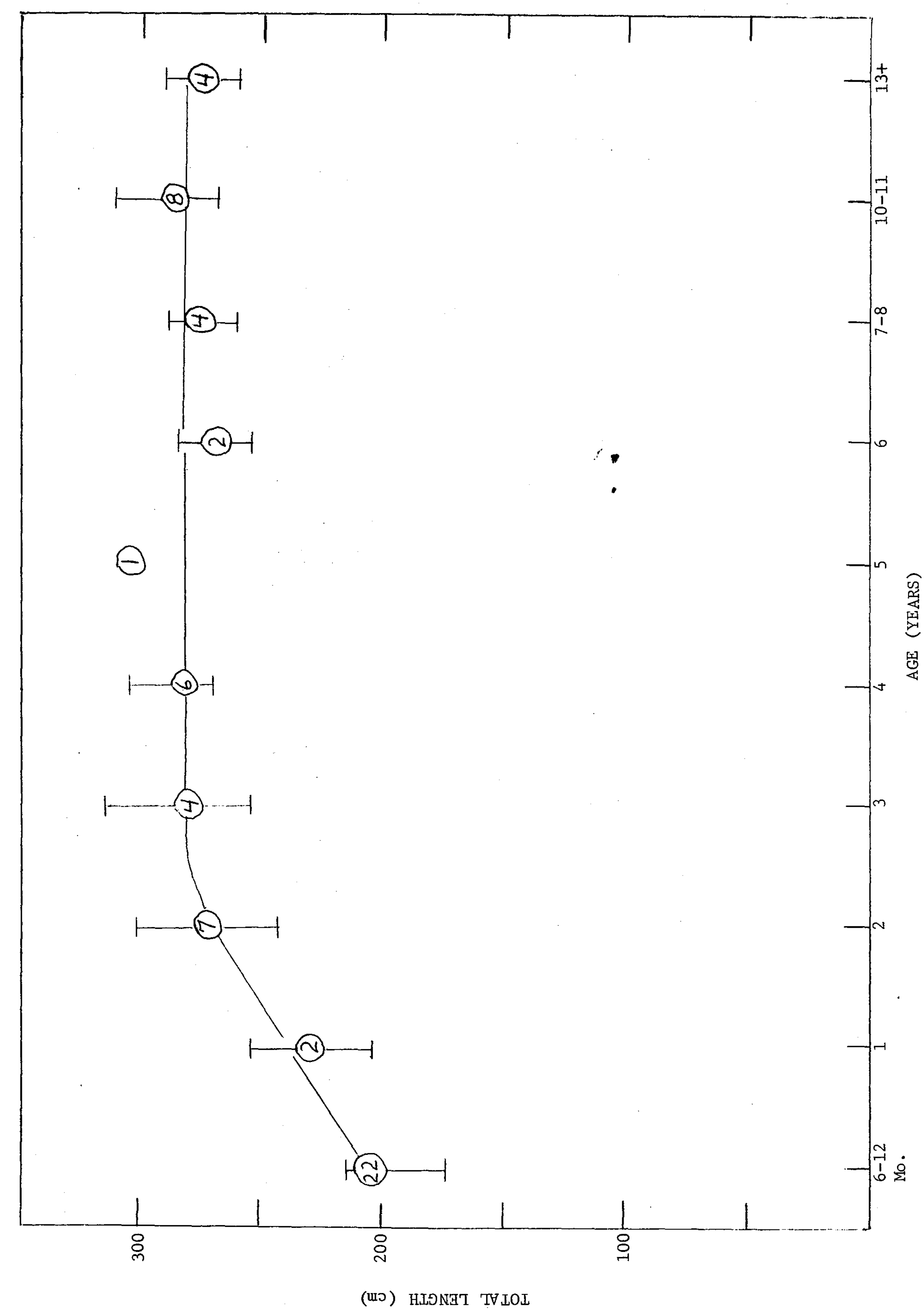


Fig. 7. Total body length of male and female moose obtained in GMU 20A and 20B during all seasons, 1971 to 1973.



the study area may reach maximum body mass and skeletal dimensions during their third year.

Body mass or weight is a widely used measure of growth rate and indicator of physical condition (Klein, 1970). Nevertheless, skeletal measurements better reflect growth rate since they are not subject to short-term fluctuations associated with fullness of the digestive tract, seasonal accumulation and utilization of fat reserves, etc. (Klein, 1964, 1965). In addition, skeletal measurements are generally easier to obtain than body weight from large animals.

Total length, and to a lesser extent hind foot length, and shoulder height best reflected a pattern of age specific growth. Heart girth involves measurements of the skeleton as well as overlying muscle and fat, and therefore reflects the mass of the animal more closely than skeletal growth (Brandy et al., 1956). Chest heights were recorded to evaluate the potential performance of the animal in deep snow for this study.

Moose have been reported to reach maximum body size within two to four years in other areas. Blood et al. (1967) noted that moose in Alberta increased in weight until three and one-half years of age, or perhaps longer, while Verme (1970) found that females in Michigan reached maximum size in two and one-half years, and males increased in size until three and one-half years old. Rausch (1959) found that female moose in southcentral Alaska grew very little beyond wear age class III (two to four years).

However, other workers have reported that moose grow in both weight and skeletal size for several years. Skunke (1949) noted the moose in Sweden increase in weight until 7 to 10 years of age, and LeResche and Davis (1971) indicated that growth of moose on the Kenai Peninsula in Alaska may continue throughout the life of the animal. After reviewing the European and American studies, Jordan et al. (1970) concluded that body growth continued until year six in females and year 11 in males.

In interior Alaska maximum body weights occurred during fall. The average weight for two bulls and five cows collected during mid-October, well into the rut, was 507 kg. The heaviest animal was a 4-year-old bull weighing 546 kg, while the next heaviest was a 4-year-old cow weighing 524 kg (Table 5).

Body weights of moose reported from other areas are generally less than those cited here. The heaviest bull and cow weighed by Blood et al. (1967) in Alberta were 478 and 429 kg, respectively, while Verme (1970) found a maximum weight of 506 and 385 kg for a bull and cow in Michigan, respectively. Rausch (1959) noted that few bulls exceed 545 to 635 kg in Alaska, and reported a weight of only 517 kg and a body length of 287 cm for the largest bull he examined. LeResche and Davis (1971) reported a weight of 445 kg for the largest cow handled at the Kenai Moose Research Center, Alaska.

Moose in interior Alaska apparently experience considerable seasonal fluctuation in body weight. Average body weights for moose older than three years (see Tables 3, 4, 5) were 338 kg in December through May, 409 kg in June, and 507 kg in October. These values indicate a 33 percent weight loss in animals between fall and winter and spring. Although sample sizes were not large, and some of the weights obtained during winter and spring were from "winter-killed" moose, it is apparent that substantial seasonal fluctuations in weight of moose in interior Alaska normally do occur.

Jordan et al. (1970) concluded that seasonal weight fluctuations in moose amounted to 6.6 percent for females and 10.3 percent for males. However, Rausch (1959) and LeResche and Davis (1971) reported seasonal weight fluctuations of 20 percent and 15-30 percent, respectively, for moose in southcentral Alaska. Verme (1970) found that a "winter-killed" bull in Michigan had lost 33 percent of his pre-winter weight.

Energetic demands of lactation resulted in a substantially lower body weight during the summer than for non-lactating females (Table 6). Average body weight of four non-lactating females was approximately 12 percent greater than that of lactating females. Each group included 2-year-old animals. Energy requirements for lactation are discussed in greater detail in a recent publication (Gasaway and Coady, 1973). Sequential weights of cows at the Kenai Moose Research Center indicated a weight loss of 8 to 18 percent associated with calving and rearing young (LeResche and Davis, 1971).

Rapid growth rates and large body size of moose reported in this study suggest favorable range conditions. Growth of ungulates in both body mass and skeletal dimensions is closely related to plane of nutrition (Brandy et al., 1956). Maximum size and growth rates have been positively correlated with quantitative and qualitative aspects of the food supply for numerous ungulates, including reindeer (Klein, 1964, 1968), and black-tailed deer (*Odocoileus hemionus columbianus*) (Cowan and Wood, 1955). LeResche and Davis (1971) indicated that low growth rates and small body size of moose on the Kenai Peninsula may be due to relatively poor range conditions. Klein (1968) further suggested that quantitative aspects of the food resource was important in determining growth rate andbody size. Thus, range "carrying capacity" must consider winter periods when physiological requirements of animals are low and food supply is critical, and summer periods when physiological demands for reproduction, fat deposition, and body growth are high and high quality food is important.

Klein (1965) has discussed the annual nutritional cycle of deer. Winter nutritional requirements, though reduced, are generally in excess of available forage quantity, resulting in a gradual weight loss throughout the winter. During summer nutritional requirements are relatively great although high quality forage may be relatively abundant. This physiological cycle is apparently controlled largely through genetic mechanisms, since Wood et al. (1962) reported that captive black-tailed deer fawns stopped growing and adults lost weight during fall and winter, even though a high quality ration was available throughout the year.

Table 6. Weight and total length of lactating and non-lactating cow moose over 2 years of age during June in interior Alaska (GMU 20A).

Non-lactating	No.	Mean	Range
Weight	4	429	395-463
Total length	4	264	242-275
Lactating	**No.**	**Mean**	**Range**
Weight	4	379	367-390
Total length	4	276	269-284

Large fluctuations in body weight of adult moose reported in this study may also reflect adequate nutritional status and favorable range conditions. Nordan et al. (1968) reported that captive black-tailed deer maintained on a low plane of nutrition exhibited smaller annual fluctuations in body weight than deer fed a high quality ration. The magnitude of the annual cycle was apparently related to the amount of fat deposition during summer months which determines the ability of the animal to effectively participate in reproductive activities and its success in surviving the winter.

Reproduction: Thirty female reproductive tracts collected between February and May 1971 from moose two years old or older were examined. Twenty-one (70%) of the animals were pregnant. Of 13 females obtained from the inhabited Fairbanks area, only seven (54%) were pregnant. Fourteen (82%) of the remaining animals, obtained from the uninhabited Tanana Flats were pregnant. Three of five (60%) adult females examined during April 1973 on the Tanana Flats were pregnant. No yearlings examined at any time were pregnant.

Ovarian analyses from approximately 70 female moose older than calves have not been completed at this time.

Pregnancy rates observed in this study during the winter of 1970-1971 and during April 1973 were somewhat lower than those reported by other workers. Edwards and Ritcey (1958), Pimlott (1959), Rausch (1959), Simkin (1965), Rausch and Bratlie (1965), and Houston (1968) reported average pregnancy rates of 75, 81, 94, 87, 90, and 90 percent for females older than yearlings in British Columbia, Newfoundland, Alaska, Ontario, Alaska, and Wyoming, respectively. Edwards and Ritcey (1958) included animals collected during October in their calculations, and therefore may not have detected some pregnancies or pregnancies resulting from later oestri. Pimlott (1959) reported variation in pregnancy rates of 74 to 87 percent among moose from different areas of Newfoundland. A similar range of pregnancy rates has been reported by Cheatum and Severinghaus (1950) for white-tailed deer (*Odocoileus virginia*) in New York.

Low pregnancy rates observed in this study are difficult to explain. There is little evidence in the literature for resorption, abortion, or stillbirth among cervids. Only two out of 283 reproductive tracts examined by Pimlott (1959) indicated resorption, while Rausch (1959) found no definite indication of mortality among embryos or fetuses in Alaskan moose. However, resorption in moose has been recorded by several workers in the USSR, particularly following severe winters (in Markgren, 1969). Thus, the possibility of intrauterine death contributing to the low pregnancy rates in the Fairbanks area must be considered.

Another potential cause of low pregnancy rates may be due to non-breeding of females. While this has never been implicated as a factor contributing to low calf production in Alaska, the possibility of females not being bred under certain situations, either because of low bull:cow ratios or because of continuous anoestrus during the normal breeding season, cannot be discounted.

