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THE UNIVERSITY OF ALBERTA

BIOENERGETICS AND BEHAVIOR OF MOOSE (*Alces alces*) IN THE ASPEN-DOMINATED BOREAL FOREST

by

© LYLE ALFRED RENECKER

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF DOCTOR OF PHILOSOPHY

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled BIOENERGETICS AND BEHAVIOR OF MOOSE (*Alces alces*) IN THE ASPEN-DOMINATED BOREAL FOREST submitted by LYLE ALFRED RENECKER in partial fulfilment of the requirements for the degree of DOCTOR OF PHILOSOPHY in WILDLIFE PRODUCTIVITY AND MANAGEMENT.

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Abstract

The two main aspects of the energy budget, expenditures and assimilation, were studied to understand how moose (*Alces alces*) survive in northern climates. The research centered on four main areas: (a) seasonal environments; (b) seasonal energetics; (c) comparative digestive physiology; and (d) resource-use behavior.

Metabolic rate and thermoregulatory responses were monitored simultaneously in three adult moose on selected days in all seasons. Body weight and energy expenditure varied in a marked annual cycle with maximum values occurring during summer/early autumn and seasonal minima during winter. Moose were extremely cold tolerant, however, their respiration rates increased when ambient temperatures were above -5°C and 14°C during winter and summer, respectively.

Digestion of different diets, including browse, in a browser (moose), grazer (cattle) (*Bos taurus*) and mixed feeder (wapiti) (*Cervus elaphus nelsoni*) was compared. Fermentation capacities of these ruminants were similar when animals were given equal time for adaptation to diets, however, moose consistently propelled labelled aspen particles faster through the rumen than particles of other feeds. Flow rates of particulate matter were significantly correlated with flow of solutes in moose, but only weakly related for wapiti and not correlated in cattle. The digestive strategy of moose (browser) may be related to rapid rumen turnover and passage of large particles for efficient use of cell contents in lignified browse. The plasticity observed in wapiti may reflect their efficiency of comminution.

Dry matter intake was quantified for two free-ranging moose using the bite-count technique and ratio of total dry matter in the feces to percent indigestibility of dietary dry matter. During the 1-year period, daily dry matter intake ranged from 37.8 g/kg $BW^{0.75}$ in January to 128.5 g/kg $BW^{0.75}$ during summer and consumption rates (g/min) increased asymptotically with forage biomass. The net energy requirement for maintenance of free-ranging moose cows was calculated to be 400 KJ/kg $BW^{0.75}$.

Time-energy budgets were analyzed using an index which predicted metabolic rate from radio-telemetered heart rate. Energy expenditures increased with level of activity and movement. Daily energy allocated towards rumination was greater than for other activities in most seasons except during late spring when forage was highly digestible which reduced the requirements for comminution. Seasonal trends indicated that moose adjust rumination time and chewing efficiency in relation to fibrousness of diet. Moose were highly susceptible to heat stress in summer and altered daily behavioral patterns and utilized wetlands to minimize energy expenditures.

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SCIENTIFIC AND COMMON NAMES OF PLANT SPECIES LISTED IN THE TEXT

BROWSE

Amelanchier alnifolia Nutt.	saskatoon[1]
Betula papyrifera Marsh.	white birch
Cornus stolonifera Michx.	red-osier dogwood
Corylus cornuta Marsh.	beaked hazel
Lonicera dioica L.	twinning honeysuckle
Lonicera involucrata (Richards.) Banks	bracted honeysuckle
Picea glauca (Moench) Voss.	white spruce
Populus balsamifera L.	balsam poplar
Populus tremuloides Michx.	trembling aspen
Prunus virginiana L.	chokecherry
Ribes hirtellum Michx.	gooseberry
Rosa acicularis Lindl.	rose
Rubus idaeus var. *strigosus* (Michx.) Maxim	red raspberry
Salix bebbiana Sarg.	Bebb's willow
Salix planifolia Pursh.	willow
Salix petiolaris Anders.	willow
Salix discolor Muhl.	pussy willow
Shepherdia canadensis (L.) Nutt.	soapberry
Symphoricarpos occidentalis Hook.	western snowberry
Viburnum edule (Michx.) Raf.	low bush cranberry

FORBS

Achillea millefolium L.	yarrow
Cirsium arvense (L.) Scop.	Canada thistle
Epilobium angustifolia L.	fireweed
Lathyrus ochroleucus Hook.	yellow peavine
Medicago sativa L.	alfalfa
Mentha arvensis L.	common mint
Taraxacum offinicale Weber	dandelion
Trifolium hybridum L.	alsike clover
Trifolium repens L.	white clover
Typha latifolia L.	cattail
Urtica gracilis Ait.	stinging nettle

GRAMINOIDS

Agropyron repens (L.) Beauv.	quackgrass
Agropyron trachycaulum (Link) Malte	wheat grass

Bromus ciliatus L.	brome grass
Bromus inermis Leyss.	brome grass
Carex stipata Muhl.	sedge
Carex atherodes Spreng.	sedge
Carex bebbii Olney	sedge
Carex rostrata Stokes	sedge
Carex disperma Dew.	sedge
Phleum pratense L.	timothy
Poa compressa L.	Canada blue grass
Poa pratensis L.	Kentucky blue grass

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[1] Gray's Manual of Botany (M.L. Fernald. 1970. D. Van Norstrand Comp., Toronto 1632 pp.) was used as the source of botanical nomenclature.

SCIENTIFIC AND COMMON NAMES OF ANIMAL AND INSECT SPECIES LISTED IN THE TEXT

MAMMALS

Aepyceros melamous Lichtenstein	impala[1]
Alcelaphus buselaphus Pallas	hartebeest
Alces alces L.	moose
Bison bison L.	American bison
Bos grunniens L.	yak
Bos taurus L.	domestic cattle
Canis lupus L.	wolf
Capreolus capreolus L.	roe deer
Cephalophus niger Gray	duiker
Cervus elaphus L.	red deer
Cervus elaphus nelsoni Bailay	wapiti
Connochaetes taurinus Burchell	wildebeest
Damaliscus lunatus Blaine	topi
Giraffa camelopardalis L.	giraffe
Kobus ellipsiprymnus Ogilby	waterbuck
Litocranius walleri Brooke	gerenuk
Madoqua kirkii Gunther	dik-dik
Nesotragus moschatus Von Duben	suni
Odocoileus hemionus Rafinesque	mule deer
Odocoileus hemionus columbianus Richardson	black-tailed deer
Odocoileus virginianus Zimmerman	white-tailed deer
Oreamnos americanus De Blainville	mountain goat
Oryx beisa Ruppell	oryx
Oryx gazella L.	gemsbok
Ovibos moschatus Zimmerman	muskox
Ovis aries L.	domestic sheep
Ovis canadensis Shaw	bighorn sheep
Ovis dalli Nelson	Dall's sheep
Ovis musimon Pallas	mouflon
Rangifer tarandus tarandus L.	reindeer
Redunca spp.	reedbuck
Rupicapra rupicapra L.	chamois
Synercus caffer Sparrmann	buffalo
Tragelaphus imberbis Blyth	kudu
Ursus spp.	bear

INSECTS

Chrysops spp.	deer fly
Culicidae spp.	mosquito
Haemotobia irritans	horn fly
Tabanus spp.	horse fly

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[1] Grzimek's Animal Life Encyclopedia Vol. 13, Mammal's IV (Grzimek, B. 1972. Van Norstrand Comp., Toronto 566 pp.) was used as the source of animal nomenclature.

ACRONYMS AND ABBREVIATIONS USED IN TEXT

ADF	acid detergent fiber
ADL	acid detergent lignin
ARC	Agricultural Research Council
BW	body weight
Cell	cellulose
cm	centimeter
CP	crude protein
CWC	cell wall constituents
d	day
DE	digestible energy
DDMI	digestible dry matter intake
DM	dry matter
DMI	dry matter intake
Dy	dysprosium
e	emissivity of globe surface
EE	energy expenditure
FDM	daily fecal dry matter excretion
g	gram
ha	hectare
HC	hemicellulose
hr	hour
°K	degrees Kelvin
K	convective coefficient for a specified 10.2 cm diameter globe
kd	rate constant for digestion
kg	kilogram
kJ	kilojoule
kp	rate constant for passage
LIG	lignin
LPS	large particle size
ME	metabolizable energy
MFN	metabolic fecal nitrogen
MHz	Megahertz
mm	millimeter
MPS	mean particle size
NBD%	percent digestibility of dry matter in nylon bag
NDF	neutral detergent fiber
OM	organic matter
OMI	organic matter intake
QRS	the Q, R and S waves of a normal electrocardiogram
RHL	radiant heat load
RQ	respiratory quotient
RTT	rumen turnover time
SD	standard deviation
SE	standard error
σ	sigma
STP	standard, temperature and pressure
ta	ambient temperature (°C)
Tg	tg + 273 (°K)
tg	temperature of globe (°C)
Tr	rectal temperature (°C)
Tsk	skin temperature (°C)

T wave	electrical currents as ventricles of the heart recover from a state of depolarization
V	air velocity

I. GENERAL INTRODUCTION

A. Emergence of Ruminants

Since their appearance during the Eocene, ruminants (*Artiodactyla: Ruminantia*)[1] have radiated in great variety, largely replacing perissodactyls and proboscids by the Miocene. This evolutionary success usually has been attributed to the perfection of ruminant digestion. One explanation for their trophic development is related to security ("Eat and Run" Hypothesis), whereby early ruminants fed rapidly then processed this food later in a safe place without risk of predation (Foose 1982, Van Soest 1982). However, the most popular interpretation argues that they adapted digestively to vegetation with a high fiber content. Differentiation of anatomical features in ruminants, which accompanied pregastric fermentation, by detoxifying chemical defenses in plant tissue (Detoxification Hypothesis), provided greater latitude for dietary choice (Freeland and Janzen 1974). Ruminants evolved the necessary dentitious and digestive machinery to extract energy from fibrous foods (Moir 1968) available in the cooler climates of the Miocene (Digestive Efficiency Hypothesis) (Foose 1982, Van Soest 1982). This differentiation involved pregastric retention of digesta, rumination and microbial fermentation. A wide variety of more specific adaptations enabled this group to extract nutrients from many different fibrous plant materials (Foose 1982).

B. Adaptive Radiations of Ruminants

Trophic Adaptation

A characteristic feature of ruminants is a four-chambered stomach consisting of rumen, reticulum, omasum and abomasum. Diets of browse, forbs and grass are retained in the rumen until adequate nutrients are extracted from fibrous material and particle-size reduction

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[1] Grizmek's Animal Life Encyclopedia Vol. 13, Mammal's IV (Grizmek, B. 1972. Van Nostrand Comp., Toronto 566 pp.) was used as the source of animal nomenclature.

has occurred. Based on the degree of specialization in forage selection and digestive anatomy, ruminants have been classified into three groups (Hofmann 1973) : (a) browsers (concentrate selectors), (b) grazers (grass or roughage feeders) and (c) mixed or intermediate feeders.

Browsers

Browsers differ from other ruminant groups both in foraging strategy and adaptations of the digestive tract. Typically, as a group, they consume plant species (browse) and parts (twigs and foliage) high in readily fermentable cell solubles and avoid fibrous fractions of plant material which would impede digesta flow. Extensive ruminoreticular papillation has developed which facilitates absorption of volatile fatty acids produced from rapidly fermented substrates. Rumens of selective feeders are small and lack well-developed barriers which would delay passage of digesta. Members of this group have developed relatively large salivary glands in relation to body weight (Hofmann 1973); high flow rates of saliva increase the buffering capacity of the rumen during rapid fermentation (Kay et al. 1980) and may accelerate passage of sugars through the ruminoreticulum for absorption in the small intestine (Hofmann 1985).

Typically, browsers are small and include the diminutive dik-diks (*Madoqua* spp.) and suni (*Nesotragus moschatus*) and the small forest-dwelling duikers (*Cephalophus* spp.) which largely consume fruits, forbs and dicotyledonous foliage (Hofmann 1973). Browsers rely on high quality foods with rapidly fermentable substrates which will supply adequate energy to compensate for the metabolic constraints of a small body size. Consequently, concentrate selectors do not have the ability to expand diets to include fibrous forages (Foose 1982). Intake is constrained largely by the ability of the animal to find high quality foods, maximize forage consumption and maintain high rates of passage.

Browsers also include the black-tailed deer (*Odocoileus hemionus columbianus*), white-tailed deer (*Odocoileus virginianus*), roe deer (*Capreolus capreolus*), kudu (*Tragelaphus* spp.), gerenuk (*Litocranius walleri*) and the larger giraffe (*Giraffa* spp.) and moose (*Alces alces*) (Hofmann 1973, 1982, 1985). These species select mainly tree and shrub foliage. However, species in northern latitudes eat woody twigs during winter. Nevertheless, these large browsers have a small ruminoreticulum and are faced with a similar need for high quality forages which maintain rapid passage rates.

Grazers

Grazers (bulk or roughage feeders) occupy a niche at the other trophic extreme. They consume larger quantities of fibrous grass which are retained for extended periods in the capacious rumens by numerous, well-developed pillars to allow more complete digestion. Thus, foraging is limited to a few periods throughout the day. Rumino-reticular fill can comprise 11% to 20% of the live body weight of grazers in comparison to <11% for a browser (Kay et al. 1980). Because mouth parts are large, restricting selective foraging, grazers rely heavily on rumination for fragmentation of particles to optimum fineness for passage.

Grazing ruminants rely more or less on open grasslands. Among the bulk feeders, domestic cattle (*Bos taurus*), American bison (*Bison bison*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*) and waterbuck (*Kobus ellipsiprymnus*) are classified as fresh grass eaters dependent on water (Hofmann 1973, Van Soest 1982) while the hartebeest (*Alcelaphus buselaphus*), topi (*Damaliscus lunatus*) and mouflon (*Ovis musimon*) are classified as roughage grazers (Hofmann 1973) which are capable of more selective feeding on green leaves of grasses (Kay et al. 1980). Other grazers like the oryx (*Oryx beisa*) and gemsbok (*Oryx gazella*) are classified as dry region grazers (Hofmann 1973).

Mixed Feeders

Transitional to digestive extremes of browsers and grazers are the mixed feeders which consume browse, forbs and grass according to seasonal changes in quality and availability. In general, rumen anatomy and morphology of intermediate species is better adapted for greater digestive capacities of more fibrous diets than concentrate selectors.

Among this group of opportunistic feeders are the wapiti (*Cervus elaphus nelsoni*) (Church and Hines 1978), red deer (*Cervus elaphus*) and reindeer (*Rangifer tarandus tarandus*) (Hofmann 1985) which can seasonally change the mucosal absorptive surface of the rumen in response to diet fibrosity (Hofmann 1985). Another intermediate feeder with the ability to adjust ruminoreticular and hindgut capacity is the chamois (*Rupicapra rupicapra*) (Hofmann 1982).

C. Body Size and the "Bell-Jarman" Principle

Body size is related to both food requirements and digestive capacity in ruminants. Ungulates must extract adequate nutrients from ingested food to meet metabolic requirements. Larger animals are expected to require greater absolute food quantities than smaller herbivores, but energy requirements scale to approximately body weight $^{0.75}$ (Kleiber 1975) whereas storage capacity of the ruminoreticulum scales isometrically (Van Soest 1982). This confers on small selective feeders a penalty of high maintenance costs per unit of body weight but limited digesta storage capabilities (Parra 1978, Demment and Van Soest 1985).

Nutrient requirements of browsers are met through selection of concentrated nutrients in fruits, foliage and forbs which may have higher rates of passage (Hofmann 1985). Alternatively, grazers with a large body size have lower metabolic requirements per kg body weight and can tolerate more fibrous diets of slowly digesting grasses. However, the greater absolute requirements of large body size constrain these ruminants from selective feeding (Hanley 1982).

This pattern is the basis of the "Bell-Jarman Principle" which states that body size and social behavior of ungulates is a function of the quality and quantity of the food resources that they exploit (Bell 1969, 1971, Jarman 1974). More specifically, it contends that body size is the mechanism which determines interspecies differences in diet selection depending on the limitations of quality and quantity of forage resources (Bell 1969, 1971, Jarman 1974). Consequently, apparent trade-offs between time-energy constraints and food acquisition will determine the limitations of each herbivore (Hanley 1982). For example, because forage intakes cannot exceed the capacity of the gastrointestinal tract, small selective feeders are expected to extend foraging times in search of concentrated sources of cell solubles which are digested to meet high metabolic requirements, however, costs must not exceed benefits (Hanley 1982). In comparison, larger grazers must adhere to the other extreme where the constraints of quality are relaxed, but greater absolute volumes of forage are required (Bell 1969, 1971). Intermediate feeders are opportunistic with greater diet flexibility and are expected to alternate seasonally between these options. Other adaptations, such as specialized processes of prehension, permit grazers with large mouth parts to forage more rapidly while ingesting large quantities of fibrous forages or small selective feeders with small mouths to select high quality foods and plant parts.

Although the activities of ungulates are largely directed to forage acquisition, they must satisfy these needs within the constraints of environmental risks (predation and thermoregulation) (Moen 1973) and social obligations (Geist 1974, Jarman 1974). Animals mitigate thermal imbalance and increase energy assimilation through behavior within the limits of their physical and physiological adaptations. They optimize these trade-offs between searching time and feeding time in terms of foraging efficiency, activity patterns and habitat selection. Thus, the ability of each ruminant species to interface between the environment and its nutritional needs is dependent on anatomical, physiological and behavioral adaptations.

D. The Enigmatic Moose

Moose are a particularily interesting species because they apparently violate the "Bell-Jarman Principle" ~~in~~ terms of body size and expected foraging strategy. It is surprising to find a large ruminant species (moose) aligned along the relatively selective gradient of a browser in northern latitudes where forage resources are limited and the seasonal growth pulse is short. Although their large body size can clearly be considered an advantage in terms of cold tolerance, ability to cope with deep snow cover and to defend themselves against wolves, large size may create a precarious energy budget. Moose must consume large absolute quantities of widely dispersed forage, high in lignin as well as cell solubles, and must not waste time and energy capturing or processing food. Their success may be linked to their ability to harvest food efficiently and selectively. However, time spent foraging is a function of both energy demands and environmental constraints. Although the large body size benefits animals which live in cold climates, it also imposes constraints on daily energy expenditures through thermal stress. Moose must attempt to ameliorate these circumstances and not preempt foraging since considerable time must be allocated for the search and capture of concentrated sources of nutrients. Analysis of the seasonal time-energy constraints and digestive adaptations of this ungulate will provide clues which may lead to investigations to unravel the complexities of this apparent trophic exception to the "Bell-Jarman Principle".

E. Approach and Thesis Organization

I designed this study to provide explanations for the unusual trophic strategy of moose. The major aim has been to define seasonal changes in plant-animal interactions. Specifically, I sought to determine how a large concentrate selector, the moose, responds to the extreme seasonal and boreal environment in terms of energy expenditures, digestive function and resource-use behavior.

The overall study consisted of the following main components:

A. To determine seasonal changes in quality of the dietary composition (i.e. plant species) found in the study area.

B. To estimate seasonal changes in energy expenditures of the moose.

C. To assess the comparative digestive capabilities of moose, wapiti and cattle.

D. To quantify behavioral aspects of resource-use by moose.

The synthesis from the integration of results of parts A, B, C and D gives an integrated account of how moose cope with seasonal nutritional constraints in their habitat.

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PART A. SEASONAL ENVIRONMENTS

II. STUDY AREA, ANIMALS AND FACILITIES

This research was conducted at the Ministik Wildlife Research Station (SEC 26 TP50 R21), which is located 48 km SE of Edmonton, Alberta (Fig. II.1). The station is situated on the Cooking Lake moraine within the southern fringe of the boreal mixed-wood forest (Rowe 1972). Environmental descriptions have been provided by Gates (1980) and Nietfeld (1983). This information is common and applicable to all subsequent parts of the overall study.

A. Geology and Soils

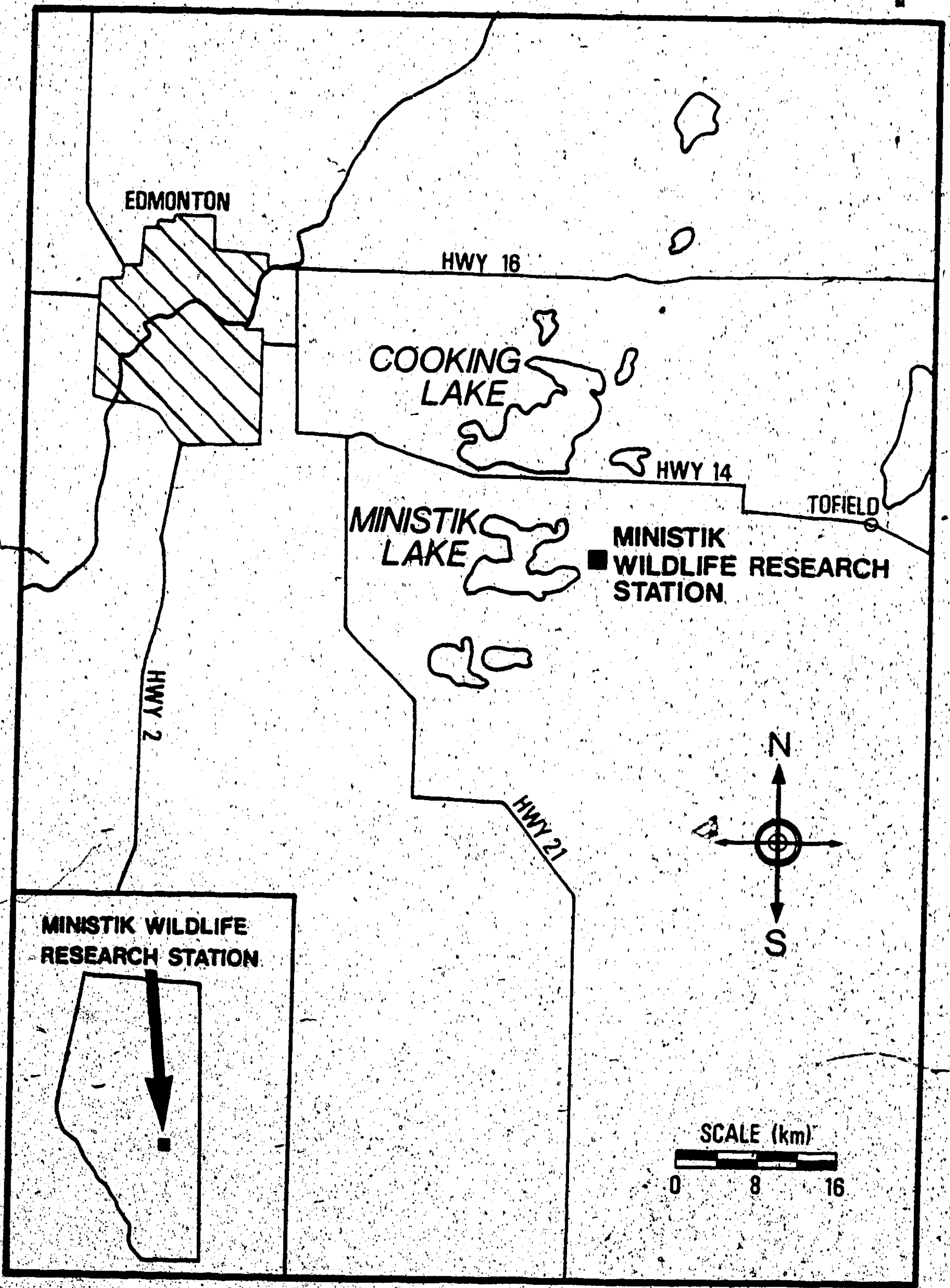
This morainic area is underlain by Upper Cretaceous shales, shale-sandstone and sandstones (Bayrock and Hughes 1962). Surface till deposited by the most recent glacial advance of the Pleistocene has formed an undulating complex of hills and closed depressions - the Cooking Lake Moraine. There are numerous seasonal and permanent bodies of water (sloughs). These wetlands form incomplete drainage systems throughout the area. The level of water in the sloughs represents the local water table where the soil till is impervious.

The Ministik Lake area is situated on Luvisdic soils derived from calcareous, fine-grained till (Bowser et al. 1962, Crown 1977). The forest soils of the Cooking Lake area are classed as Orthic Gray Luvisols, whereas the poorly drained mineral soils are classed as Humic Luvic Gleysols. Organic soils are often found in depressions.

B. Climate

The winters of this area are typically cold and dry with January ambient temperatures which range from -49°C to 10°C (Olson 1985). Summer temperatures are generally warm with a mean June to September temperature of 15°C. Annual precipitation averages 500 mm, with 25% as snowfall (Anon. 1980). Generally, accumulations of snow occur in late November and persist until April.

Fig. II.1. Geographical location of the Ministik Wildlife Research Station, Alberta.


EDMONTON
HWY 16
COOKING LAKE
HWY 14
TOFIELD
MINISTIK LAKE
MINISTIK WILDLIFE RESEARCH STATION
HWY 2
HWY 21
N
S
MINISTIK WILDLIFE RESEARCH STATION
SCALE (km)
0
8
16

C. Vegetation

The boreal mixed-wood forest zone is composed of a mixture of forest and grassland in a mosaic pattern with numerous aquatic communities (Bird 1966). Important factors which shape these communities have been weather, fire and man. However, since man has become a dominant force, the effects of fire have declined while agriculture has become more important.

The vegetation is primarily mixed deciduous-coniferous forests with a mosaic of open grasslands, sedge meadows and sloughs. In the closed canopy poplar forest, trembling aspen (*Populus tremuloides*)[2] and balsam poplar (*Populus balsamifera*), with lesser amounts of white birch (*Betula papyrifera*), are the dominant trees. White spruce (*Picea glauca*) infrequently forms pure stands, but isolated individuals are relatively common. Major shrub species of the understory are beaked hazel (*Corylus cornuta*), low-bush cranberry (*Viburnum edule*), red-osier dogwood (*Cornus stolonifera*), bracted honeysuckle (*Lonicera involucrata*), twinning honeysuckle (*Lonicera dioica*) and gooseberry (*Ribes* spp.). Sites with a lower density of trees or near the ecotones between communities support chokecherry (*Prunus virginiana*), saskatoon (*Amelanchier alnifolia*), red raspberry (*Rubus idaeus* var. *strigosus*), soapberry (*Shepherdia canadensis*) and western snowberry (*Symphoricarpos occidentalis*). Dense stands of willow (*Salix* spp.) also occur in moist low areas or near the perimeter of sloughs and drainage areas. Common forbs within this vegetation zone include fireweed (*Epilobium angustifolium*), Canada thistle (*Cirsium arvense*), dandelion (*Taraxacum officinale*), peavine (*Lathyrus* spp.) and white clover (*Trifolium repens*), with common mint (*Mentha arvensis*) and cattail (*Typha latifolia*) in wetland communities. Common graminoids are wheat grass (*Agropyron trachycaulum*), brome grass (*Bromus* spp.) and sedge (*Carex* spp.) from moist areas.