Of 22 fetuses examined between February and May 1971, 15 were female and 7 were male. Sex ratios at birth for most species of mammals are generally near 1:1, or slightly in favor of males (Robinette et al., 1957). However, among some species under favorable environmental conditions, males tend to predominate. Rausch (1959) listed several factors which may influence sex ratios at birth, including age structure of the population, reproductive history of the female, nutritional status before and after birth, and severity of the winter. Generally under adverse conditions males tend to suffer the greatest intrauterine mortality, and this factor, considering the severity of the 1970-1971 winter, may have been responsible for skewed fetal sex ratios observed here (assuming intrauterine mortality occurs in moose).

On June 27, 1972 a female moose fetus was collected from a 3-year-old cow on the Tanana Flats (Coady, 1973). Based on fetal growth rates reported by Rausch (1959), measurements (weight, 6.71 kg; girth, 42 cm; total length, 70 cm) indicated that the fetus was approximately six to eight weeks from term. Since the gestation period for moose in North America is about 240-246 days (Peterson, 1955; Rausch, 1959), conception of the above fetus may have occurred during December. Normally, the peak of conception occurs around the first of October for moose in Alaska (Rausch, 1959).

Markgren (1969) reported that although births during April and early May are rare in Sweden, calving during midsummer is quite common, and births during August, September, and even October have been recorded. Although occasionally reported verbally, the only written account known to this author of a late pregnancy in North American moose was of a pregnant cow shot in Alaska on the lower Tanana River in September (Davis, 1952).

Late pregnancies indicate conceptions decidedly later than during the main periods of oestrus. Recurrence of oestrus in moose has been reported by Edwards and Ritcey (1958), Rausch (1959), and Markgren (1969). Data presented by Edwards and Ritcey (1958) indicate an interval of approximately one month between successive oestri. Males are apparently capable of breeding for a considerable period during the fall since Rausch (1959) found spermatozoa in the epididymis from mid-August to December. Thus, the late pregnancy observed in this study suggests conception during a third or fourth oestrus.

Several factors contributing to conception after an initial oestrus have been suggested. Russian data (in Markgren, 1969) indicate that the "heat" during which the cow will allow copulation lasts less than 24 hours, while Altmann (1959) reports for American moose that the bull stays with a cow for only 7 to 12 days. Therefore, a bull conceivably may not be available for mating during an initial oestrus. Other Russian information cited in Markgren (1969) indicates that young (primarily yearlings) and nutritionally deficient cows may have delayed oestri.

Although exceptions to and irregularities in most physiological processes can be found, "normality" of nearly all individuals is the rule. Among moose populations the synchrony and uniformity of oestrus cycles and subsequent calving among the overwhelming majority of the population under widely varying environmental conditions remains the most remarkable phenomenon.

Femur Marrow Fat: Percent fat in femur bone marrow was analyzed from 65 adult and 61 calf moose examined between February and May 1971 (Fig. 8). A significant difference ($P < 0.01$) in marrow fat between adults dying from malnutrition and from unnatural causes (road and railroad accidents, shooting, etc.) was found, while a similar comparison between calves revealed no significant difference ($P > 0.50$). Duncan's new multiple range test indicated no significant difference in marrow fat between moose dying from unnatural causes in remote areas and from apparent wolf (*Canis lupus*) predation, and between moose shot in May and from malnutrition (Fig. 9). Marrow fat of animals dying from apparent wolf predation, unnatural causes near Fairbanks, and shooting in May were intermediate in value and not significantly different. Moose which appeared to be in the poorest physical condition were selected for shooting.

Quantative analysis of depot fat has frequently been used as a criterion of physical condition of animals, and various procedures for determination of total body fat, subcutaneous fat, abdominal fat, perinephric fat, and bone marrow fat have been reviewed (Cheatum, 1949; Riney, 1955; Smith, 1970). Riney (1955) noted that deposition or mobilization of fat, in response to favorable or unfavorable conditions, occurs first in subcutaneous depots, followed by abdominal, perinephric, and bone marrow depots. Thus, fat mobilization from bone marrow tissue probably occurs only after other fat reserves have been largely depleted.

Marrow fat values have been used to evaluate physical condition of white-tailed deer (Ransom, 1965), elk (*Cervus canadensis*) (Greer, 1968, 1969), moose (LeResche, 1970), pronghorn (*Antilocapra americana*) (Bear, 1971), and caribou (*Rangifer tarandus*) (Miller, 1972). Greer (1968) noted that elk in excellent physical condition have marrow fat values of 82 to 99 percent, while marrows from "winter-killed" elk contain less than 1 percent fat. Mech (1970) found that only 15 percent of wolf-killed adult moose examined on Isle Royal had low marrow fat content. Relatively low mean marrow fat content among all groups of adult moose dying from unnatural as well as natural causes (Fig. 9) reflects the severity of the 1970-1971 winter and the poor physical condition of most animals. However, it is interesting to note that moose dying from unnatural causes in remote areas had both the highest marrow fat and the highest pregnancy rate of any group of animals.

While marrow fat from adult moose collected in this study clearly reflects a difference in nutritional status of the animal, samples from calves were uniformly low (Fig. 8). Among young animals Abrams (1968) reported that the sequence of tissue development is nervous system, skeletal system, musculature, and finally fat. Thus, fat is apparently a "luxury" which moose calves in interior Alaska, if anywhere, cannot afford.

Fig. 8. Average percent fat (circles), standard deviation (triangles), and range (bars) in femur bone marrow of male and female moose dying from malnutrition and unnatural causes in GMU 20A and 20B between February and May, 1971. Number in circles indicate sample size.

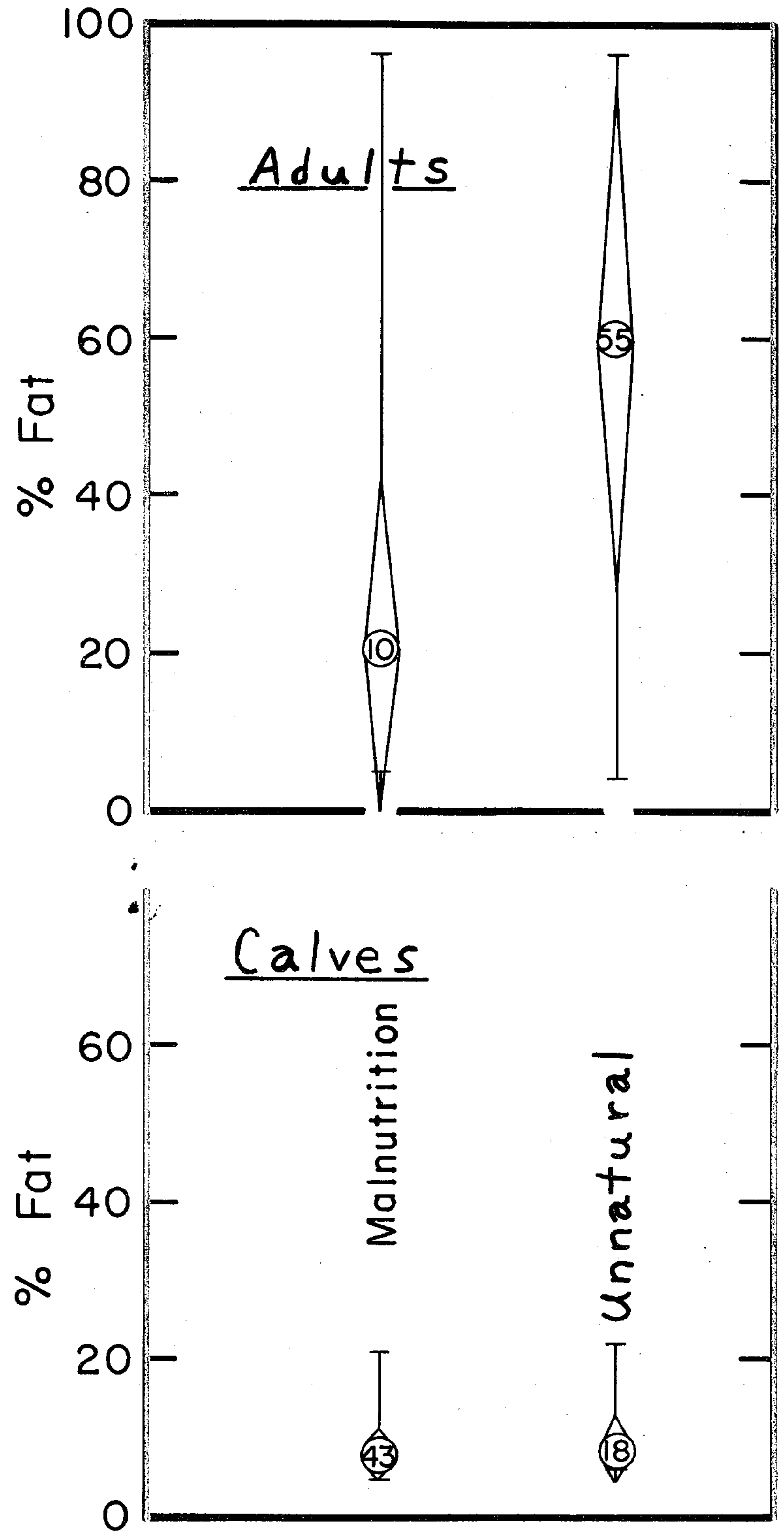
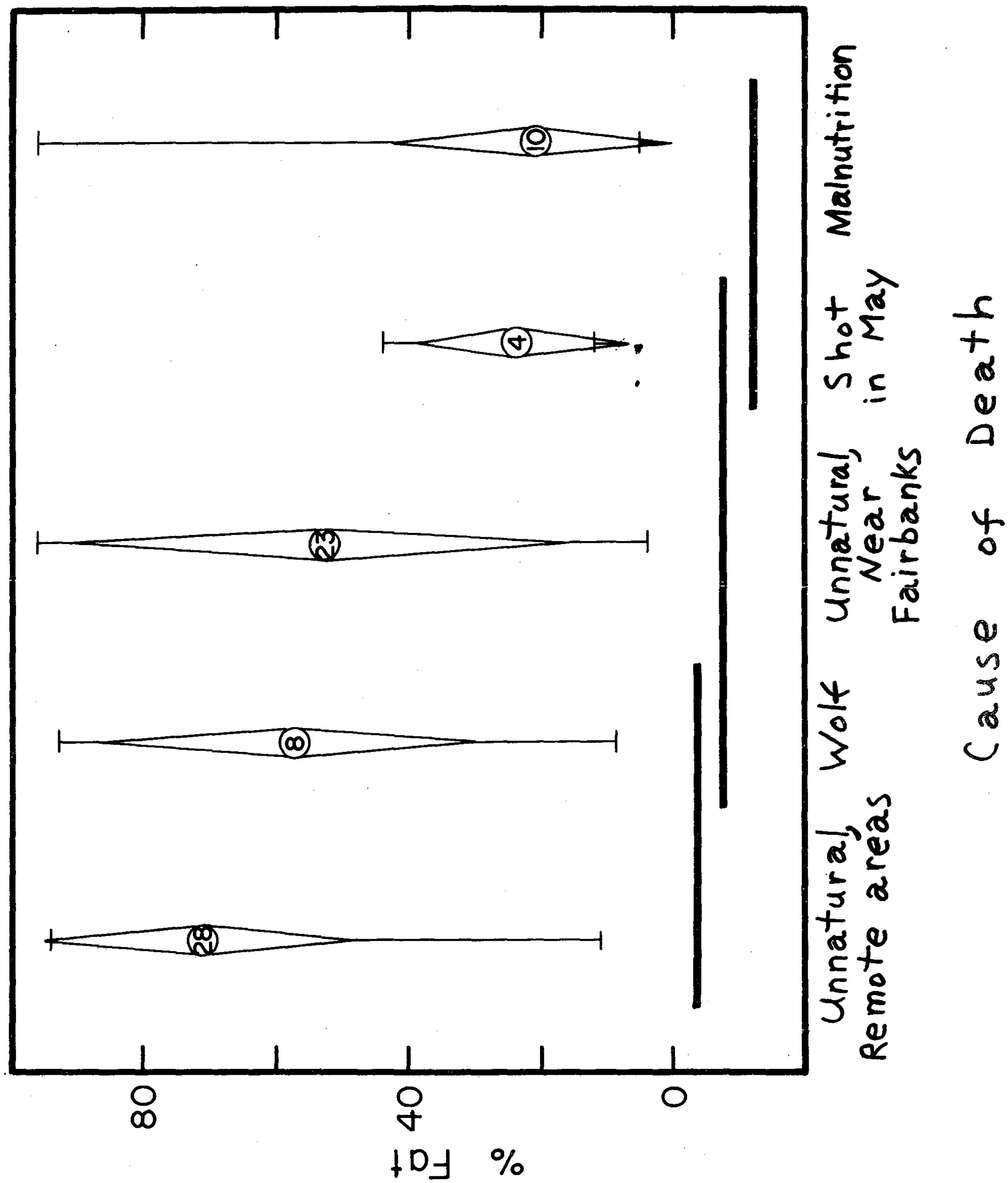


Fig. 9. Average percent fat (circles), standard deviation (triangles), and range (bars) in femur bone marrow of male and female adult moose dying from various causes in GMU 20A and 20B between February and May, 1971. Number in circles indicate sample size. Solid bar indicates no significant difference between sample means as measured by Duncan's new multiple range test.