Representative habitats have been identified, by Gates (1980), as willow, poplar forest, upland grassland, lowland grassland and sedge meadows. Floristically diverse areas experiencing old-field succession have regeneration by clonal growth of trembling aspen and balsam poplar. The general habitat composition of the 65 ha enclosure, situated at Ministik, is illustrated in

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[2] Gray's Manual of Botany (M.L. Fernald 1970. D. Van Norstrand Comp., Toronto 1632 pp.) was used as the source of botanical nomenclature.

Fig. II.2, and more detailed descriptions will be given in subsequent chapters.

D. Pen Facilities

The Ministik Wildlife Research Station is approximately 265 ha in size enclosed by a 2 m game fence. Internal fencing divides the area into two pens of 200 ha and 65 ha in area. A central facility consists of several holding pastures, isolation pens and staunchions. Alleyways provided access to corrals and chutes which were used to move animals into a central restraining facility equipped for weighing animals.

E. Study Animals

Captive moose used in this study were five cows (Alice, Annie, Daisy, Elly and Eve) and two bulls (Morey and Rocky). These animals were enclosed within either a 2 or 5 ha pasture. The 65 ha enclosure was used for animals during free-ranging experiments.

Animals fitted with ruminal fistulas consisted of one moose cow (2.5 years old, Ellsie) and one bull (1.5 years old, Ralph), two wapiti steers (5 years old) and two Charolais-cross steers (5 years old). These animals were maintained in "The Wildlife Unit" at the University of Alberta Experimental Farm in Edmonton.

F. Literature Cited

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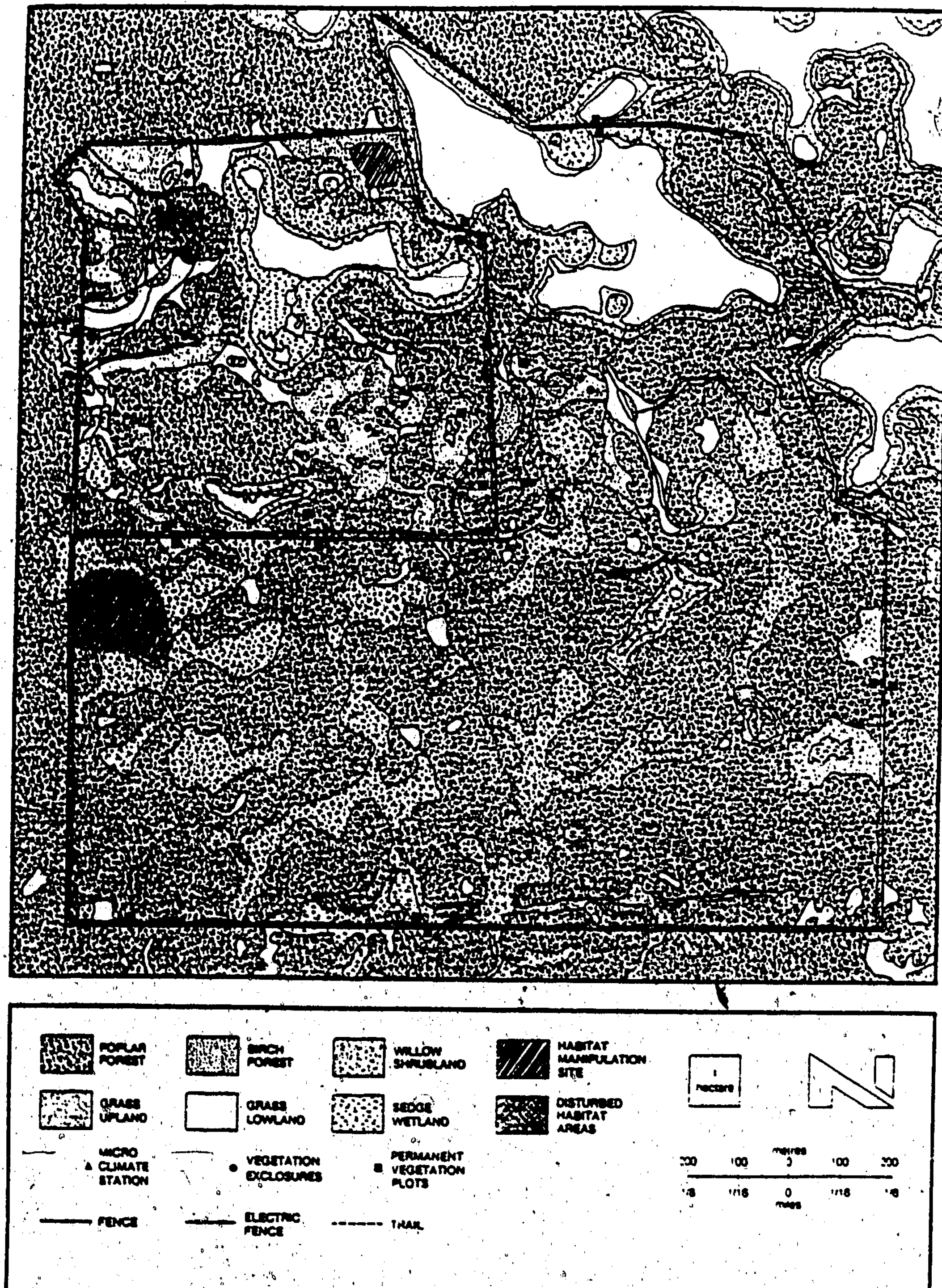
Fig. II.2. Distribution of habitats at the Ministik Wildlife Research Station, Alberta.



MINISTIK WILDLIFE RESEARCH STATION PRELIMINARY VEGETATION MAP

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III. SEASONAL QUALITY OF FORAGES[3]

A. Introduction

Forage quality is one of several important criteria determining range carrying capacity for moose. Although attention usually has been directed to the critical winter period, summer can also be considered a nutritionally critical period for northern wild ungulates, since body condition must be regained during a short growing season to ensure reproductive success, growth and winter survival (Julander et al. 1961, Klein 1970).

Diet-digestibility is a key measure of forage quality, but is both laborous and expensive to determine from pen feeding (*in vivo*) trials. *In situ* nylon-bag digestion using ruminally-fistulated animals allows rapid evaluation of numerous plant species and appears to be a reliable index of *in vivo* digestibility (Demarquilly and Chenost 1969, Orskov et al. 1980). It has the advantage that the quality of forages can be assessed in the natural environment of the rumen. Chemical methods are least expensive but correspondence with digestibility is often weak, particularly among forage classes (Van Soest 1982). Recently, near-infrared reflectance techniques have been used to estimate fibrous fractions (Park et al. 1983), crude protein and dry matter digestbility of forages (Mathison et al. 1985). However, these techniques and calibrations have not been applied to native forages.

There is little information on the digestibility of native forages in the aspen boreal forest let alone quantitative relationships between digestibility and chemical composition. Stewart et al. (1977) studied seasonal changes in quality of forages consumed by moose in Saskatchewan. Bishoff (1981) examined chemical composition of selected forage plants in Elk Island National Park, Alberta during winter and summer. Crude protein and *in vitro* dry matter digestibility of forages used seasonally by wapiti at the Ministik Field Station were investigated by Nietfeld (1983). To fill this perceived gap and provide a basis for evaluating seasonal

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[3] A version of this chapter has been accepted for publication. Renecker, L.A. and R.J. Hudson. 1987. Oikos (accepted).

changes in diet and habitat selection, this study was designed to determine seasonal changes in chemical composition of forbs, grasses, sedge and browse species used by moose in boreal mixed-wood habitats in relation to *in situ* digestibility.

B. Methods

Forages were collected in the Ministik Lake area (outside the 65 ha enclosure) from May, 1982 to October, 1983 to estimate seasonal nutrient supplies. In addition to forb, grass, sedge and browse species listed in Chapter II, bark from several species of trees and leaf litter were evaluated since they were important food items for moose in the study area, at least, seasonally (Chapter X).

Samples of 100 to 500 g (wet weight) of plant parts were collected from different habitat types every 2 to 4 weeks. Changes in plant phenology and quality were used as the basis for separation of seasons. An attempt was made to collect only plant parts used by moose based on observations reported in Chapter VIII. Current annual growth was selected from browse species as determined by the previous bud scale scar, avoiding the large diameter sprout growth. Only green parts of forbs, grasses and sedges were sampled, except subsequent to senescence and prior to spring green-up. Leaf litter and bark from trees were collected to simulate portions consumed by moose (Chapter VIII) (Renecker and Hudson 1985).

Forages were clipped and oven-dried at 50°C for 48 hours, then ground through a 20 mesh screen of a Wiley Mill. During spring and summer, leaves and woody stems of browse species were separated for comparative analysis. Forage samples were analyzed in duplicate for crude protein (CP) by the macrokjeldahl technique according to A.O.A.C. (1965). Neutral detergent fiber (NDF=cell wall constituents (CWC)), acid detergent fiber (ADF) and acid detergent lignin (ADL) were determined in duplicate by sequential analysis according to the methods of Goering and Van Soest (1970). Cell solubles were considered to be (100-CWC), hemicellulose (includes some fiber-bound proteins) as NDF-ADF, cellulose as ADF-ADL and lignin (LIG) as ADL-Ash Content (Van Soest 1982).

Triplicate 3 g samples of ground forage were weighed into nylon bags (pore size of 10 microns) and placed in the ventral sac of the rumen of a fistulated moose (Renecker et al. 1982) maintained on a combination of pelleted aspen-concentrate feed (Schwartz et al. 1985), chopped alfalfa and fresh browse diet. The bags were removed after 48 hours, washed and oven-dried at 60°C to constant weight according to the procedure of Orskov et al. (1980). Dry matter digestibility was calculated as the percent change in the dry weight of the bag contents.

C. Results and Discussion

In Situ Digestibility

Percent digestibility of dry matter using the nylon bag technique (NBD%) varied markedly among seasons ($P<0.05$) and forage types ($P<0.005$). For each forage, NBD% decreased as plant tissue matured (Fig. III.1). Values ranged from 26.5% for sedge during early spring to 73.5% for grasses in early June. Grasses and sedges attained maximal digestible dry matter during green-up, which occurred 1-2 weeks prior to leaf flush for browse species. Appearance of new plant growth depended on the duration of winter snow cover; growth was delayed during May, 1982. Digestibility of leaves varied markedly from 55% for white birch to more than 77% for beaked hazel. Differences in NBD% of woody tissues were less during May with the exception of white birch which was estimated to be 32%. With advancing plant phenology, white birch twigs continued to be significantly ($P\leq0.05$) less digestible than other woody plants reaching a seasonal low of 21% during early September.

Inter-specific comparisons of browse are summarized in Table III.1. Throughout winter, twigs of balsam poplar, trembling aspen and willow were most digestible. The least digestible woody species in each season was white birch. Reichardt (1981) and Palo (1984) found that birch stems contain large quantities of secondary plant metabolites which increased with fiber content of stems thereby reducing dry matter and protein digestibility (Choo et al. 1981). As a result, winter twigs of white birch containing 27% lignin and other secondary

Fig. III.1. Seasonal change in nylon bag digestibility of four forage (browse, grass, sedge and forb species) classes between May 1982 and October 1983 in the Ministik Lake area, Alberta.

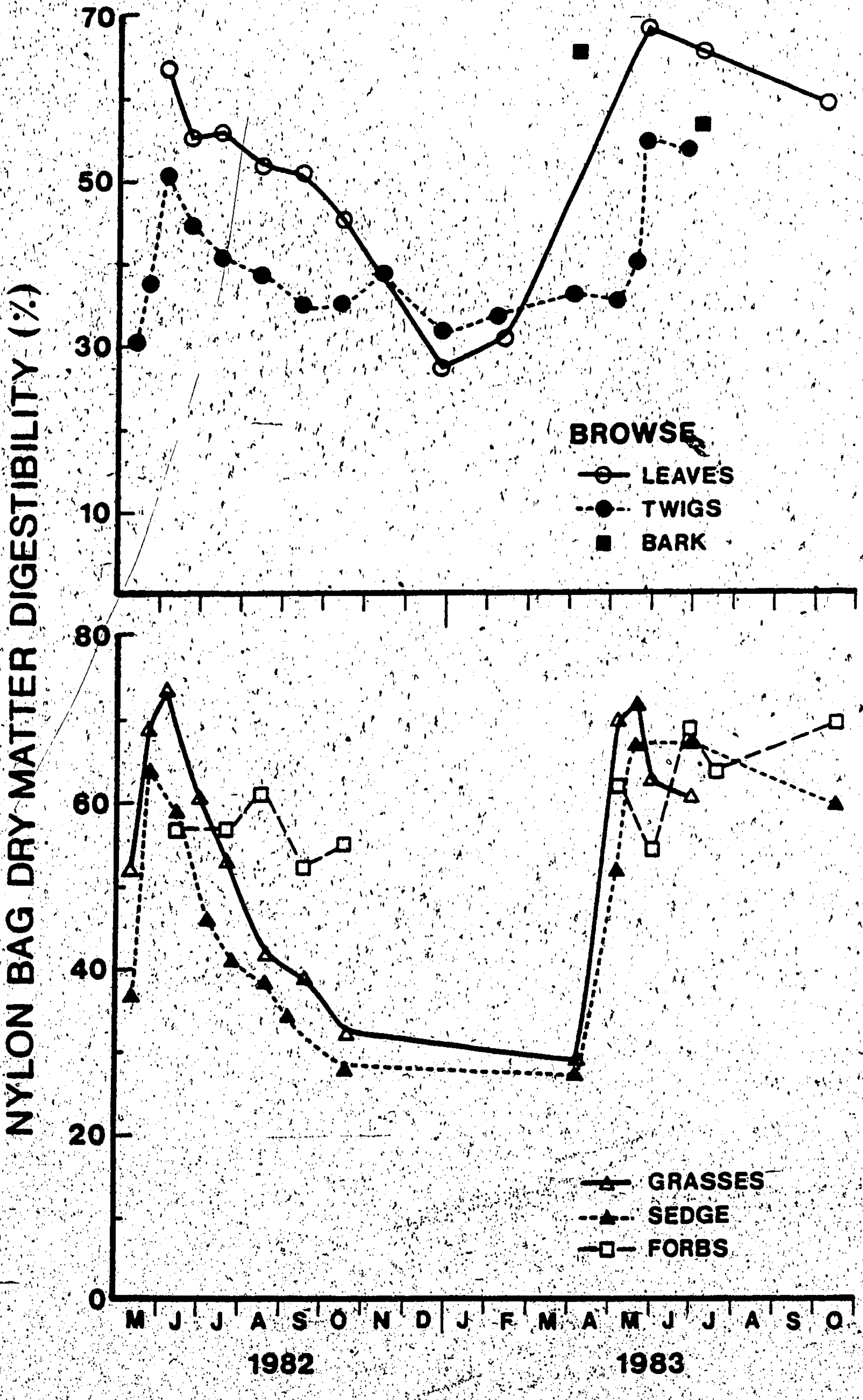

NYLON BAG DRY MATTER DIGESTIBILITY (%)
70
50
30
10
BROWSE
LEAVES
TWIGS
BARK
80
60
40
20
0
GRASSES
SEDGE
FORBS
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
1982
1983

Table III.1. Seasonal changes in nylon bag dry matter digestibility (NBD%) and crude protein (CP) content (%) of dry matter of browse species in Ministik Lake area, Alberta between May 1982 and October 1983.

Species[1]	Winter		Early Spring		Late Spring		Summer		Autumn	
	NBD%	CP(%)	NBD%	CP(%)	NBD%	CP(%)	NBD%	CP(%)	NBD%	CP(%)
Balsam Poplar										
Twigs	39.4	7.6	41.9	6.8	51.1	12.1	48.4	8.6	42.8	8.0
Leaves	--	--	--	--	73.9	19.7	61.1	13.7	--	--
Beaked Hazel										
Twigs[2]	29.8	5.6	29.6	5.4	54.9	11.4	37.8	6.7	33.7	5.2
Leaves	--	--	--	--	77.4	23.6	55.1	13.8	--	--
Chokecherry										
Leaves	--	--	--	--	--	20.9	--	--	--	--
Gooseberry										
Leaves	--	--	--	--	50.6	19.0	--	--	--	--
Bracted Honeysuckle										
Leaves	--	--	--	[illegible]	65.0	17.9	67.4	10.8	68.3	8.8
Low-Bush Cranberry										
Twigs	30.1	5.3	32.2	5.6	38.6	8.6	37.9	8.5	35.1	5.2
Leaves	--	--	--	--	59.8	18.5	58.0	12.6	--	--
Red-Osier Dogwood										
Twigs	30.3	5.3	33.7	6.5	48.8	12.9	42.6	7.8	38.6	6.8
Leaves	--	--	--	--	64.7	20.9	56.5	12.6	40.5	9.1
Red Raspberry										
Leaves	--	--	--	--	60.5	20.9	57.0	13.6	57.8	12.4
Rose										
Leaves	--	--	--	--	64.6	20.7	70.2	12.8	--	--

Table III.1. Seasonal changes in nylon bag dry matter digestibility (NBD%) and crude protein (CP) content (%) of dry matter of browse species in Ministik Lake Area, Alberta between May 1982 and October 1983.

Saskatoon										
Twigs	31.8	5.5	30.3	5.8	47.4	14.9	32.6	10.4	33.8	5.8
Leaves	--	--	--	--	54.2	20.6	49.5	14.5	--	--
Soapberry										
Twigs	--	11.8	--	--	--	--	--	--	--	--
Leaves	--	--	--	--	--	26.9	--	17.7	--	--
Western Snowberry										
Leaves	--	--	--	--	[illegible]	15.0	61.3	17.5	59.5	12.3
Trembling Aspen										
Twigs	44.9	8.3	45.4	7.1	55.4	13.5	47.1	10.1	44.3	8.6
Leaves	--	--	--	--	55.7	22.1	51.3	13.8	51.3	12.8
White Birch										
Twigs	20.7	7.4	25.8	7.9	32.2	9.9	23.4	8.0	22.8	8.5
Leaves	--	--	--	--	53.3	23.0	45.2	13.2	--	--
Willow										
Twigs	38.1	6.5	35.3	7.4	42.8	13.6	39.6	--	32.0	7.7
Leaves	--	--	--	--	60.2	21.0	50.3	15.8	42.3	12.0
Bark[1][2]	--	--	65.4	3.8	--	--	56.2	--	--	--
Leaf Litter[1][3]	27.1	8.0	30.9	6.1	--	--	--	--	49.3	8.2

[1] subsamples were derived from 1 sample of 100-500 g (wet weight) of material.
[2] bark was collected from trembling aspen, balsam poplar and willow.
[3] leaf litter consisted of fallen leaves from primarily trembling aspen, balsam poplar and beaked hazel.

compounds were extremely resistant to microbial degradation in the rumen. Differences in NBD% among browse species remained large during late spring, however these differences were not great enough to affect animal use as moose select from a wide variety of species during this period (see Chapter XI). Most leaf material from these shrubs exceeded a NBD% of 60% with the exception of gooseberry, saskatoon, western snowberry, trembling aspen and white birch. In autumn, green leaf growth was found only on shrubs established in habitats protected from early frosts. Bracted honeysuckle, rose, red raspberry and western snowberry maintained NBD% above 57% into late October. This allowed moose to maintain diet digestibility by foraging selectively during this period (Renecker and Hudson 1985, 1986).

Dry Matter and Leaf-Stem Ratios

Percent dry matter (DM) content of forages varied seasonally reflecting the stage of growth. Generally, lowest values occurred in late spring and increased throughout summer. The most marked change in DM content was observed in grasses and forbs between the new growth of spring and autumn when growth was complete. During the growing season, twigs showed consistently higher DM values than leaves. Subsequent to senescence and leaf fall, DM content of leaves was substantially higher than both twigs and bark as a result of desiccation of leaf litter. Twigs increased moisture content during late winter in reponse to warmer temperatures. From spring to autumn, bark was least variable differing only 8.5% in DM value, which probably reflected the high proportion of cell wall in this material.

Leaf material contributed to a substantially larger proportion of the current annual growth with maturity (Table III.2). The leaf-to-stem ratio peaked during early summer and then declined with senescence and finally with leaf fall which occurred during autumn. A considerably lower leaf-to-stem ratio during early August was apparently caused by a period of high temperatures and low precipitation.

Table III.2. Mean leaf-to-stem ratios for current annual growth of browse species[1] from June 7 to October 13, 1982 based upon a dry weight:dry weight ratio[2].

Collection date	Leaf-to-Stem Ratio (±SE)
June	
7	1:0.33 (±0.02)
25	1:0.29 (±0.02)
July	
3	1:0.32 (±0.05)
17	1:0.26 (±0.04)
August	
5	1:0.49 (±0.05)
16	1:0.33 (±0.04)
September	
3	1:0.53 (±0.06)
15	1:0.52 (±0.05)
October	
1	1:2.26 (±0.68)
13	1:30.5 (±9.60)

---

[1] Browse species included balsam poplar, willow, beaked hazel, low bush cranberry, saskatoon, rose, bracted honeysuckle, red raspberry, western snowberry, red-osier dogwood and white birch.

[2] Subsamples were derived from a 100-500 g (wet weight) sample of current annual growth.

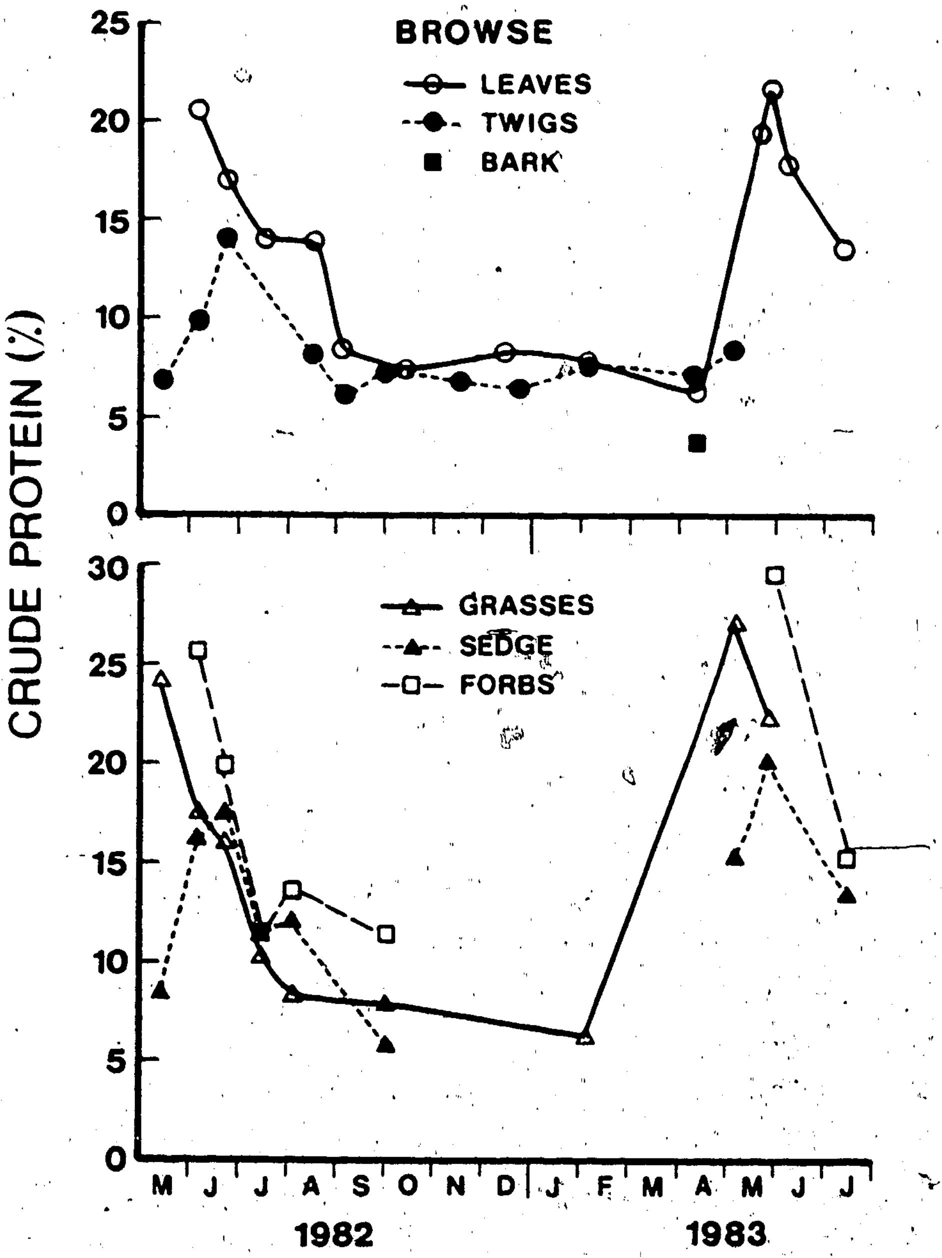
Crude Protein

Crude protein (CP) content in all forages varied significantly ($P < 0.05$) with season. Values ranged from 5-15% for woody twigs to 6-27% for grasses, with only small deviations occurring between September and April with a mean (±SE) of 7.3±0.4% CP for the winter period.

Crude protein, as a percentage of DM, increased in spring following increases in moisture content as observed by Stewart et al. (1977). Generally, CP of grasses peaked first during early May followed by leaves, forbs, twigs and sedge during late May and early June (Fig. III.2). By early September, CP had declined steadily to 8.5±1.1% except for a brief late summer green-up. In autumn, protein levels depended on senescence, abscission and time of first frost, with green forbs and leaves of willow and aspen containing more than 12% CP (Table III.1). After abscission in September, fallen leaves contained approximately 8.2% CP. However, this level decreased continuously to a spring low of 6.1% CP with leaching by autumn precipitation and winter freeze-thaw cycles. Lowest levels were recorded for bark of aspen and balsam poplar during April. Nevertheless, free-ranging moose consume large quantities of bark prior to spring green-up (Renecker and Hudson 1985).