Winter Mortality of Moose: Due to unusually early and heavy snow during the winter of 1970-1971, winter mortality throughout a large portion of interior Alaska was relatively high. In addition to deaths resulting from malnutrition, numerous animals attracted to plowed roads and railroads were killed by vehicles. Moose deaths resulting from natural and accidental causes in the Fairbanks area occurred primarily between December 1970 and May 1971. During this period the Alaska Department of Fish and Game office in Fairbanks received over 400 reports of dead, dying, and nuisance moose near Fairbanks. Approximately 250 of those reports were received during February and March.

Between December 1970 and May 1971, 154 moose dying from natural and accidental causes were examined. Calves were the most common age group in the sample. Male and female calves died in approximately equal numbers, while among adults females tended to predominate (Fig. 10). The sex ratio of both dead calves and adults may, in part, reflect the sex ratio in the population of the two age groups. In the Susitna River Valley in southcentral Alaska, Pitcher (per. comm.) also found that approximately equal numbers of male and female calves predominated among winter-killed moose during 1970-71. Among adults, however, males died in higher proportion than they were found in fall sex and age composition counts.

The relationship between winter weather conditions and winter mortality was first reported by Severinghaus (1947) for deer, and recently discussed by Bishop and Rausch (1973) for moose. Severity of winter snow conditions in the Fairbanks area (Fig. 11) is reflected by survival of moose calves in the Fairbanks area to 1 year of age (Fig. 12). Calf survival over the two winters of the most severe snow conditions (1965-66 and 1970-71) was exceptionally low, while a gradual increase in the ratio of yearlings per one hundred females occurred following winters of less severe snow conditions. In Fig. 11, the dotted line indicates the average chest height of calves, while the solid line indicates the average chest height of adult moose.

Moose-Snow Relationships

The following has been taken, in part, from a recent publication by Coady (1973).

The structural, physical, and mechanical properties of a snow cover vary greatly, depending on conditions of deposition and subsequent metamorphism. Seasonal snow covers behave in an extremely dynamic fashion, and the only completely predictable phenomenon is change itself. Metamorphic processes which take place within a seasonal snow pack have been described by numerous workers (Bader et al., 1939; Formozov, 1946; Gold, 1958; Kingery, 1960; Benson, 1967, 1969; Trabant, 1970). While wind action is a major factor affecting snow as it precipitates (Sommerfeld, 1969), diagenetic processes resulting from temperature, time, and settling (Keeler, 1969) begin immediately after deposition. All features of a snow pack reflect post-depositional changes as much or more than they reflect the character of snow at the time of deposition. High temperature relative to the melting point of snow and steep temperature

Fig. 10. Age specific sex ratio of moose killed in GMU 20A and 20B during winter, 1970-71.

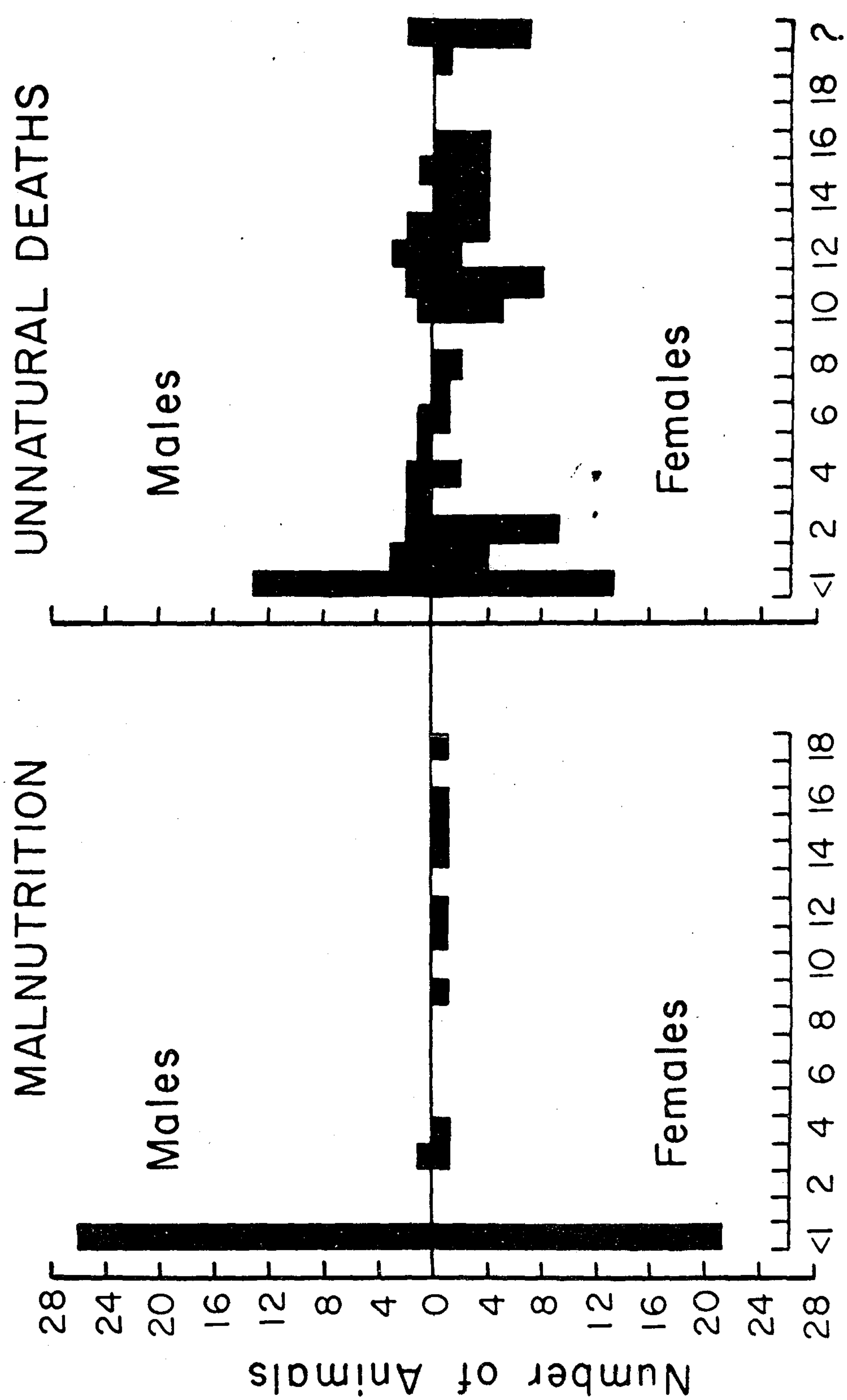


Fig. 11. Relative yearly snow severity near Fairbanks, Alaska, calculated by plotting snow depth on ground on the last day of the month, between October and April, and determining the relative area under the curve with a planimeter. Data are taken from National Weather Service Records from Fairbanks.

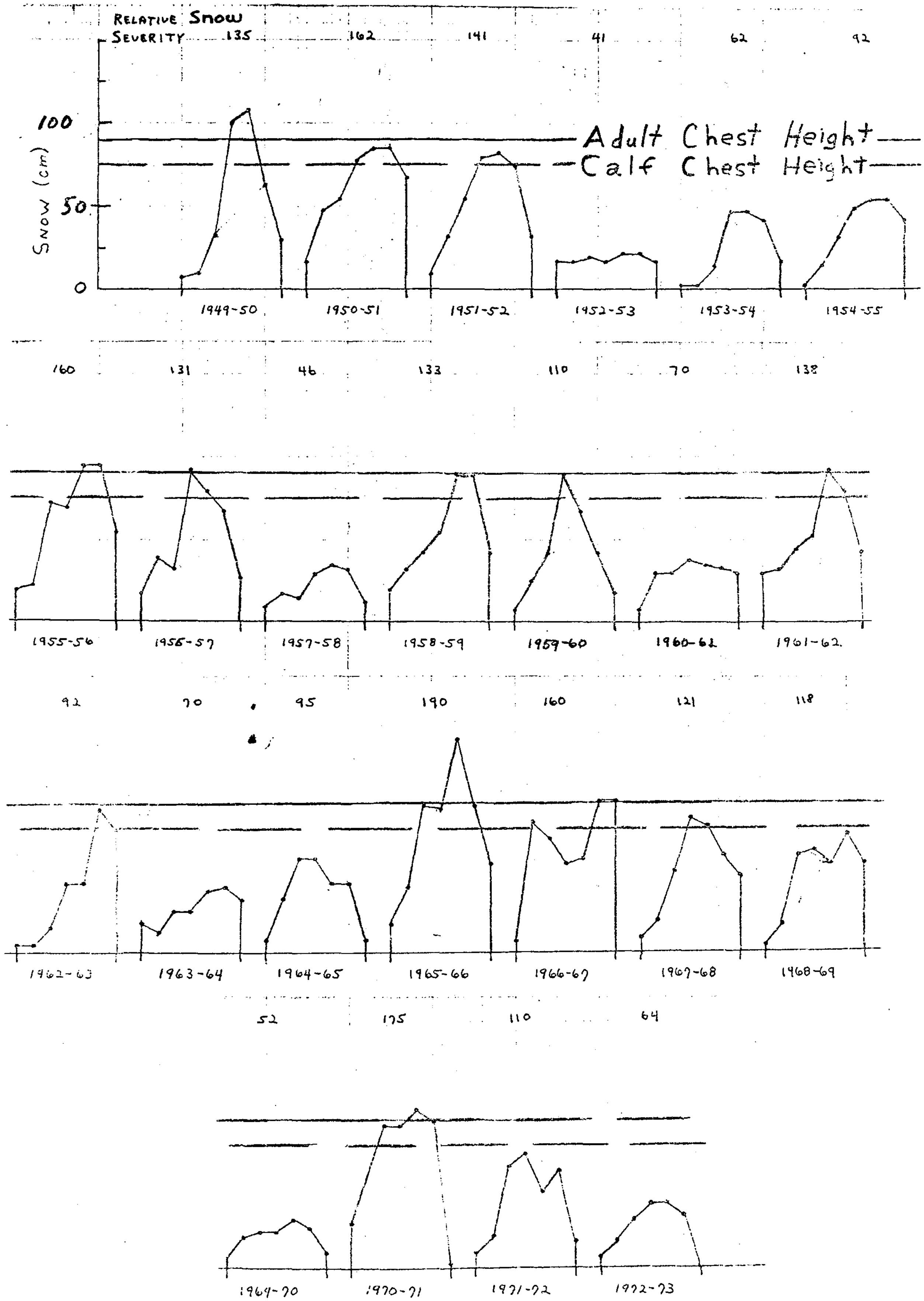
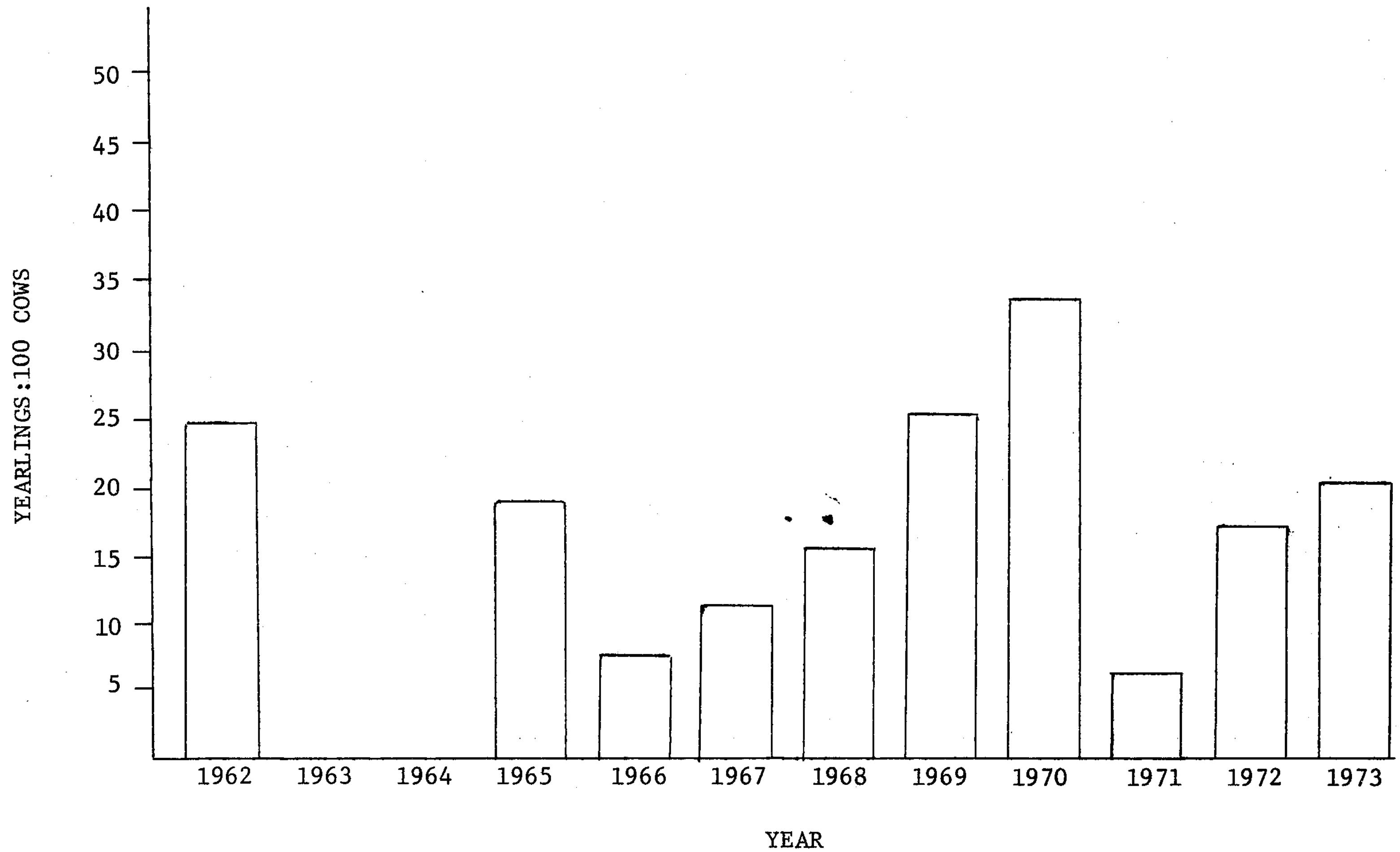