Protein is an essential dietary nutrient for maintenance, growth and reproduction. The minimum requirement for CP in rations of domestic cattle has been estimated to be around 6-8% (ARC 1980) before intake and digestibility are depressed. Similarily, minimum CP requirements of deer are estimated to be 5-7% (Bissel and Strong 1955, Wallmo et al. 1977, Holter et al. 1979). If these values are applied to moose, then the CP content in forage samples collected from September to spring green-up was at the minimum level necessary for maintenance of rumen and body functions. Deciduous foliage and forbs exhibited CP levels from May to August which were higher than the estimated 13% required for growth and production in deer (Murphy and Coats 1966, French et al. 1956).

Fig. III.2. Crude protein content of four forage classes (browse, grass, sedge and forb species) from May 1982 to July 1983 collected in the Ministik Lake area, Alberta.


BROWSE
LEAVES
TWIGS
BARK
GRASSES
SEDGE
FORBS
CRUDE PROTEIN (%)
25
20
15
10
5
0
30
25
20
15
10
5
0
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
1982
1983

Fiber Composition

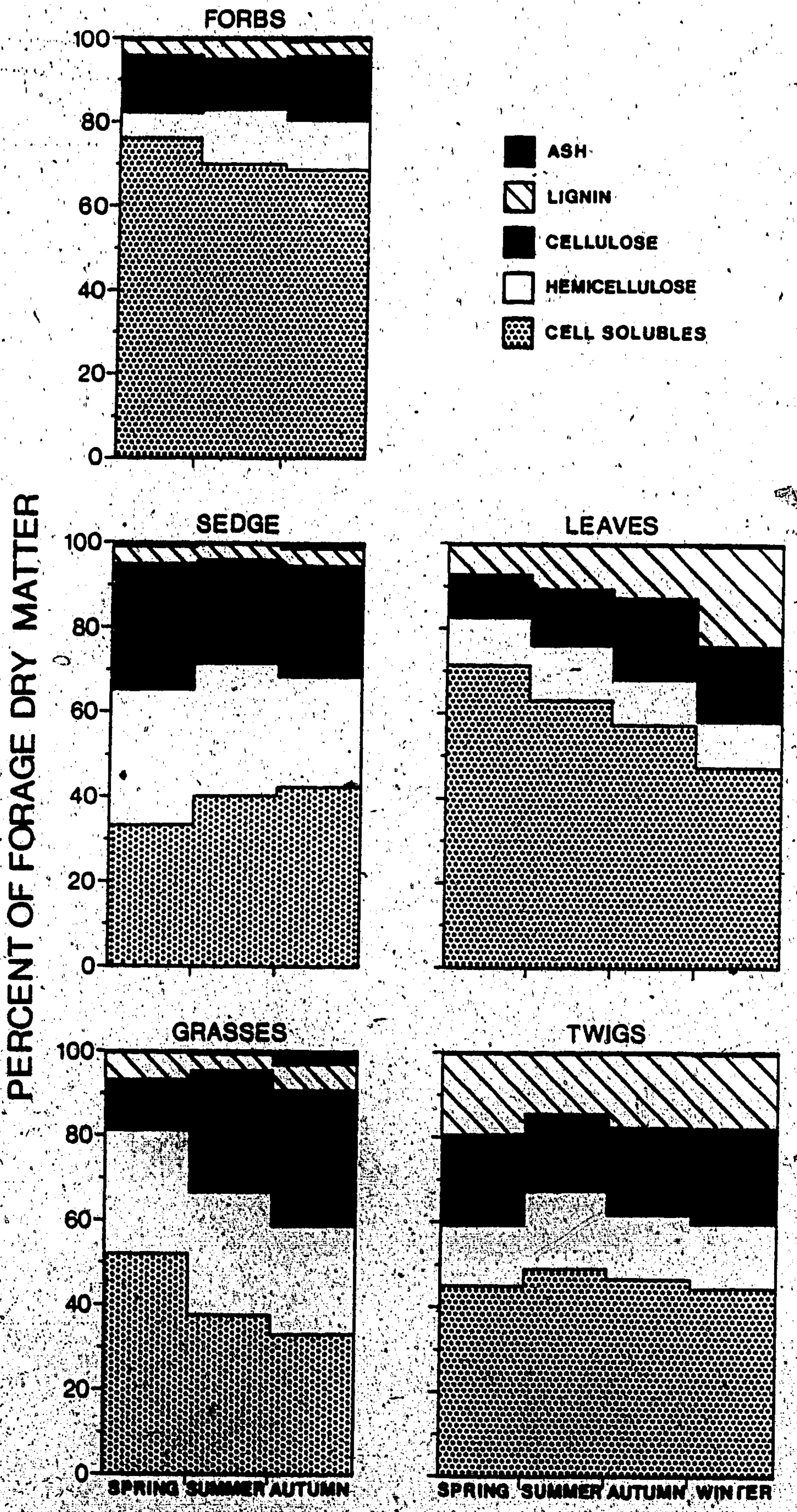
Changes in fiber components were closely associated with plant phenology and compared favorably with studies in this and other areas (Short et al. 1972, Blair et al. 1977, Oldemeyer et al. 1977, Stewart et al. 1977, Eastman 1983). Cell wall constituents of foliage and grasses showed significant ($P < 0.05$) variation among seasons and forage classes.

The greatest differences in fiber content occurred between the succulent growth of spring and the dormant material of winter. Rapid new growth, which is associated with spring, decreased dry matter concentration and structural carbohydrates in browse, leaves, forbs and grasses (Fig. III.3). Concomitantly, high levels of rapidly digestible cell solubles (100 - CWC%) were associated with green plant material during the early stages of growth when meristematic activity was high (Blair and Epps 1967). Concentrations of CWC in sedges and twigs were lowest during summer. Elongation of woody twigs and growth of cooler sedge meadow habitats may have been affected by a persistant snow cover until early May, 1982 and absence of substantial spring precipitation. As the growing season progressed and forages matured, the fibrous fraction of plant material increased as cell solubles decreased.

Grasses, Sedge and Forbs

Grasses and sedge were generally higher in CWC and lower in lignin than other forage classes (Fig. III.3). A large portion of this cell wall material was hemicellulose. Similar tissue differences have been documented for grass species in comparison to forbs and browse (Gaillard 1965, Milchunas et al. 1978). The virtually nondigestible lignin fraction remained relatively constant and low throughout the annual period with only a marginal decrease during summer. Mertens (1973) suggested that the lignin component of grasses may delay rates of passage more than higher lignin content of legumes as a result of the long, cylindrical fiber shape of grasses. The need to delay passage of grasses and sedges likely allows time for digestion of cellulose and hemicellulose in the cell walls. Perhaps because moose lack specific delaying mechanisms and large rumen volumes, they rarely feed on grasses or sedge during winter and only infrequently during summer and autumn

Fig. III.3. Cell wall composition of leaves and woody twigs from current annual growth of browse species during spring, autumn and winter seasons. Cell wall composition of grass, sedge and forb species during spring, summer and winter seasons in the Ministik Lake area, Alberta.


FORBS
SEDGE
LEAVES
GRASSES
TWIGS
PERCENT OF FORAGE DRY MATTER
0
20
40
60
80
100
ASH
LIGNIN
CELLULOSE
HEMICELLULOSE
CELL SOLUBLES
SPRING
SUMMER
AUTUMN
WINTER

pe[illegible] (Renecker and Hudson 1986).

Browse Species

Leaves from deciduous trees and shrubs had a consistently lower precentage of CWC than that of twig portions (Fig. III.3). Levels of CWC in woody twigs did not vary significantly ($P > 0.05$) with season, ranging between 45% for willow in late May to 63% for saskatoon during winter. However, the lignin component of the CWC in browse leaves showed a significant ($P < 0.01$) increase as the deciduous growth matured, ranging from 4.7% in red-osier dogwood during June to 26% for winter leaf litter. This trend, accompanied by a decrease in cellular contents, agrees with results for similar browse species in other areas (Oldemeyer et al. 1977, Eastman 1983).

If portions of older wood were consumed, then levels of cell solubles would decrease because of the more lignified and thicker cell walls (Blair et al. 1977, Penner 1978). Moose have also been observed to discriminate between plant parts of deciduous trees and shrubs during spring and summer, "stripping" only succulent leaves as food (Renecker and Hudson 1985). This rapidly growing tissue contains a high proportion of cell contents which are highly digestible (Chapin 1980). Separate analysis of leaves and woody tissue during the growing season is an important consideration for analyzing feeding behavior of moose.

Relationship of Digestibility to Forage Composition

Forage analysis by wet chemistry provides a good estimate of the digestibility of forages used by domestic animals (Van Soest 1982). It is often a less satisfactory correlate of the digestibility of browse but little work on this aspect has been done. In this study, chemical composition was found to be as good as a predictor of *in situ* digestibility of browse as of grasses but the relative importance of components varied (Table III.3). For browse, lignin and DM were the best single predictors while for grasses and sedges, crude protein gave the highest correlation.

Table III.3. Simple linear regression of dry matter digestibility of forages in nylon bags suspended in the rumen of a fistualted moose and tissue composition of forage classes sampled in the Ministik Lake area, Alberta from May 1982 to October 1983.

Regressions on Digestibility	N	a	b	SEb	r²
Browse Species					
Dry Matter	18	98.73	-1.23	0.18	0.74 ***
Crude Protein	17	24.59	1.88	0.50	0.47 ***
Cell Wall Content	12	81.48	-0.88	0.20	0.65 ***
Hemicellulose	12	45.24	-0.41	0.52	0.06 N.S.
Cellulose	12	65.30	-1.41	0.42	0.42 **
Lignin	12	66.12	-1.65	0.78	0.78 ***
Grasses and Sedge					
Dry Matter	25	77.99	-0.76	0.55	0.55 ***
Crude Protein	17	20.81	2.20	0.31	0.77 ***
Cell Wall Content	9	123.12	-1.29	0.47	0.52 *
Hemicellulose	9	-12.40	1.99	1.30	0.25 N.S.
Cellulose	9	79.39	-1.38	0.44	0.59 **
Lignin	9	62.75	-3.85	4.51	0.09 N.S.

N.S. not significant at the 0.05 level.
* significant at the 0.05 level.
** significant at the 0.025 level.
*** significant at the 0.005 level.

Correlation coefficients were highly significant ($P<0.005$) when hemicellulose (HC), cellulose (CELL) and lignin (LIG) were combined to predict NBD% in browse twigs and leaves:

$$Y=0.21\ HC-0.76\ CELL-1.34\ LIG+71.99\ (r^2=0.83).$$

and grasses and sedges:

$$Y=1.44\ HC-0.99\ CELL-2.73\ LIG+41.30\ (r^2=0.71).$$

In grasses and sedges, the smaller portion of lignin in the cell wall appeared to have a larger effect on its NDB% than for other forage classes.

Other workers have provided predictive relationships between fiber components of forages and digestibility (Van Soest 1965, Oldemeyer et al. 1977, Cederlund and Nystrom 1981, Choo et al. 1981). Associative effects of physical inhibitors or secondary metabolites are often important but their effects are masked when digestibility is determined by *in situ* methods (Oh et al. 1966, Van Soest 1967, Mould 1980). Therefore, these results probably would not hold where the diets of moose are predominantly of a single plant species.

D. Conclusions

The nutritional quality of forages used by moose in aspen boreal habitats was sufficiently high during spring and summer to permit growth and deposition of tissue. However, during winter, forage digestibility was depressed and marginally adequate for maintenance as a result of increased fiber and decreased protein. Renecker and Hudson (1985) found that moose reduced dietary intake (by about 65%) when forage quality was depressed during winter.

Leaf litter, an important early winter forage, was only marginally lower in NBD% and CP than woody stems, but probably more abundant and therefore may lend more nutritive value to moose during winter. Although bark was relatively low in CP, it was highly digestible and could serve as a supplemental source of rapidly fermentable carbohydrate in spring. The importance of two forage resources, leaf litter and bark, is often overlooked.

Although grasses are quite digestible, they are still less digestible and pass more slowly out of the ruminoreticulum of moose than aspen browse (Chapter VII). The heavy dependance of moose on foliage and twigs must be related to relative rates of digestion and passage (Mertens 1973). Because moose are concentrate selectors (Hofmann 1973), relying on energy from highly digestible material while propelling slowly-digested fibrous fractions through the gastrointestinal tract, they are unable to exploit grasses and sedges which would require long retention times and large rumen capacity to optimize digestibility.

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PART B. SEASONAL ENERGETICS

IV. TELEMETERED HEART RATE AS AN INDEX OF ENERGY EXPENDITURE[a]

A. Introduction

Indirect calorimetry, the most widely used method for determining metabolic rate, requires the collection of expired air. Although respiration chambers permit highly controlled environmental conditions, they inhibit normal activity. Mobile gas collecting techniques, such as the face mask method (Mattfeld 1974, Renecker et al. 1978, Kautz et al. 1981, Pauls et al. 1981, Parker and Robbins 1984) or tracheotomy (Mautz and Fair 1980), can be used on animals under less confined conditions to compute energy expenditures more applicable to free-ranging circumstances.

The use of heart rate as a correlate of metabolic rates of unrestrained animals has been explored in a variety of studies. An index can be established from repeated simultaneous measurement of heart rate and energy expenditure over a range of thermal conditions, nutritional planes or activity levels. This predictive relationship has been applied in wild ungulates, including mule deer (*Odocoileus hemionus*) (Kautz et al. 1981), white-tailed deer (Holter et al. 1976, Mautz and Fair 1980), wapiti (Robbins et al. 1979, Pauls et al. 1981) and moose calves (Renecker et al. 1978, Chermnykh and Mochalov 1987). Robbins et al. (1979) and Mautz and Fair (1980) expressed doubt in the usefulness of the calibrated heart rate index based on poor correlations. However, strong positive correlations between oxygen consumption and pulse rate were reported by other workers (Holter et al. 1976, Renecker et al. 1978, Pauls et al. 1981) with restrained wild ungulates.

Radiotelemetry transmitters have been constructed to detect and transmit pulse rate or QRS pattern. These remote monitoring devices avoid the consequent interference with natural behavior because no recording leads are required. Recent investigations have reported successful transmission of heart rate from unrestrained ungulates using several transmitter designs.

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[a] A version of this chapter has been published. Renecker, L.A. and R.J. Hudson. 1985. Comp. Biochem. Physiol. 82A: 161-165.

Systems have been developed which are mounted on a harness for external placement with surface electrodes (Johnston et al. 1980, Pauls et al. 1981). Miniturization and reduced power requirements have resulted in the development of completely implantable units (Jacobsen and Stuart 1978) and implantable packages with an external repeater transmitter neck collar (Cupal et al. 1976). An improved design of the repeater system, described by Weeks et al (1977), has been tested with variable success with mule deer (Freddy 1984), wapiti (Lieb and Marcum 1979), moose (Renecker et al. 1982, Renecker and Hudson 1983) and bighorn sheep (*Ovis canadensis*) (R. Weeks, personal communication). Jacobsen and Stuart (1978) described a completely implantable system which has been implanted successfully in black-tailed deer (Jacobsen et al. 1981) and moose (Renecker et al. 1982, Renecker and Hudson 1983).

The objective of this study was to evaluate heart rate as a correlate of energy expenditure in tethered moose. This chapter presents revised equations based on data collected over a period of 22 months.

B. Methods and Materials

Three hand-reared moose cows (No. 135, 447 and 449) were maintained in a 2 ha pasture at the Ministik Wildlife Research Area near Edmonton, Alberta on an aspen-concentrate ration described by Schwartz et al. (1985). Animal weights varied between 280 and 420 kg and animals were 2.5 to 5.5 years old.

Telemetry System

Heart rate was obtained by telemetry from two types of implanted transmitters designed for a battery life of 2 years. One transmitter unit (Model HR13) described by Weeks et al. (1977), with electrode leads of 8 and 56 cm, relayed a signal to a transceiver neck collar (Model RRF-3, Wyoming Biotelemetry, Inc.). The other system was completely implantable (Jacobsen et al. 1981) with electrode lengths of 15 and 56 cm (Model ECG-1-1000, J. Stuart Enterprises). Each transmitter was tuned to a specific frequency within the range of 150.880 to

151.880 MHz. The implantable transmitter (manufactured by Wyoming Biotelemetry, Inc., Model HR13) measured 30 mm x 30 mm x 10 mm, weighed 20 g and was manufactured to transmit a maximum distance of 46 cm to the repeater-type neck collar at a frequency of 100 KHz. The implant from J. Stuart Enterprises measured 14 cm long x 3 cm in diameter and weighed 125 g.

The data receiving system consisted of a receiver (TRX 48A, Wildlife Materials, Inc.), a digital data processor (TDP-2, Telonics) connected to a pulse period to pulse-rate converter (J. Cupal Consulting Engineer) installed in a dual channel recorder (TDR-1, Telonics) and a 12-volt Globe-Union Gel Cell. Signals were received on two 11-element yagi antennae with a cophasing unit (Wildlife Materials, Inc.) mounted on a 18.3 m tower. A rotor was installed on the ~~antennae~~ standpipe to allow manual rotation of the antennae from the central laboratory.

Surgical Procedures

Prior to surgery, animals were fasted 24 hours to reduce the possibility of bloat and regurgitation. Each animal was anaesthetized with an intramuscular injection of etorphine (0.025±0.002 mg/kg) and xylazine (1.08±0.17 mg/kg). Atropine (0.5 ml; 0.60% solution w/v distilled deionized water) was administered to prevent excessive salivation and stabilize heart rate. The larger, completely implantable unit was sutured initially, using absorbable suture material, into a polypropylene mesh pocket to prevent implant movement and later this was substituted with non-absorbable silk suture when the pouch separated after 30 days. Before surgery, trocars and polypropylene mesh were sterilized in a mixture of chlorhexidine or zepharine chloride cold sterilant and water (1:1 or 1:750, respectively) for a minimum of 20 minutes. They were then rinsed in sterile saline.

The implant procedure followed those of Freddy (1977). Three incisions were made in the ventral side of each animal. A 3 cm diagonal incision was opened anterior to the anticipated implant site, near the loose folds of skin at the base of the neck, about 5 cm off midline. A pouch was dissected bluntly in a natural pocket for insertion of the implant. Initially, this incision was 8 cm for the completely implantable unit but was reduced to 5 cm when placed at the anticipated midpoint of this transmitter. Incisions (3 cm) were made near midline at the anterior and posterior end of the sternum. The anterior incision was offset laterally by 5 cm from midline. The electrode leads were passed from the neck pocket to the appropriate areas, the bared ends were sutured into position in the underlying sternal muscle with nonabsorbable silk suture material and then incisions were closed with absorbable suture material. Postoperative treatment with topical and intramuscular antibiotics reduced infection. Animals were given an intravenous injection of diprenorphine (0.051±0.004 mg/kg) to reverse the effect of the anaesthetic.

C. Energy Expenditure

A face mask constructed from plexiglass and expanded neoprene, with one-way valves made from dental dam, was used to collect respired air from non-fasted, tethered moose. Trials of simultaneous measurement of oxygen consumption and heart rate were conducted on selected days of above average, average and below average air temperatures from January, 1982 to October, 1983. A 10 minute collection of respiratory gas was made from each animal with a face mask and meteorological balloons during standing and lying postures. Volume was measured with a dry test meter and oxygen extraction on a Beckman Oxygen Analyzer (Model 7003). Calculations of metabolic rate were based on the calorific equivalent of 20.46 KJ/l of oxygen at STP (MacLean 1970). Pulse rate of the cardiac cycle was monitored simultaneously and expressed as body weight$^{-0.25}$ to standardize measurements for changes in body weight (Brody 1945).

Least squares regression analysis was used to compute fitted linear and exponential lines for the data. Slopes and intercepts of computed lines were statistically compared with a t-test for confidence intervals (Sokal and Rohlf 1981). The confidence intervals for calculated intercepts were determined from a computed asymptotic standard deviation (Jennrich 1981).

D. Results and Discussion

Evaluation of Telemetry System

Several obstacles which prohibited long-term measurement of heart rate of moose had to be overcome. No occurrence of tissue infection was observed with these procedures under field conditions. With experience, duration of surgery was reduced to less than 45 minutes.

Operating life of the completely implantable unit was less than 2 months as a result of electrode breakage. This problem was rectified by braiding numerous strands of pacemaker wire. Recently, Weeks et al. (1977) strengthened the electrode leads of the repeater-type system eliminating this problem. However, the repeater-type system failed because the bared electrode tips, at the anterior of the sternum, pulled out of the muscle. This was solved by increasing the anterior lead to 38 cm and the use of nonabsorbable suture material. Defective batteries reduced the operational time of implanted transmitters to less than six days on one occasion.

Transmitter rejection occurred in three cases. Following skin abrasion, the largest completely implantable unit was rejected through the skin layer at 4 to 5 months after the implant operation. The animal was not in poor health and the area healed rapidly. This problem could be eliminated by further reinforcement of the neck pocket with polypropylene mesh. Chronic implants of the repeater-type system have been in operation for over one year in penned and free-ranging moose.

System Performance

Field testing of the two telemetry systems was conducted for more than two years. Effective line-of-sight range of the transceiver neck collar was 3200 m and about 500 m for the completely implantable unit. Signal strength was influenced by topography with effective range declining when animals moved into topographic depressions. Also, orientation of the animal affected maximum transmitting range of the completely implantable unit reducing signal strength when the animal was monitored from the side of the body where the transmitter was not positioned. Initially, heart rates were not transmitted from animals equipped with repeater-type systems when their heads were lowered and the transceiver neck collar moved out of range of the implant. A modified identification neck collar (Freddy 1977) placed anterior to the repeater-type neck collar maintained a maximum distance of about 30 cm between the implant and the external transceiver unit.

Signal quality was not reduced as a result of motion artifact and "T" wave. Violent movement, such as shaking and running, generated virtually no artifact. An improved electronic design of the repeater-type unit reduced electrode movement artifact and generated "T" waves (Weeks et al. 1977). Nevertheless, some unwanted signal noise was apparent on the strip chart recordings. Signal quality was further improved by a second generation model of a microprocessor, described by Cupal (1977), which processed heart pulse rate signals within predefined limits. Unfiltered artifact and noise were separated by visual inspection of the changes in pulse width. In addition, this pulse-rate converter was self-calibrating at hourly intervals and generated a moving average over either 2, 4 or 8 heart rate pulses. The device was inoperative when room temperature approached 0°C. This problem may be eliminated by installation of a strap heater in the compartment containing the electronic circuitry.

Heart Rate and Energy Expenditure

Results of the trials in this study indicated a close relationship between energy expenditure and heart rate. There was a significant ($P<0.001$) linear and exponential association between heart rate and metabolic rate for individual animals (Table IV.1). Generally, the highest correlation coefficients, ranging between 0.94 and 0.98, were observed with an exponential equation.

Comparisons between regression coefficients indicated there was no significant difference ($P>0.05$) between slopes of individual regression lines for the three moose. Lund (1974) and Kautz et al. (1981) suggested that the variation in slope may result from age, seasonal effects and differences in physical condition. Since age and time of calibration were

Table IV.1. Regression of metabolic rate (kJ/kg $BW^{0.75}$/hr) on heart rate (b/min/kg $BW^{-0.25}$) for three moose cows from winter 1982 to autumn 1983 at the Ministik Wildlife Research Station, Alberta.

Animal	Regression type	N	a	b	SEb	r
135	Linear	8	-9.617	0.1283	0.0151	0.96 ***
	Exponential	8	4.794	0.0063	0.0441	0.94 ***
447	Linear	86	-12.671	0.1678	0.0038	0.98 ***
	Exponential	86	5.910	0.0062	0.0008	0.98 ***
449	Linear	86	-24.554	0.2003	0.0078	0.94 ***
	Exponential	86	3.262	0.0080	0.0011	0.96 ***
Combined data	Linear	180	-15.170	0.1692	0.0055	0.91 ***
	Exponential	180	4.675	0.0068	0.0009	0.94 ***
Computed regression*	Linear		-15.614	0.1821		
	Exponential		4.655	0.0071		

*** r-correlation coefficients significantly different from zero ($P<0.001$).
* Weighted mean equation from regression of individual animals.

similar for the three cows, physical condition may have accounted for most of the variability. There was no significant difference in the intercepts for moose no. 135 and 449 ($P>0.05$), but there was a significant difference for moose no. 447 ($P<0.05$). Webster (1967) and Brockway and McEwan (1969) attributed the variability between domestic sheep to nervous disposition. Kautz (1978) suggested that a consistently higher heart rate for given energy expenditure in mule deer may result from level of nervousness, level of conditioning, sex and body weight differences. In addition, small significant differences among intercepts would be more easily shown when determined from a large sample, which may be reflected by animals no. 447 and 449.

An overall pooled equation was computed from weighted regression coefficients (weight equal to error degrees of freedom) and averaged intercepts (Fig. IV.1). If this relationship was used to predict the mean metabolic rate for individual animals, then estimates would differ 4.2% (1.5 KJ/kg $BW^{0.75}$/hr) to 5.1% (2.7 KJ/kg $BW^{0.75}$/hr) from those calculated with individual regressions for moose no. 447 and 449, respectively. The mean equation overestimated metabolic rate predicted by the individual regressions of moose no. 135 by 9%. The reduction in accuracy in this case was probably a result of a small sample size.

Respiratory Rate Index

Significant correlations ($P<0.01$) also were detected between respiratory rate and energy expenditure (Table IV.2). A similar relationship was detected for moose calves which were monitored in a respiratory chamber (Renecker et al. 1978). In both cases, heart rate was a better predictor of metabolic rate than respiratory rate. The change in breathing rate probably reflected dissipation or conservation of heat by increasing or reducing evaporative water loss, respectively, rather than energy costs (Hargrove and Gessaman 1973).

Fig. IV.1. Relationship between metabolic rate and heart rate for individual moose between winter 1982 and autumn 1983 at the Ministik Wildlife Research Station, Alberta. The solid line is the fitted line for individual moose and the broken line is the pooled regression for the three animals.