Fig. 12. Survival of moose to one year of age as indicated by spring sex and age composition counts in GMU 20A. Data are taken in part from Rausch (1971).



gradients are effective in promoting vapor transport, a major cause of metamorphism. Constant fluctuations in air temperature and accumulation rate of snow cause continual changes in both thermal and gravitational forces which are perceptible within days or even hours.

The properties of snow can be divided into fundamental and derived characteristics. A discussion of fundamental properties, which include size, shape, orientation, and packing of particles, is beyond the scope of this review. While fundamental properties of a snow cover do bear a relationship to the mechanical properties and are important for a complete understanding of snow metamorphism, they are probably of minor significance in ungulate snow ecology (Pruitt, 1971a).

Derived properties of snow are those which depend on fundamental properties for their magnitude and rate of change (Keeler, 1969). Generally, they are more easily measured than fundamental properties, and are useful indices to the nature of snow. Although derived properties are numerous and diverse, relatively few are generally measured to characterize a snow cover. The most commonly measured derived properties used in biological work are depth, temperature, density, and hardness.

Physical characteristics of moose affecting their mobility in snow have been related to height of the animal and weight-load-on-track of the feet. When moose sink into snow to depths approaching chest height and are forced to "plow" or bound through the snow, energy required for movement is greatly increased. However, snow depths below chest height may hinder movement by increasing resistance to movement of the legs. Weight-load-on-track is a measure of the weight per unit area on the feet, and reflects the extent to which a moose may be supported by a substrate. Under situations in which snow will partially or fully support a moose, resistance to and energy required for movement may be reduced.

Procedures for measuring chest heights and track loads have recently been described in detail. Kelsall (1969) measured chest heights from the tip of the thoracic limb, with leg extended perpendicular to the body, diagonally to the sternum. The measurement may slightly overestimate actual chest height since the leg may be less extended on a standing than on a decumbent animal. In many studies hoof load, or weight on hooves alone, has been used to measure the bearing surface of the legs. However, Kelsall and Telfer (1971) and Telfer and Kelsall (1971) indicated that the entire foot from the tip of the hoof to the dew claws supports an ungulate in soft snow, and described a procedure for measuring foot areas and calculating foot loads. Foot loads measured by the previous technique are probably minimal since the measurement does not allow for spreading of hooves and angular placement of legs in snow. However, the actual foot load is probably somewhat greater since only when standing is weight supported on only two feet. In addition, Kelsall (1969) thought that as much as three-fifths of the weight of a standing ungulate is distributed on its forefeet.

The significance of chest heights and track loads of moose reflecting adaptation to snow was first shown by studies in Russia and later in North America. Nasimovich (1955) reported that chest heights of adults averaged 105 cm or greater. Kelsall (1969) found that average chest heights of male moose in Eastern Canada increased from 81.9 cm for calves, to 98.9 cm for yearlings, and 104.7 cm for animals older than four years. Kelsall and Telfer (1971) found an average chest height of 106 cm for male moose older than four years in Western Canada. Similar chest heights of 84, 96, and 104 cm for 60 calves, yearlings, and moose older than two years, respectively, have been found in interior Alaska.

Nasimovich (1955) noted that moose on the Kola Peninsula in Russia were unaffected by snow depths of 40 to 50 cm, while movement was definitely impeded by depths of 60-70 cm. At 60-70 cm calves frequently followed in the trail of adults. Nasimovich (1955) concluded from the Russian literature that snow depths of 90 to 100 cm may be considered critical to moose, since at that depth winter mortality substantially increased. Kelsall (1969) reported similar observations from Eastern Canada, noting that movement was unrestricted by depths of 44 cm and severely restricted by depths of 70-99 cm. Snow depths greater than 90-100 cm were critical for moose unless of very short duration. Ritcey (1967) and Prescott (1968, in Telfer 1970) found that depths of 60-70 cm restricted mobility of moose in British Columbia and Nova Scotia, respectively. In Alaska substantial winter mortality has occurred in several areas of the state when snow depths exceeded 90 cm for several months.

The above data suggest that snow depths up to 40 cm, or depths approximately equal to the carpus or tarsus height, cause little or no hindrance to movement. From 40 to 60-70 cm, or depths approaching two-thirds of the chest height, movement is only slightly restricted. At depths greater than 70 cm movement is definitely impeded, while at depths greater than 90 cm, or approximately equal to or slightly less than chest height of standing moose, movement is greatly restricted to the extent that adequate food intake may become impossible. Calves, because of their shorter legs, may be restricted by snow depths somewhat less than those affecting adults, while large males may be least affected by deep snow. Differential movement of sex and age groups during winter reported by several workers (LeResche, 1973; Pulliainen, 1973) may reflect, in part, the relative ability of the different groups to move in deep snow.

Heights of moose from interior Alaska and the Kenai Peninsula have been compared to illustrate that leg length in moose may be adaptive to snow conditions. In interior Alaska in winter moose habitat snow depths of 70 cm or more, that persist for several months are the rule, and depths in excess of 90 cm are not unusual. On the Kenai Peninsula, however, depths in winter moose habitat range near 40 cm for short periods, and seldom reach 60 cm. Since chest heights of moose from the Kenai Peninsula were not available, a ratio of shoulder height to total length was used to reflect relative differences in leg length and presumably in chest height of moose from the two areas. Average ratio for 31 fully grown moose from the Interior was .68, while that of 64 similar animals from the Kenai Peninsula was .59. Similar ratio for 18 calves 6 to 12 months of age from the Interior, and 50 calves from the Kenai Peninsula were .72 and .70, respectively. Average shoulder heights of moose from the Interior and from the Kenai Peninsula were 182 cm and

172 cm for adults, and 148 cm and 141 cm for calves, respectively. Thus, both relative and absolute height of moose is lower, particularly among adults, from the Kenai Peninsula than from interior Alaska.

Variations in body size of animals may be due to genetic or nutritional differences. Since data from the Kenai Peninsula were obtained from moose on relatively poor range (LeResche and Davis, 1971), and data from the Interior were from moose on relatively good range (Coady, 1973), differences in skeletal dimensions of animals from the two areas may reflect nutritional differences. While nutritionally related differences in skeletal growth do occur (c.f. Klein, 1964), there is little reason to expect that poor range on the Kenai Peninsula is responsible for preferential growth of body length over foreleg length. Thus, while nutritional deficiencies may account for smaller absolute shoulder height of Kenai Peninsula moose, it is probably not responsible for reduced height of animals relative to length.

While long legs *per se* are not necessarily an adaptation to deep snow (e.g., height facilitates the browsing habit), the selective advantage to moose of increased leg length in regions of deep snow is obvious. Therefore, observed differences in relative height of moose between the Kenai Peninsula and the Interior in Alaska are probably of genetic origin and may be related to differences in snow conditions between the two areas. Nasimovich (1955) noted that reindeer from the taiga zone where deep, soft snow is common have longer legs than those animals from tundra areas. Nevertheless, additional studies would be useful.

Nasimovich (1955) reported that the average track load of "several moose" in Russia was 420 g/cm^2. This value presumably represents the total foot load, and not just hoof load, of the animal. Kelsall and Telfer (1971) measured average foot loads of approximately 710 g/cm^2 for male moose four years and older during December in Western Canada. Higher average hoof loads of 789 to 922 g/cm^2 were found by Kelsall (1969) for similar aged male moose from two areas of Eastern Canada. However, the higher values were measured prior to rut, while the lower hoof loads were obtained following the rut and presumably after considerable weight loss.

Foot loads of moose in interior Alaska are not uniform but vary with age of animal and with season. Average foot load decreased from 593 g/cm^2 for eight adult cows in October to 432 g/cm^2 for 19 adult cows between April and June. Thus, as winter progresses and snow depth and hardness increase, foot loads of adults decrease due to seasonal loss of body weight. Foot loads of nine calves between April and June averaged 317 g/cm^2, over 100 g/cm^2 less than adults during the same season. Thus, the shorter legs of calves may in part be compensated for by lower foot loads. No seasonal increase in hoof size was noted for Alaskan moose, as Pruitt (1959) reported for caribou.

Snow density has been related to track depth of moose. Kelsall and Prescott (1971) concluded from their extensive observations that snow densities of 0.10 to 0.19 g/cm^3 do not support moose, densities of 0.20

to 0.29 g/cm^3 provide some support, and densities of 0.30 to 0.39 g/cm^3 limit foot penetration to approximately 50 percent of the snow depth. Nasimovich (1955) reported that snow densities of 0.20 to 0.22 g/cm^3 provide little support to a running moose, while densities of 0.24 to 0.26 g/cm^3 limit foot penetration to two-thirds of the total snow depth. However, under these conditions, moose experience difficulty lifting legs from holes in the snow.

Kelsall (1969) and Kelsall and Prescott (1971) were unsatisfied with attempts to relate ungulate support to snow hardness. Theoretically, a standing moose should be supported by a vertical snow hardness equal to or greater than its track load (Kelsall, 1969; Kelsall and Prescott, 1971). However, Kelsall and Prescott (1971) found the support capacity of snow to be extremely variable, depending on the presence or absence of surface crusts and the hardness of underlying snow layers. Both white-tailed deer and moose frequently broke through crusts that should easily have supported the animal. Moose, with maximum track loads of 1,000 g/cm^2, broke through crusts of 8,000 g/cm^2 at the surface, 10,000 g/cm^2 at 15 cm, and 90,000 g/cm^2 at 34 cm. Moose also broke through crusts of 20,000, 10,000, 30,000, 40,000 and 25,000 g/cm^2 to ground level at a depth of 73 cm. On other occasions moose were supported by surface crusts of 2,000 to 30,000 g/cm^2. Peek (1971a) noted that surface crusts of 7,500 g/cm^2 supported moose in Minnesota. In interior Alaska extremely hard crusts are unusual, although an adult moose walking on a trail penetrated 20 cm in 30 cm deep snow when the hardness was 2,000 to 4,000 g/cm^2. On another occasion both a cow and calf walking on a trail penetrated 39 cm in 90 cm deep snow when the hardness was 1,000-2,000 g/cm^2.

Preliminary attempts to use the Rammsonde penetrometer to quantify the support capacity of snow for moose have been attempted. The integrated ram hardness (R_i) was calculated for the total ram hardness of the snow to foot penetration depth (Table 1). Average R_i ranged from 188 to 570 kg/cm for penetration depths of 22 and 42 cm, respectively. Although not immediately evident from the limited data above, further study may reveal a predictable relationship between R_i and depth of foot penetration in or resistance to movement through snow.

Throughout most of the circumboreal range of moose and within favorable habitat, snow conditions that significantly benefit moose by providing support apparently are seldom extensive or persistent. Even on the tundra of Alaska where snow density and hardness are very great, the snow cover in winter riparian habitat provides little or no support to moose. In other areas supporting crusts are usually extremely localized, and are apparently rarely consistent enough to facilitate travel. Murie (1944), Nasimovich (1955), Kelsall and Prescott (1971), Peek (1971a), and others indicated that snow conditions which only partially support moose may make movement more difficult and hazardous because of the resistance to movement of legs provided by the dense snow and/or the danger of abrasion from hard crusts. Snow conditions in which depth of penetration is variable may require an animal to expend more energy recovering from breaking through crusts and climbing onto crusts than would be required to move through deep snow offering no support. However, dense, hard snow offering uniform support, such as ski or snow machine trails, may be extensively used.

Comparison of foot loads of moose from different regions may indicate adaptation to varying snow conditions. In Western Canada Kelsall and Telfer (1971) measured average foot loads of 710 g/cm^2 for adult moose during December, whereas in interior Alaska I report foot loads of 593 g/cm^2 for adults during October. Normal snow conditions at the collection site in Western Canada were not given, but presumably snow depth and hardness were at least as great as those in interior Alaska. Although I followed procedures described by Kelsall and Telfer, possible differences in measuring foot area must be considered.

The influence of snow on seasonal movements of moose has been reported by several workers, although quantitative observations are relatively limited. The greatest effort to document and review relationships between snow and moose migrations has occurred in the USSR (Formozov, 1946; Nasimovich, 1955; Knorre, 1959, 1961; Egorov, 1965; Heptner and Nasimovich, 1967 in Van Ballenberghe and Peek, 1971). However, significant contributions have also been made in Europe (c.f. Pulliainen, 1973) and in North America (Edwards and Ritcey, 1956; Ritcey, 1967; Knowlton, 1960; Houston, 1968; Kelsall and Prescott, 1971).

Nasimovich (1955) drew several conclusions from the copious Russian literature regarding the influence of snow on moose migrations in both mountains and flatlands of the USSR. Basically, in regions where maximum snow depth averages less than 50 cm and deep snows are of short duration, extensive seasonal migrations are uncommon, although local movements may occur. However, in areas where maximum snow depths in excess of 70 cm persist for long periods, seasonal movements occur from areas of deep to less deep snow. The longest migrations, ranging from 150 to 300 km, occur among animals living on flat terrain, although migrations of 100 to 150 km are common across divides or to lower elevations in mountainous regions. Gradual movements generally occur between October and January, and may coincide either with the first lasting snow cover or with snow depths of 25 to 45 cm. However, some animals migrate before snowfall while others remain in summer habitat until snow depths reach 60 to 70 cm.

Pulliainen (1973) reviewed the literature describing relationships between snow and moose migrations in Scandinavia. Movements in most areas are closely correlated with prevailing snow conditions. Gradual movements from high to low elevations usually begin in November or December, although they may be delayed or may not occur during years of little snow. Some animals, particularly cows with calves, begin migrating at first snowfall, while others, particularly bulls and cows without calves, remain at high elevations until snow depths reach 60 to 70 cm. However, formation of icy crusts may initiate downward migration of almost all animals (Krafft, 1964). Return to summer range is usually abrupt, and occurs during May after snow melt has exposed patches of ground.

In North America several early workers, including Murie (1934) on

Isle Royal, Hosley (1949) in Maine, Bauman (1941, in Hosley) in Yellowstone Park, Murie (1944) in Alaska, and Hatter (1946, in Hosley) have commented on snow depths and moose movements. However, Edwards and Ritcey (1956) in British Columbia were the first to present detailed observations on the relationships between moose migrations and snow conditions. They found that a gradual altitudinal movement from 1525-2135 m to 760-1220 m during fall and winter coincided with a gradual increase in snow depths on summer range. A rapid return to higher elevations during spring coincided with a rapid snow melt. Segregation of winter and summer ranges was not complete, although most animals had departed higher elevations by the time snow depths reached 75 cm. Upward movement to summer range was initiated when melting had reduced snow depths to 30 to 45 cm. Cold temperatures appeared to moderate the effect of snow by speeding movement downward in the fall and retarding movement upward in the spring.

Ritcey (1967), also in British Columbia, noted that deep snows at high elevations were responsible for the fall and winter movement to elevations below 1050 m. Arrival on winter range generally began in November when snow depths were less than 15 cm, and continued throughout the winter. Departure from winter range began in late February or March, while snow depths were as great as 125 cm but declining.

Kelsall and Prescott (1971) and Telfer (1967a, b) in the Canadian Maritime Provinces, studied winter segregation of white-tailed deer and moose in relation to moose sickness induced by *Parelaphostrongylus tenuis*. Although segregation was not complete, deer generally wintered at elevations below 200 m, while moose remained at elevations above 200 m. Snow depths of 85-90 cm above 200 m did not initiate downward migration of moose, even though snow depths were more favorable and browse more abundant at lower elevations. However, relatively high density and hard crusts due to winter thaws and rains may provide some support to moose, thereby reducing the effective snow depth (Telfer, per. comm.).

In Montana Knowlton (1960) and Stevens (1970) reported that deep snows in summer range above 1830-2135 m initiated movements to lower elevations. Movements were gradual, and frequently lasted from December to March. Harry (1957) in Wyoming reported that increasing snow depths at high elevations resulted in a gradual downward movement and concentration of moose in mountain valleys by December. Snow conditions associated with these studies in Montana and Wyoming were not reported. However, Houston (1968) in Jackson Hole, Wyoming, found that downward movements from 2190 m to winter range at lower elevations began in late December in response to snow depths of about 80 cm on the summer range. Movement to spring and summer range began in late March in response to a snow crust formation capable of supporting mooose and in response to disappearance of snow from south and east slopes. Moose densities on winter range were 10 moose/km^2 in Montana (Stevens, 1967:7 in Stevens, 1970) and 19 moose/km^2 in Jackson Hole (Houston, 1968).

Seasonal movements of moose in response to snow in Alaska have been noted by some workers. Rausch (1958) reported that an early snowfall in 1956 at high elevations in southcentral Alaska caused an early migration in November to lowland areas. Rausch concluded from his extensive observations that snow influences but does not cause seasonal movements of moose.

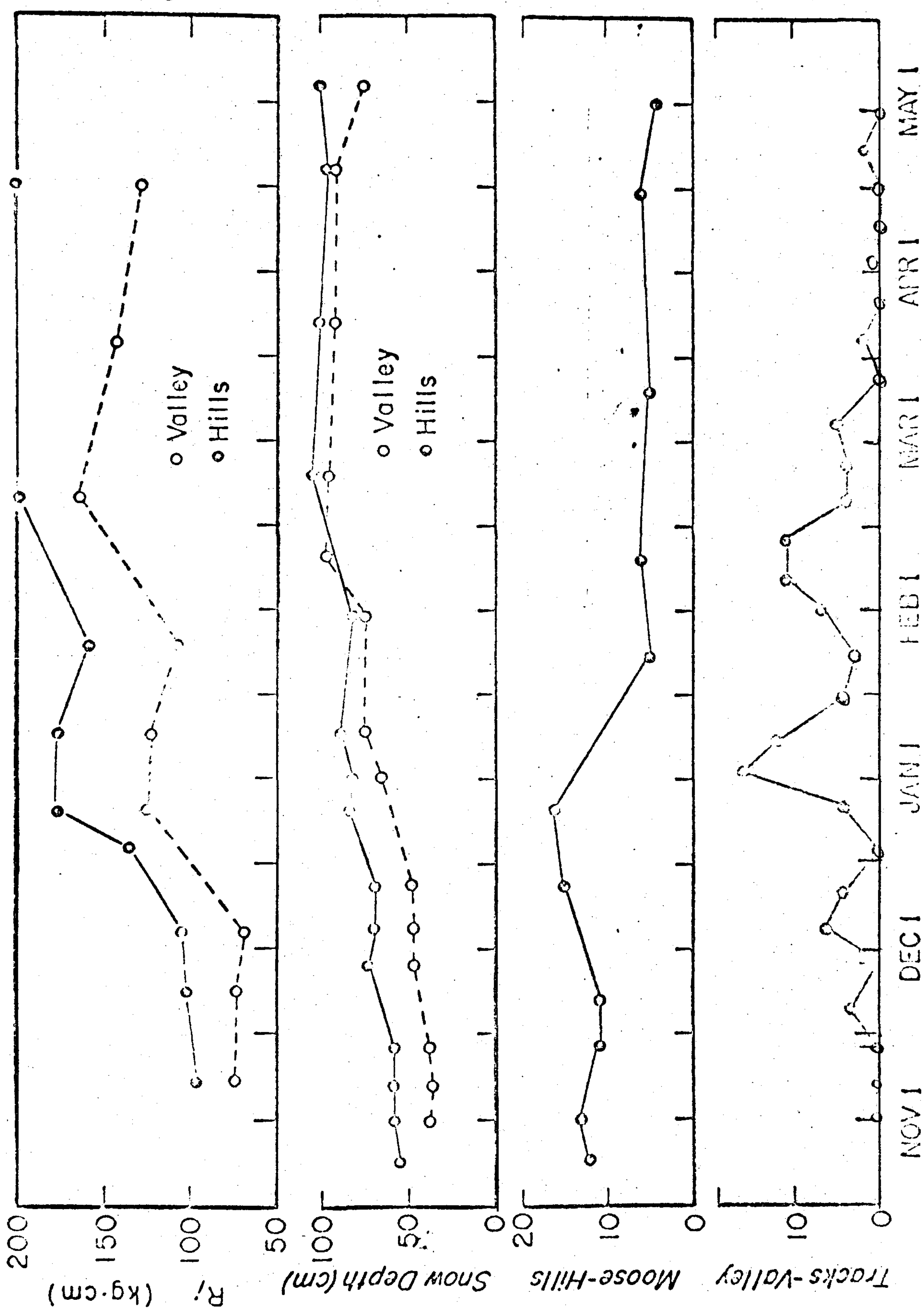
Fall migrations in hills and mountains of interior Alaska generally occur as a gradual downward movement between December and February or March. The extent, time, and composition of the migrating animals appear to be closely related to snow conditions. In late November and early December, 1970, snow depths of 90 cm (55 cm above average) at elevations of 600 to 915 m in hills near Fairbanks apparently caused an abrupt downward migration of moose to elevations below 300 m. Over 1200 animals were seen on or moving toward low elevation riparian habitat during 23 hours of Alaska Department of Fish and Game aerial surveys in early December. Almost no animals were found on the usual upland fall and early winter range. Snow depths of 110 to 120 cm persisted until early April and moose remained along rivers until mid-March when they apparently dispersed into adjacent timbered areas. Similar observations during 1970 were reported by Bishop (1971) for western interior Alaska, where snow depths of 60 cm during the end of November apparently precipitated an early movement of moose from upland areas to lower elevation riparian habitat, where they remained until late March.