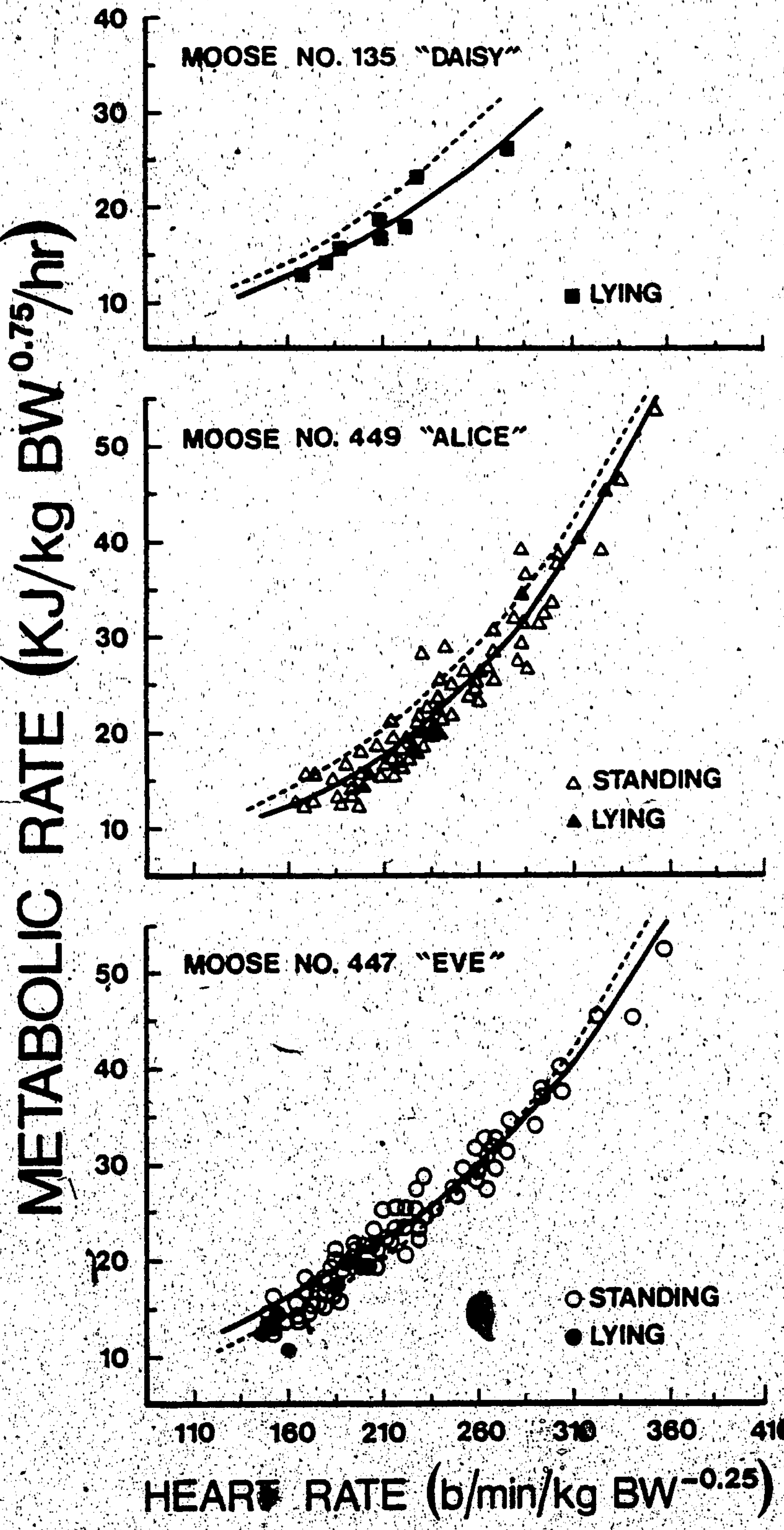
MOOSE NO. 135 "DAISY"
■ LYING
MOOSE NO. 449 "ALICE"
△ STANDING
▲ LYING
MOOSE NO. 447 "EVE"
○ STANDING
● LYING
10
20
30
40
50
110
160
210
260
310
360
410
METABOLIC RATE (KJ/kg BW^0.75/hr)
HEART RATE (b/min/kg BW^-0.25)

Table IV.2. Regression of metabolic rate (kJ/kg $BW^{0.75}$/hr) on respiratory rate (breaths/min) for three moose cows from winter 1982 to autumn 1983 at the Ministik Wildlife Research Station, Alberta.

Animal No.	Regression Type	N	a	b	SEb	r
135	Linear	8	11.901	0.6912	0.1133	0.93 **
	Exponential	8	13.256	0.0327	0.0662	0.91 **
447	Linear	86	17.793	0.4884	0.0545	0.70 ***
	Exponential	86	18.815	0.0170	0.0384	0.71 ***
449	Linear	86	16.189	0.3713	0.0364	0.74 ***
	Exponential	86	17.535	0.0132	0.0256	0.73 ***

*** r-correlation coefficients significantly different from zero ($P<0.001$).
** r-correlation coefficients significantly different from zero ($P<0.01$).

E. Conclusions

Long term implants with good transmitting range have been developed for monitoring heart rate. Improved surgical techniques, low-powered miniturized curcuits, prevention of moisture leakage and reduced signal artifact make heart rate telemetry a practical field method for remote monitoring of physiological changes in heart rate of free-ranging animals. This technique can be used for studying activity budgets, responses to novel stimuli and environmental conditions as well as energy expenditures.

Although factors may confound the relationship between energy expenditure and pulse rate of the heart, the high correlation coefficients indicate that the heart rate index was a good predictor of energy expenditure in adult moose. Although calibration for the individual animals generated the most accurate predictors of metabolic rate, differences between the weighted mean equation and individual estimates of mean energy expenditure were less than 10% for three moose cows. Therefore, this weighted mean equation could be used to study energy expenditures of adult free-ranging moose cows.

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V. SEASONAL ENERGY EXPENDITURES AND THERMOREGULATORY RESPONSES [8]

A. Introduction

Seasonal metabolic rhythms occur in a number of northern wild ruminants including mule deer (Freddy 1984; Parker and Robbins 1984), white-tailed deer (Silver et al. 1969, Sauer 1973, Holter et al. 1976, Jacobsen 1978; Moen 1978), wapiti (Lieb and Marcum 1979, Pauls et al. 1981; Parker and Robbins 1984), bighorn sheep (Chappel and Hudson 1980) and bison (Christopherson et al. 1979). The amplitude of these cycles varies widely among species. Although conditions of measurement have not been highly standardized, small cervids appear more cyclic than large bovids but whether this is related to phylogenetic relationships, body size or digestive strategy is not clear. Information on moose, a large browser, may help to resolve this question.

Circannual thermoregulatory responses provide an indication of the adaptive limits of wild ruminants. The lower critical temperature is usually defined as the temperature at which metabolic rate increases to maintain homeothermy. Upper critical temperature is similarily defined as the temperature at which metabolism increases in response to heat and is associated with hyperthermia. Parker and Robbins (1984) described seasonal changes in thermal sensitivity of both mule deer and wapiti and reviewed much of the current literature on other wild ruminants.

Data on seasonal cycles of metabolic rate (Regelin et al. 1985), feed intake (Schwartz et al. 1984, Renecker and Hudson 1985a) and body weight (Schwartz et al. 1987, Renecker and Hudson 1985a) of moose have been published recently. Although the metabolic response of calves to cold has been studied (Renecker et al. 1978), this is one of the first studies on seasonal thermal sensitivity of adult females. Specific objectives were to: (i) determine seasonal changes in energy expenditure, heart rate and body weight of adult moose and (ii)

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[8] A version of this chapter has been published: Renecker, L.A. and R.J. Hudson. 1986. Can. J. Zool. 64: 322-327.

relate seasonal thermoregulatory responses of moose cows to ambient temperature.

B. Methods and Materials

Seven hand-reared moose (two males, five females), ranging in age from 12 to 70 months, were maintained within a two ha enclosure at the Ministik Wildlife Research Area, near Edmonton, Alberta, on a pelleted aspen-concentrate ration (Schwartz et al. 1985) offered *ad libitum*. Although data on body weight changes were taken on all animals, only two cows were suitably trained for measurement of metabolic rate by indirect calorimetry.

Bioenergetic Parameters

Metabolism trials were conducted from winter 1982 to autumn 1983 on two adult female moose (Eve and Alice), tethered in individual open wooden-rail stalls. During March, November (1982) and April (1983), Alice and Eve were fasted for periods of 50 to 59 hr and metabolic rate was measured at selected intervals. Normally, animals were standing quietly but, on several occasions, opportunistic measurements were made when they were bedded.

Respiratory gases were collected, using a face mask and several neoprene meteorological balloons (expired capacity of 350 l), as described by Renecker and Hudson (1985b). Volume of gas expired in each 10 min sample period was measured by emptying the balloon through a dry test meter and oxygen concentration by passing a sample through a Beckman Oxygen Analyzer (Model 7003). Metabolic rates were calculated from oxygen consumption assuming, in the absence of measurements for RQ, a calorific equivalent of 20.46 KJ/l of oxygen at STP (MacLean 1970).

Heart rates were recorded simultaneously with the collection of respiratory gases using telemetry systems described in Chapter IV and Renecker and Hudson (1985b) and expressed as body weight$^{-0.75}$ (Brody 1945). Heart rate and respiratory rate were averaged over each sample period.

Rectal and skin temperatures were measured after each collection, if possible, with a tele-thermometer (YSI Model 46 TUC) and a rectal probe (YSI Series 400). Skin temperatures were taken at three sites (mid-thigh, side and shoulder) on each side of the animal.

Thermal Environment

Air temperature was recorded with an alcohol thermometer installed in a Stevenson screen. Windspeeds were determined with an anemometer mounted, at 1 m height, adjacent to the stalls. A globe thermometer mounted on a camera tripod in an adjacent stall and set about mid-height to the flank of the moose was used to determine black-body temperature. It consisted of a 10.2 cm copper ball cock painted mat black with a thermometer inserted through a black rubber plug. Air temperature, black-globe temperature and wind velocity readings were converted to radiant heat load using the formula of Bond and Kelly (1955):

$$\text{RHL} = K/e\sqrt{v}\,(tg - ta) + \sigma\, Tg^4$$

where RHL = radiant heat load (watts/cm^2), K = convective coefficient for a specified 10.2 cm diameter globe, e = emissivity of globe surface (assumed to be 0.95), v = air velocity (cm/sec), tg = temperature of globe (°C), ta = temperature of air (°C), σ = Stefan-Boltzman Constant (5.67×10^{-12} $\text{watts/cm}^2/^\circ\text{K}$), and Tg = tg + 273 (°K).

Statistical Analysis

Linear, curvilinear and two-phase regression techniques (least squares methods) (Draper and Smith 1981, Jennrich 1981, Ralston 1981) were used to summarize relationships between thermoregulatory responses and environmental conditions and to define upper critical temperatures. Two-phase regression techniques allowed solution of unknown slopes and point of intersection of two trends using dummy variables and a quadratic curve (Draper and Smith

1981). Iterative procedures were used to compute maximum likelihood estimates (Ralston 1981).

C. Results

Seasonal changes in average meteorological measurements are presented in Fig. V.1. During winter, ambient temperatures ranged between -32°C and 6°C with warmer temperatures occurring during chinook conditions. Daily maximum heat loads were measured during July and August when black-globe temperatures ranged between 28°C and 42°C, but were generally low during 1983 when wind speeds were slightly higher. During the annual cycle, wind speeds ranged from 0 to 26 m/sec.

D. Body Weight

Weight followed a seasonal cycle in both sexes despite unlimited availability of high quality feed (Fig. V.2). During late May and early June, weight gains ($\bar{x} \pm SE$) of cows averaged 1.03 ± 0.40 kg/d while bulls gained 0.90 ± 0.33 kg/d. Declining or static weights occurred during periods of high ambient temperature. During the rut, bulls lost up to 1.3 kg/d while cows lost over 0.70 kg/d. After the breeding season, weights of bulls increased until early winter when weights of both sexes declined by 7% to 25% reaching lowest values during late April and early May. During late winter, losses of 0.57 kg/d were recorded.

Weight gains during the third trimester of gestation ranged between 0.8 to 3.8 kg/d for the one cow that was pregnant. There was a loss of 13.6% in body weight at parturition which reflected the weight of the conceptus.

Seasonal Metabolic Rates

Resting metabolic rates (Fig. V.3) followed a seasonal cycle which appeared to increase during the second year of the study. Energy expenditures of two standing fed moose cows (Eve and Alice) ranged from 430 kJ/kg $BW^{0.75}$/d in December-March to 940 kJ/kg $BW^{0.75}$/d in July.

Fig. V.1. Annual fluctuations in ambient temperature (Ta), black-globe temperature (Tg) and radiant heat load (RHL) from January 1981 to September 1983 at the Ministik Wildlife Research Station, Alberta. Solid lines were fitted by eye.