The response of moose to winter weather factors has been studied in interior Alaska since 1971. For example, relationships between moose movement and snow conditions during 1971-1972 were examined on a study area near Fairbanks (Fig. 13). "Tracks-Valley" indicates the seven-day total of fresh moose tracks crossing a one-half mile long transect in a valley. The valley is located at 245 m elevation, and represents typical winter riparian moose habitat. "Moose-Hills" indicates the number of moose counted during frequent intensive aerial surveys in a 75 km^2 drainage above the valley transect. The upland site ranges from 550 to 670 m elevation, and consists of mixed conifer and deciduous trees and shrubs which characteristically support modest numbers of moose during summer and fall in interior Alaska. While neither "Track-Valley" nor "Moose-Hills" indicates actual number of animals, they are thought to reflect the trend of animal abundance on each site. Snow depths and integrated Rammsonde resistance of the total snow cover (R_i) in shrub communities on the two sites are also noted.

A decrease in moose observed at high elevations and an increase in fresh tracks at low elevations occurred during late December and early January. The decrease in fresh tracks in the valley during mid-January may have been related to reduced activity during extremely cold temperatures (-40° to -50°C) during that period, while the decrease in tracks after late February may have resulted from a dispersal of animals away from the riparian habitat where the transect was located. After January the number of moose in the hills remained low throughout the winter.

Snow depths at high elevations gradually increased to about 80 cm at the time of movement in late December. While lowland snow depths throughout January and early February ranged from 15 to 25 cm below those in the hills, depths at the two sites remained nearly identical during the rest of winter. The R_i of the snow cover sharply increased

Fig. 13. Relationship between moose movement between and snow depth and Rammsonde hardness at high and low elevations in the Chatanika River drainage (GMU 20B) during winter 1971-72. See text for explanation of figures.



during December preceding movement of animals. The increase resulted from both an increase in total snow depth and an increase in ram hardness of given depth increments. The dispersal of moose from lowland riparian habitat to adjacent areas during March may have been influenced by the declining R_i making travel less difficult. Dispersal from riparian habitat in March may also have been related to the lower snow depth, density and hardness in deciduous and conifer tree communities during that time. The range for snow density of settled snow at the upland shrub site increased from 0.16 - 0.24 g/cm^3 in late November to 0.20 - 0.31 g/cm^3 in late December, while the range of snow hardness for settled snow increased from 10-50 g/cm^2 to 50 - 500 g/cm^2 during the same period.

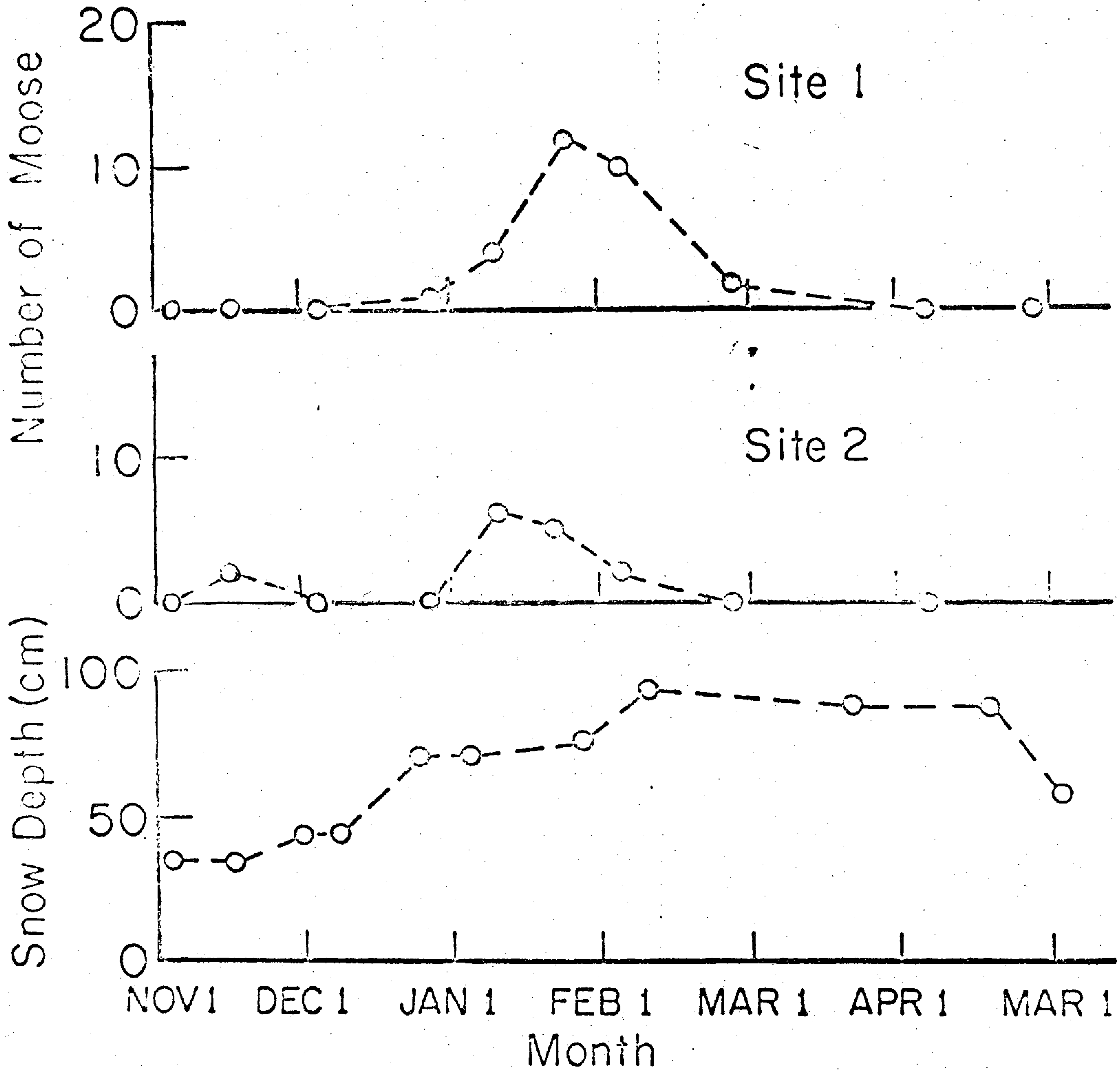
Conclusions regarding the significance between integrated Rammsonde resistance and movement of moose would be highly premature at this time. However, based upon the above data and upon similar correlations between R_i and moose behavior in other study areas during both 1971-1972 and 1972-1973, further studies using the Rammsonde penetrometer appear justified.

Movement of moose onto non-riparian lowland habitat during 1971-1972 corresponded closely with that onto riparian areas (Fig. 14). Sites 1 and 2, located 90 km from the above study area, are each approximately 1.5 km^2 in size. Land clearing 10 to 15 years ago has resulted in a dense regrowth of shrubs and low trees. Moose movement onto both sites 1 and 2 began in late December, while by early March nearly all animals had dispersed from the sites, apparently into more densely vegetated areas. Snow depths on the sites averaged about 70 cm in late December when animals began to appear, and remained near 80 to 90 cm until late April. The maximum number of animals was 11 (density 7/km^2) on site 1 in mid-January. During the preceding winter snow depths on the sites averaged 115 cm in January and the maximum number of animals during that time was 36 (density 24/km^2).

Seasonal migrations of moose in interior Alaska are not always influenced by snow conditions. Movement of some animals from lowland summer range to either upland or riparian shrub habitat may begin in August, well before snowfall occurs, and continue throughout the winter. However, while initial movements may be related to factors other than snow, the speed and extent of migration are apparently influenced by snow. During winters of early or deep snow, movement of most animals from lowland summer ranges may occur sooner and to a greater extent than during winters of late or little snow. Availability of browse as affected by snow depth may be particularly important in influencing movements over flat terrain where local differences in snow conditions are not great. For example, late snowfall may have accounted for exceptionally heavy and extensive use of some low (40 to 60 cm high) willow (*Salix pulchra*) communities on the Tanana Flats near Fairbanks during fall and early winter, 1972.

Movement to summer range in interior Alaska apparently occurs during a relatively short period after snow melt has exposed patches of bare ground. Observations of animals and tracks suggest that when snow cover persists into mid- to late May, substantial movement of animals does not occur until that time. However, an early thaw results in an

Fig. 14. Movement of moose and snow depth at two small lowland wintering sites near Fairbanks, Alaska (GMU 20B), during winter 1971-1972. Number of moose were determined by aerial count.



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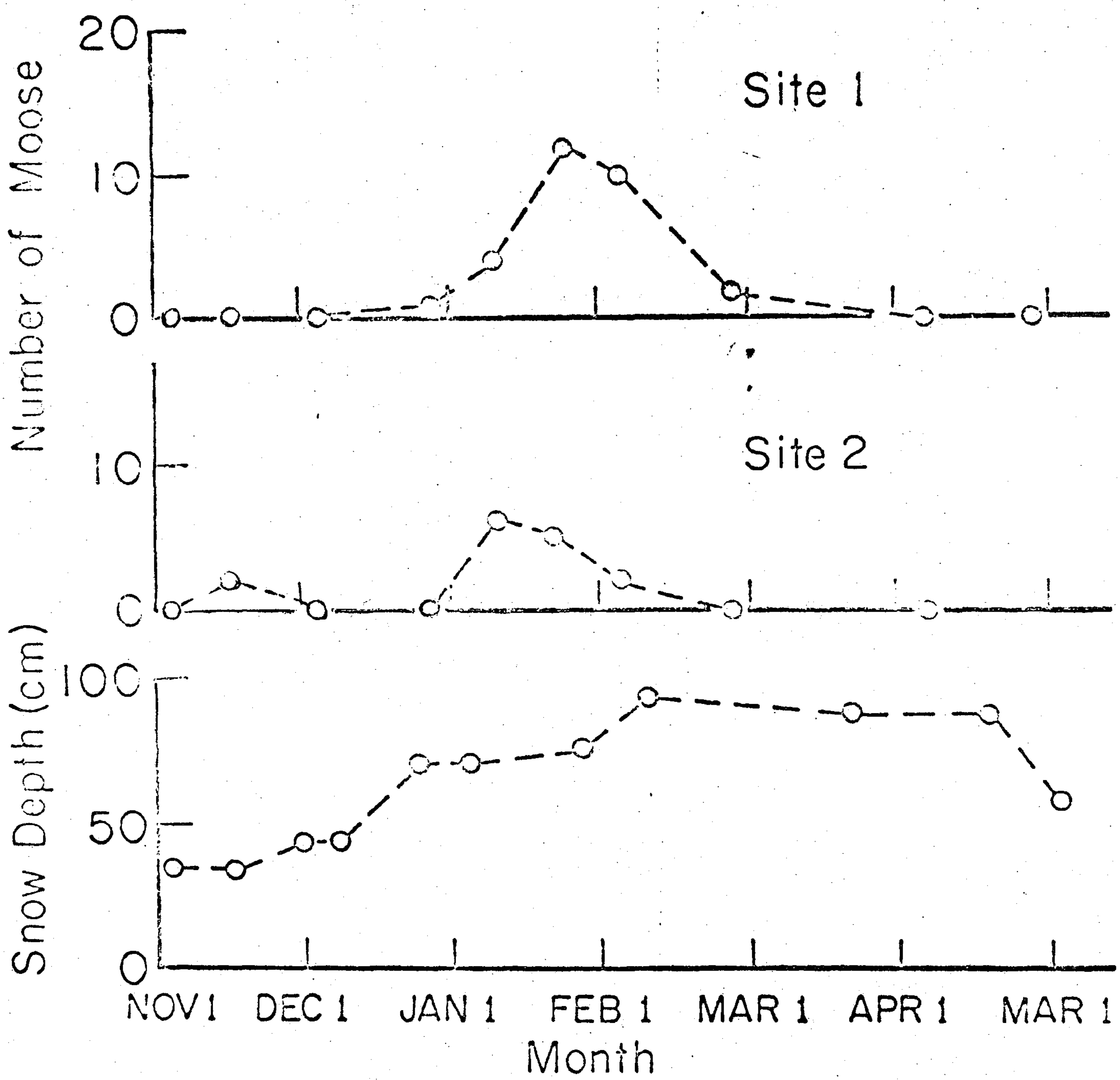

early movement to summer range during late April and early May. Advanced snow melt during spring 1973 resulted in a 70 km migration between April 10 and April 20 of a radio-collared moose from winter to summer range.

Although the above data are preliminary and highly limited in scope, they illustrate an approach to studying moose-snow relationships which may prove useful in other areas. Detailed observations of moose distribution and movements, snow parameters, and temperature and wind conditions in several areas of interior Alaska over three years will be reported in a future publication.

Habitat selection and movement on winter range in relation to snow conditions have been reported in several excellent studies (Nasimovich, 1955; Des Meules, 1964; Telfer, 1970; Berg, 1971; Peek, 1971a, b; Van Ballenberghe and Peek, 1971), and will therefore not be further considered here. However, most studies suggest an increased use of dense cover with an increase in snow depth, density, and/or hardness, and a relatively small winter home range, although actual snow conditions causing a change in habitat selection or home range size are variable.

Since February 1971, 195 moose observations, 34 aerial moose surveys, and 56 weekly track counts have been completed in the Fairbanks area. Data analyses are incomplete, and will be presented in a future report. All records are on file in the Alaska Department of Fish and Game office, Fairbanks.

Radio Telemetry

The six radio transmitters were tested on horses at Fairbanks for one day and at Kenai on Moose Research Center penned moose for two days. All transmitters and collars functioned satisfactorily during testing.

The operational life of the radio collars was as follows: one unit, seven weeks; one unit, eleven weeks; two units, seven months; two units, seven months plus (still operating). However, the signal of one currently operating transmitter was not received for seven months after it was placed on the moose. On June 18, 1973 the signal was received in the area where the moose was instrumented. It is not known whether movement of the moose out of the search area and beyond the range of the receiver or or intermittent operation of the transmitter was responsible for not receiving the signal.

During the operation of the transmitters, the moose were located a total of 158 times between November 21, 1972 and June 18, 1973. Three of the radio-collared moose remained in the Elliott Creek burn until late December, when they migrated out of the burn within 10 days of each other. One of the animals moved into a mature deciduous tree stand (elevation 600m), midway between the burn and the Chena River), and remained in that area until late April. During a period of ten days the moose then moved 55 km to a black spruce (*Picea mariana*)-bog habitat in the Tanana Flats (elevation 130 m). The other two moose moved 30 to 40 km directly from the burn to shrub communities along the Chena River and the Chena Hot Springs Road (elevation 170 m) where they remained until late April. One of the animals then occupied adjacent black spruce-deciduous tree-bog habitat. The transmitter failed on the second moose. A fourth moose remained in the burn until early April, when she moved directly into black spruce-bog habitat along the Chena River.

Monthly aerial surveys in the 90 km^2 Elliott Creek burn also indicated a gradual movement of moose out of the area.

Between the end of November and the end of December, snow depths in the burn increased from approximately 30 to 55 cm. Movement of radio-collared moose out of the burn during late December may have been influenced by rapid accumulation of snow during that time. Snow depths in the burn between mid-January and mid-March ranged between 50 and 60 cm. Therefore, the sharp decline in total number of moose in the burn between January and March was apparently not in response to increasing snow depths, but was influenced by other factors. Movement of radio-collared moose into black spruce-bog habitat during late April corresponded with the appearance of patches of bare ground at that time.

Between November and mid-April, while the ground was 100 percent snow covered, 93 percent of the collared moose located electronically were then visually spotted. However, after mid-April, with the appearance of bare ground, only 58 percent of the collared moose located electronically were visually sighted. The decrease in visibility was probably due to a number of factors, such as greater difficulty sighting moose on snow-free ground, change in habitat selection to more dense cover, and a more secretive nature with the approach of parturition.

Analysis of moose telemetry data is incomplete, and will be presented in a future publication. However, the use of radio telemetry in combination with other methods of monitoring seasonal movement patterns and habitat selection in response to various factors appears justified. However, a larger number of transmitters (20 to 25) of longer operational life (one or more years) would be of value.

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LITERATURE CITED

Abele, G. 1963. A correlation of unconfined compressive strength and ram hardness of processed snow. USA CRREL Tech. Rep. 85. 14 pp.

________. 1968. An experimental snow runway pavement in Antarctica. USA CRREL Tech. Rep. 211.

________., R. O. Ramseier and A. F. Wuori. 1965. A study of sub-surface transportation methods in deep snow. USA CRREL Tech. Rep. 160.

____. 1968. Design criteria for snow runways. USA CRREL Tech. Rep. 212.

Abrams, J. T. 1968. Fundamental approach to the nutrition of the captive wild herbivore. In M. A. Crawford, ed. Comparative nutrition of wild animals. Symp. Zool. Soc. London 21:41-62.

Alaska Department of Fish and Game. 1973. Alaska's wildlife and habitat. ADF&G. 590 pp.

Altmann, M. 1959. Group dynamics in Wyoming moose during the rutting season. J. Mammal. 40:420-424.

Bader, H., R. Haefeli, E. Bucher, J. Neher, O. Eckel and C. Thams. 1939. Snow and its metamorphism. Beitrage zur Geologie der Schweiz, Geotechniche Serie, Hydrologie, Liefereung 3, Bern. U. S. Army Snow, Ice and Permafrost Res. Establish. Transl. 14, 1954. 313 pp.

Bear, G. D. 1971. Seasonal trends in fat levels of pronghorns, *Antilocapra americana*, in Colorado. J. Mammal. 52(3):583-589.

Bee, J. W. and E. R. Hall. 1956. Mammals of northern Alaska on the Arctic Slope. Mus. Nat. Hist. Misc. Publ. No. 8. Univ. Kansas, Lawrence. 309 pp.

Benson, C. S. 1962. Stratigraphic studies in the snow and firn of the Greenland ice sheet. USA SIPRE Res. Rep. 70. 91 pp.

___________. 1967. A reconnaissance snow survey of interior Alaska. Rep. USGR-190. Geophysical Inst., Univ. Alaska, College. 71 pp.

___________. 1969. The seasonal snow cover of Arctic Alaska. Arctic Inst. N. Am. Res. Paper No. 51. 47 pp.

Berg, W. E. 1971. Habitat use, movements, and activity patterns of moose in northwestern Minnesota. M.S. Thesis. Univ. Minn., St. Paul. 98 pp.

Bilello, M. A., R. E. Bates and J. Riley. 1970. Physical characteristics of the snow cover, Fort Greely, Alaska, 1966-67. CRREL Tech. Rep. 230.

Bishop, R. 1969. Moose Report, Vol. 10. Alaska Dept. Fish and Game Annu. Proj. Seg. Rep., Proj. W-15-R-3, Work Plan K. 153 pp.

_________. 1970. Preliminary review of changes in sex and age ratios of moose and their relation to snow conditions on the Tanana Flats, Alaska. Paper presented at 6th Annu. N. Am. Moose Com. Meet., Kamloops, B. C. Feb. 1970. 14 pp. Xerox.

_________. 1971. Annual report of survey-inventory activities, Part 1, moose, deer, and elk. Fed. Aid in Wildl. Rest. Proj. Alaska, Proj. W-17-3, Vol. II. 119 pp.

_________. and R. A. Rausch. 1973. Moose population fluctuations in Alaska, 1950-72. Paper presented at the Int. Symp. on Moose Ecol., Quebec City. March 1973. 37 pp.

Blood, D. A., J. R. McGillis and A. L. Lovaas. 1967. Weights and measurements of moose in Elk Island National Park, Alberta. Can. Field Nat. 81:263-269.

Brandy, P. J., I. McT. Cowan, W. D. Kitts and A. J. Wood. 1956. A method for the assessment of the nutritional status of wild ungulates. Can. J. Zool. 34:48-52.

Bull, C. 1956. The use of the Rammsonde as an instrument in determining the density of firn. J. Glaciology 2:713-725.

Cheatum, E. L. 1949. Bone marrow as an index of malnutrition in deer. N.Y. Conserv. 3:19-22.

_____________. and C. W. Severinghaus. 1950. Variations in fertility of white-tailed deer related to range conditions. Trans. N. Am. Wildl. Conf. 15:170-190.

Chesemore, D. L. 1968. Occurrence of moose near Barrow, Alaska. J. Mammal. 49(3):528-529.

Coady, J. W. 1973. Influence of snow on behavior of moose. Paper presented at the Int. Symp. on Moose Ecology, Quebec City, March 1973. 35 pp.

Cowan, I. McT. and A. J. Wood. 1955. The growth rate of the black-tailed deer (*Odocoileus hemionus columbianus*). J. Wildl. Manage. 19(3):331-336.

Davis, H. 1952. Recollections. In Herbert L. Heller, ed. Sourdough Sagas. World Publ. Co., Cleveland.

Denniston, R. H. 1956. Ecology, behavior, and population dynamics of the Wyoming or Rocky Mountain moose, *Alces alces shirasi*. Zoologica 41(3):105-118.

Des Meules, P. 1964. The influence of snow on the behaviour of moose. Trans. N.E. Wildl. Conf. 21. 17 pp.

Dodds, D. G. 1959. Feeding and growth of a captive moose calf. J. Wildl. Manage. 23:231-232.

Edwards, R. Y. and R. W. Ritcey. 1956. The migrations of a moose herd. J. Mammal. 37(4):486-494.

______________________________. 1958. Reproduction in a moose population. J. Wildl. Manage. 22(3):261-268.

Egorov, O. V. 1965. Wild Ungulates of Yakutia. Israel Program for Scientific Translations. 204 pp.

Formozov, A. N. 1946. Snow cover as an integral factor of the environment and its importance. Moscow Society of Naturalists, Moscow, USSR. Boreal Institute, University of Alberta, Canada, Occasional Paper No. 1. 176 pp.

Gasaway, W. C. and J. W. Coady. 1973. Review of energy requirements and rumen fermentation in moose and other ruminants. Paper presented at the Int. Symp. on Moose Ecology, Quebec City. March, 1973. 37 pp.

Gold, L. W. 1956. The strength of snow in compression. J. Glaciology 2(20):719-725.

__________. 1958. Changes in a shallow snow cover subject to a temperature climate. J. Glaciology 3(23):218-222.

Greer, K. R. 1968. A compression method indicates fat content of elk (wapiti) femur marrows. J. Wildl. Manage. 32(4):747-751.

___________. 1969. Femur marrow reveals the condition of game animals. Montana Fish and Game Department, Bozeman.

Hall, E. R. and K. R. Kelson. 1959. The mammals of North America. V. 2, Ronald Press, New York.

Harry, G. B. 1957. Winter food habits of moose in Jackson Hole, Wyoming. J. Wildl. Manage. 21(1):53-57.

Heptner, V. G., A. A. Nasimovich and A. G. Bannikov. 1961. Mlekopitaiushchie Sovetskogo Soiuza. V. 1, Parnokopytnye i neparnokopytnye. Moscow, Vysshaia Shkola.

Hosley, N. W. 1949. The moose and its ecology. U. S. Fish and Wildl. Serv. Leafl. 217. 51 pp.

Houston, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton Natural History Association Tech. Bull. No. 1. 110 pp.

Jordan, P. A., D. B. Botkin and M. L. Wolfe. 1970. Biomass dynamics in a moose population. Ecology 52(1):147-152.

Keeler, C. M. 1969. Some physical properties of alpine snow. USA CRREL Res. Rep. 271. 70 pp.

____________. and W. F. Weeks. 1967. Some mechanical properties of alpine snow, Montana 1964-66. USA CRREL Res Rep. 227. 35 pp.

Kelsall, J. P. 1969. Structural adaptations of moose and deer for snow. J. Mammal. 50(2):302-210.

____________. 1972. The northern limits of moose (*Alces alces*) in western Canada. J. Mammal. 53(1):129-138.

____________. and W. Prescott. 1971. Moose and deer behaviour in snow in Fundy National Park, New Brunswick. Can. Wildl. Serv. Rep. Ser. 15. 25 pp.

____________. and E. S. Telfer. 1971. Studies of the physical adaptation of big game for snow. Pages 134-146 in A. O. Haugen, ed. Proceedings of the Snow and Ice in Relation to Wildlife and Recreation Symposium. Iowa Coop. Wildl. Res. Unit. Ames. 280 pp.

____________________________. 1973. Biogeography of moose with particular reference to western Canada. Paper presented at the International Symposium on Moose Ecology, Quebec City, March 1973. 26 pp.

Kingery, W. D. 1960. On the metamorphism of snow. Mass. Inst. Technol. Ice Res. Lab. Rep. No. 61-1. 9 pp.

Klein, D. R. 1964. Range-related differences in growth of deer reflected in skeletal ratios. J. Mammal. 45(2):226-235.

____________. 1965. Ecology of deer range in Alaska. Ecol. Monogr. 35: 259-284.

____________. 1968. The introduction, increase, and crash of reindeer on St. Matthew Island. J. Wildl. Manage. 32(2):350-367.

____________. 1970. Food selection by North American deer and their response to overutilization of preferred plant species. Pages 25-46 in A. Watson, ed. Animal populations in relation to their food resources. Blackwell, Oxford.

____________., C. C. Pearce and L. W. Gold. 1950. Method of measuring the significant characteristics of a snow cover. Nat. Res. Counc. Can. Tech. Mem. 56 pp. Mimeogr.

Knorre, E. P. 1959. Ecology of the Moose. Proceedings of the Pechora-Ilych State Nature Preserve. 7:167 pp. (in Russian).

___________. 1961. The results and perspectives of domestication of moose. Papers of the Pechora-Ilych State Reservation. 9:396 pp.

Knowlton, F. F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. J. Wildl. Manage. 24(2):162-170.

Krafft, A. 1964. Management of moose in a Norwegian Forest. The Norwegian State Game Research Insititute, 2(16):61 pp.

Lent, P. C. and D. Knutson. 1971. Muskox and snow cover on Nunivak Island, Alaska. Pages 50-62 in A. O. Haugen, ed. Proceedings of the Snow and Ice in Relation to Wildlife and Recreation Sumposium. Iowa Coop. Wildl. Res. Unit, Ames. 280 pp.

Leopold, A. S. and F. F. Darling. 1953. Wildlife in Alaska. Ronald Press Co., New York. 129 pp.

LeResche, R. E. 1970. Moose Report. Annu. Proj. Seg. Rep. Fed. Aid Wildl. Rest., Alaska Dept. Fish and Game, Juneau.

_____________. 1973. Moose migrations in North America. Paper presented at the Int. Symp. on Moose Ecology, Quebec City, March 1973. 41 pp.

_____________., R. H. Bishop and J. W. Coady. 1973. Distribution and habitats of moose in Alaska. Paper presented at the Int. Symp. on Moose Ecology, Quebec City, March 1973. 43 pp.

_____________. and J. L. Davis. 1971. Moose research report. Annu. Proj. Seg. Rep. Fed. Aid Wildl. Rest., Alaska Dept. Fish and Game, Juneau. 88 pp.

Lutz, H. J. 1960. Early occurrence of moose on the Kenai Peninsula and in other sections of Alaska. Misc. Publ. Alaska Forest Res. Center, 1:1-25.

Markgren, G. 1966. A study of hand-reared moose calves. Viltrevy 4(1): 1-42.

___________. 1969. Reproduction of moose in Sweden. Viltrevy 6(3):127-299.

Mech, L. D. 1970. The Wolf: The ecology and behavior of an endangered species. The Natural History Press, Garden City, N. Y. 384 pp.

Miller, D. R. 1972. Observations of wolf predation on barren-ground caribou in winter. Abstr. First Int. Reindeer/caribou Symp., Univ. Alaska, College.

Murie, A. 1934. The moose of Isle Royale. Univ. Michigan Mus. Zool. Misc. Publ. No. 25, Ann Arbor. 44 pp.

________. 1944. The wolves of Mount McKinley. U. S. Gov. Print. Off., Washington, D. C. 238 pp.

Nasimovich, A. A. 1955. The role of the regime of snow cover in the life of ungulates in the USSR. Moskva, Akad. Nauk SSSR, 403 pp. Translated from Russian by Can. Wildl. Serv. Ottawa.

Neiland, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. J. Wildl. Manage. 34(4):904-907.

Nordan, H. C., I. McT. Cowan and A. J. Wood. 1968. Nutritional requirements and growth of black-tailed deer, *Odocoileus hemionus columbianus*, in captivity. Pages 89-96 in M. A. Crawford, ed. Comparative Nutrition of Wild Animals. Symp. Zool. Soc. London, No. 21.

Peek, J. M. 1962. Studies of moose in the Gravelly and Snowcrest Mountains, Montana. J. Wildl. Manage. 26:360-365.

__________. 1971a. Moose habitat selection and relationships to forest management in northeastern Minnesota. Unpubl. Ph.D. Thesis. Univ. Minn., St. Paul. 250 pp.

__________. 1971b. Moose-snow relationships in northeastern Minnesota. Pages 39-49 in A. O. Haugen, ed. Proceedings of the Snow and Ice in Relation to Wildlife and Recreation Symposium, Iowa State Univ., Ames. 280 pp.

Peterson, R. L. 1955. North American Moose. Univ. Toronto Press. 280 pp.

Péwé, T. L. and D. M. Hopkins. 1967. Mammal remains of Pre-Wisconsin Age in Alaska. In D. M. Hopkins, ed. The Bering Land Bridge. Stanford Univ. Press, Stanford. 495 pp.

Pimlott, D. H. 1959. Reproduction and productivity of Newfoundland moose. J. Wildl. Manage. 23(4):381-401.

Pruitt, W. O., Jr. 1959. Snow as a factor in the winter ecology of the barren ground caribou (*Rangifer arcticus*). Arctic 12(3):159-179.

____________. 1966. Ecology of terrestrial mammals. In N. J. Wilimovsky and J. N. Wolfe, eds. Environment of the Cape Thompson Region, Alaska. USAEC Oak Ridge, Tenn. 1250 pp.

____________. 1971a. Report on International Workshop on *Rangifer* Winter Ecology, Vittangi, Sweden, March 20-28. 5 pp. Xerox.

____________. 1971b. Scandinavian-Canadian Field Workshop on *Rangifer* Snow Ecology. Arctic 24(2):145.

Pulliainen, E. 1973. Seasonal movements of moose in Europe. Paper presented at the Int. Symp. on Moose Ecology, Quebec City, March 1973. 43 pp.

Ransom, A. B. 1965. Kidney and marrow fat as indicators of white-tailed deer condition. J. Wildl. Manage. 29(2):397-398.

Rausch, R. A. 1958. Moose management studies. Job Completion Rep. Fed. Aid Wildl. Rest., 12:138 pp. Proj. W-3-R-12, Alaska Game Commission, Juneau.

____________. 1959. Some aspects of population dynamics of the railbelt moose populations of Alaska. MS Thesis, Univ. Alaska. 81 pp.

____________. 1967. Report on 1965-66 moose studies, Vol. VII, ADF&G Annu. Proj. Seg. Rep., Proj. W-15-R-1, Work Plan K. Juneau. 129 pp.

____________. 1971. Moose Report, Vol. 11, ADF&G, Prog. Rep., Proj. W-17-1, Work Plan K. Juneau. 118 pp.

____________. and R. Bishop. 1968. Report on 1966-67 moose studies, Vol. 8 and 9, ADF&G Annu. Proj. Seg. Rep. Proj. W-15-R-2 and -3, Work Plan K. 263 pp.

____________. and A. Bratlie. 1965. Annual assessments of moose calf production and mortality in southcentral Alaska. Annu. Conf. W. Assoc. State Fish and Game Commissioners, 45. 11 pp. Mimeo.

Rausch, R. L. 1951. Notes on the Nunamiut Eskimo and mammals of the Anaktuvuk Pass region, Brooks Range, Alaska. Arctic 4:147-195.

____________. 1963. A review of the distribution of holarctic recent mammals. Pages 29-43 in J. L. Gressitt, ed. Pacific Basin Biogeography. Bishop Museum Press, Honolulu.

Richens, V. B. and C. G. Madden. 1973. An improved snow study kit. J. Wildl. Manage. 37(1):109-113.

Riney, T. 1955. Evaluating condition of free ranging red deer (*Cervus elaphus*), with special references to New Zealand. New Zealand J. Sci. and Tech., Sec. B. 36(4):429-464.

Ritcey, R. W. 1967. Ecology of moose winter range in Wells Gray Park British Columbia. Proc. 4th Workshop on Moose Research and Management, Edmonton. 15 pp. Xerox.

Robinette, L. W., J. S. Gashwiler, J. B. Low and D. A. Jones. 1957. Differential mortality by sex and age among mule deer. J. Wildl. Manage. 21(1):1-16.

Severinghaus, C. W. 1947. Relationship of weather to winter mortality and population levels among deer in the adirondack region of New York. 12th North American Wildlife Conference, pages 212-223.

Simkin, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Manage. 29(4):740-750.

Skunke, F. 1949. Algen. Stokholm, Norstedt. 400 pp.

Smith, N. S. 1970. Appraisal of condition estimation methods for east African ungulates. E. Afr. Wildl. J. 8:123-129.

Sommerfeld, R. A. 1969. Classification outline for snow on the ground. USDA Forest Serv. Res. Paper RM-48. 24 pp.

Stevens, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. J. Wildl. Manage. 34(1):37-46.

Trabant, D. C. 1970. Diagenesis of the seasonal snow cover of interior Alaska. Unpubl. M.S. Thesis. Univ. Alaska, College. 48 pp.

Telfer, E. S. 1967a. Comparison of a deer yard and a moose yard in Nova Scotia. Can. J. Zool. 45:485-490.

___________. 1967b. Comparison of moose and deer, winter range in Nova Scotia. J. Wildl. Manage. 31(3):418-425.

___________. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34(3):553-559.

___________. and J. P. Kelsall. 1971. Morphological parameters for mammal locomotion in snow. Paper presented at 51st Annual Meeting of the Am. Soc. Mammal., Univ. B. C., Vancouver, June 20-24. 10 pp. Xerox.

Testlab. 1970. The Swiss Rammsonde. Special Technical Paper No. 1. 15 pp.

Van Ballenberghe, V. and J. M. Peek. 1971. Radiotelemetry studies of moose in northeastern Minnesota. J. Wildl. Manage. 35(1):63-71.

Verme, L. J. 1970. Some characteristics of captive Michigan moose. J. Mammal. 51(2):403-405.

Wood, A. J., I. McT. Cowan and H. C. Norday. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. Can. J. Zool. 40:593-603.

Wuori, A. F. 1962. Supporting capacity of processed snow runways. USA CRREL Tech. Rep. 82.

________. 1963. Snow stabilization for roads and runways. USA CRREL Tech. Rep. 83.

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