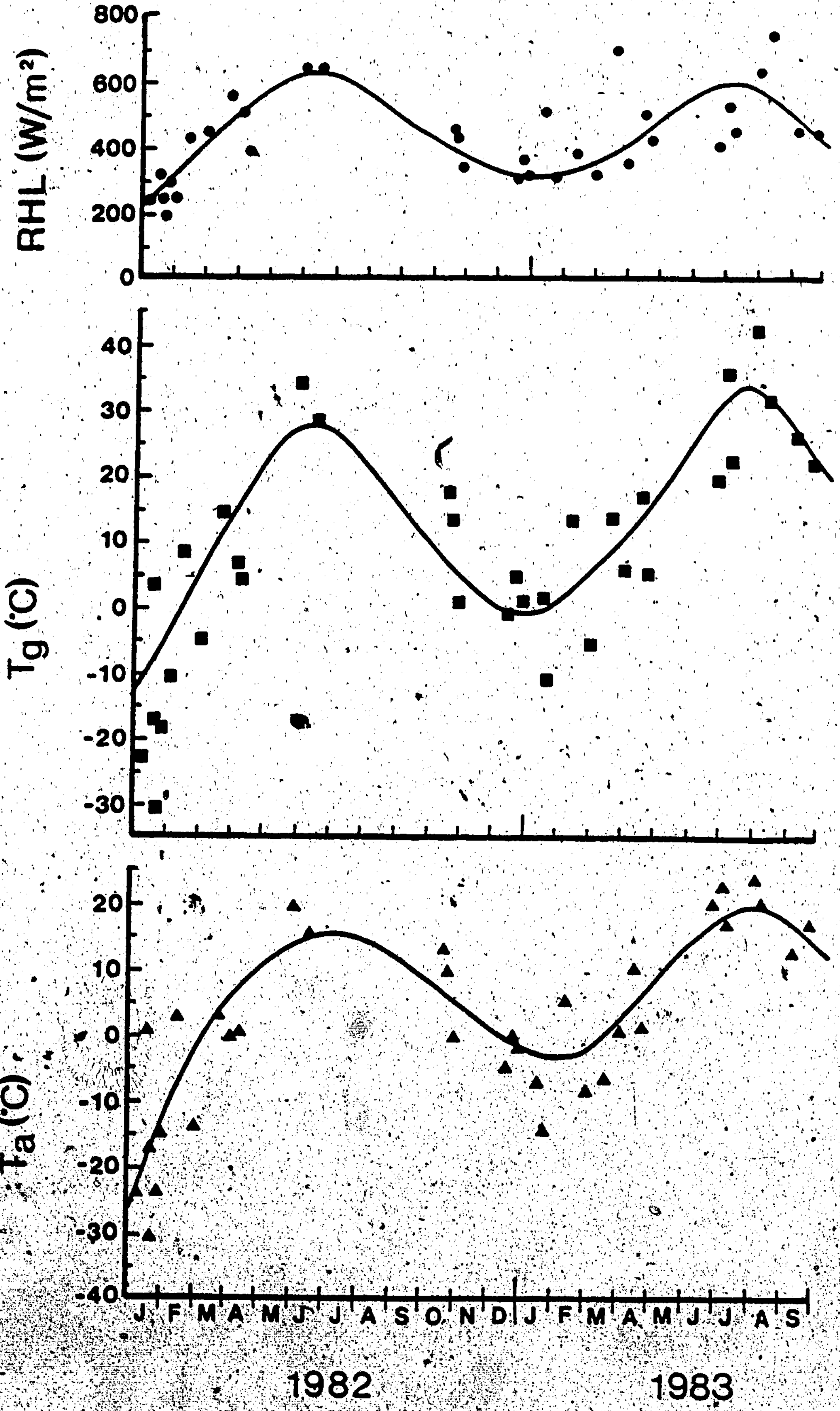

RHL (W/m²)
800
600
400
200
0
Tg (°C)
40
30
20
10
0
-10
-20
-30
Ta (°C)
20
10
0
-10
-20
-30
-40
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
1982
1983

Fig. V.2. Seasonal body weight cycle of six moose from July 1981 to April 1984 at the Ministik Wildlife Research Station, Alberta.

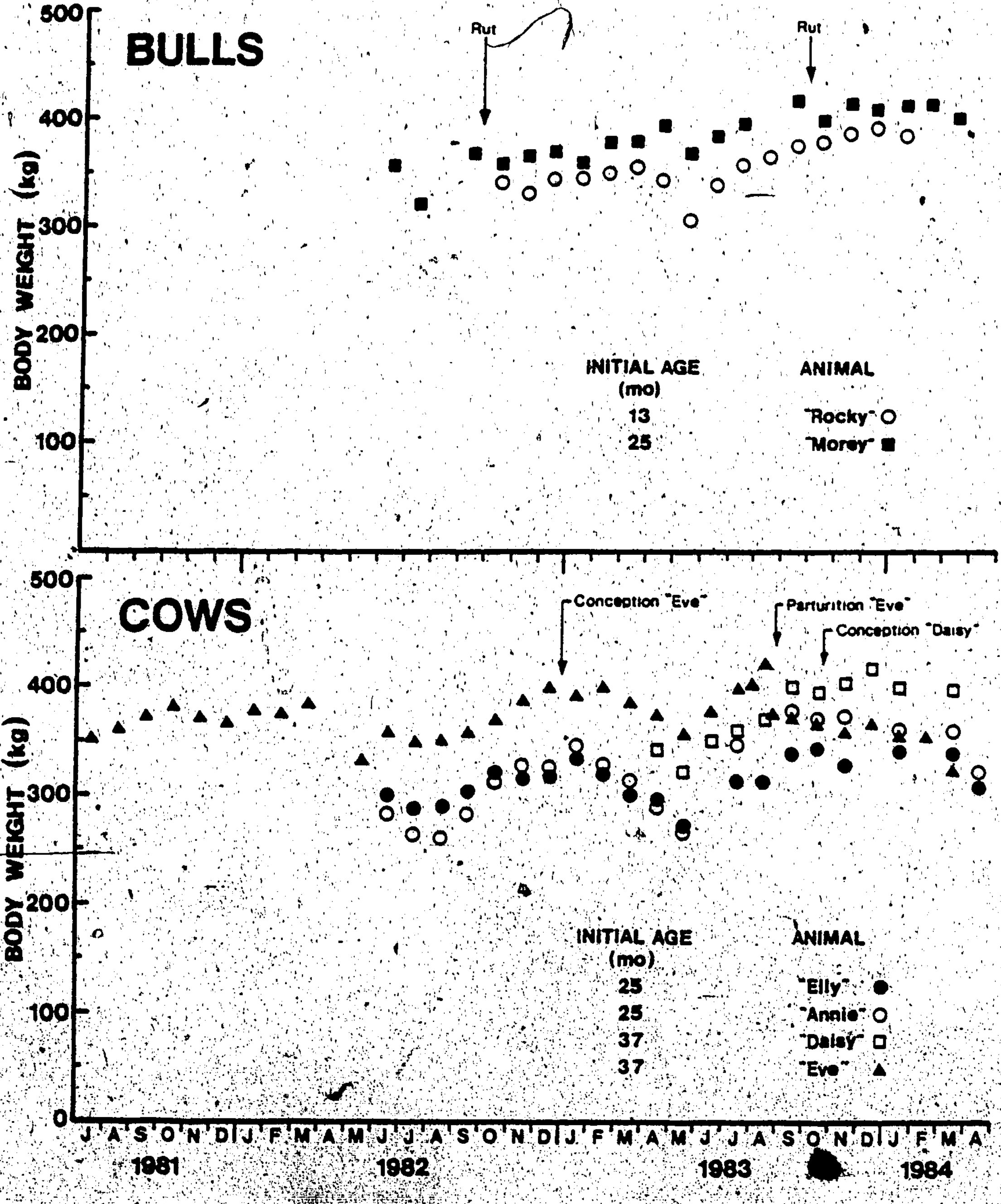
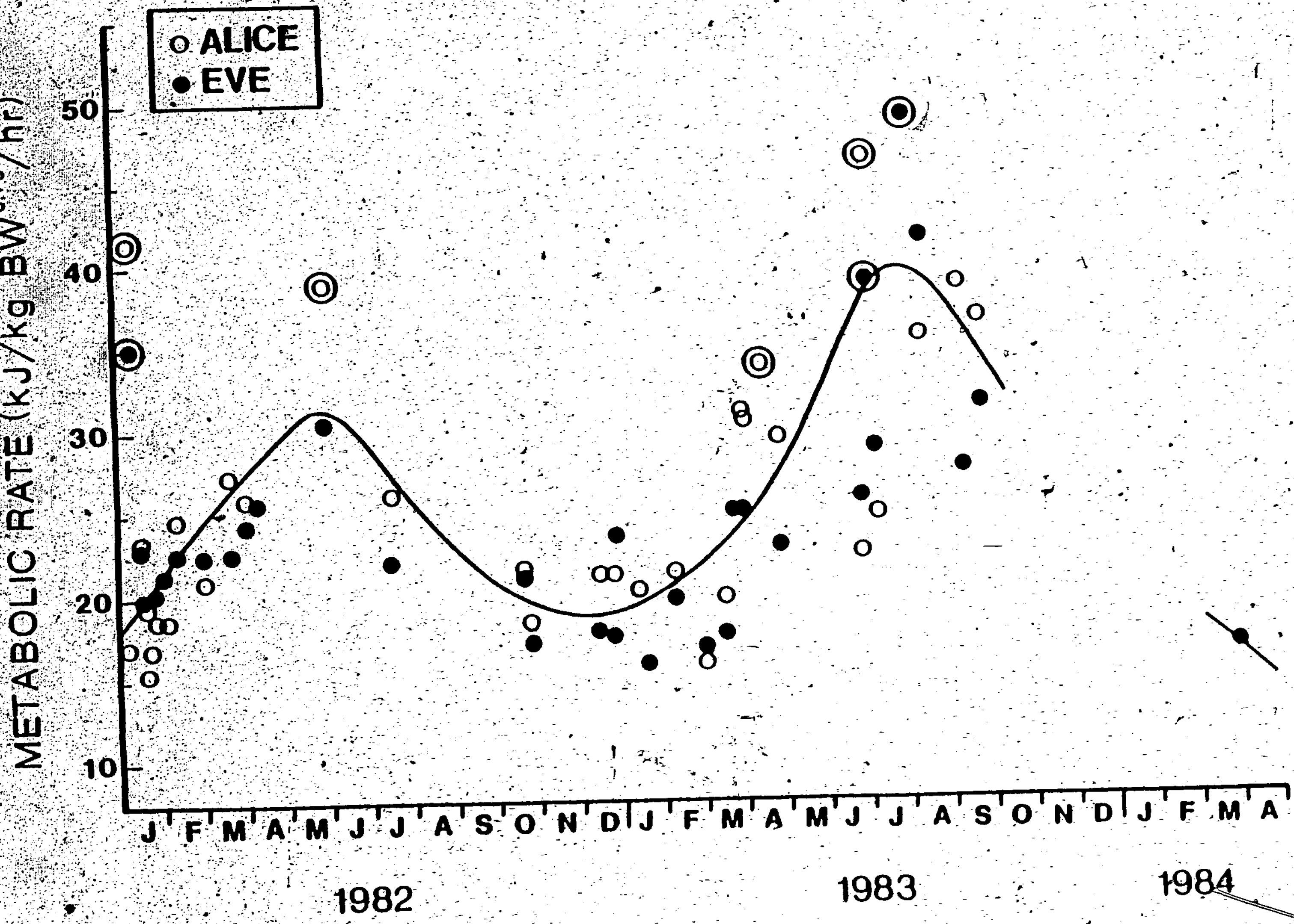

BULLS
BODY WEIGHT (kg)
500
400
300
200
100
Rut
Rut
INITIAL AGE (mo)
ANIMAL
13
"Rocky" ○
25
"Morey" ■
COWS
BODY WEIGHT (kg)
500
400
300
200
100
0
Conception "Eve"
Parturition "Eve"
Conception "Daisy"
INITIAL AGE (mo)
ANIMAL
25
"Elly" ●
25
"Annie" ○
37
"Daisy" □
37
"Eve" ▲
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1981
1982
1983
1984

Fig. V.3. Seasonal cycle of mean daily energy expenditure in two standing moose cows from January 1982 to April 1984 at the Ministik Wildlife Research Station, Alberta. Symbols enclosed with a large open circle indicate periods of chinook conditions (>3°C) during winter or high ambient temperatures (>22°C) during summer. Solid lines were fitted by eye.


ALICE
EVE
METABOLIC RATE (kJ/kg BW$^{0.75}$/hr)
50
40
30
20
10
J F M A M J J A S O N D J F M A M J J A S O N D J F M A
1982
1983
1984

Metabolic rates of the same two cows (Eve and Alice) declined by 32% to 68% (6.2 to 9.1 kJ/kg BW$^{0.75}$/hr) with fasting during trials conducted in March, November and April (Fig. V.4). Declines were most marked within the first 24 hr and approached a baseline in approximately 40 hr. These asymptotic values provided estimates of fasting metabolic rates which were approximately 310 kJ/kg BW$^{0.75}$/d in November and March and 450 kJ/kg BW$^{0.75}$/d in April.

Energy Cost of Standing

Paired measurements (n = 16) taken periodically as opportunities arose allowed calculation of the energy cost of standing. The energy increment between lying and standing postures was 4.2 ± 0.6 KJ/kg BW$^{0.75}$/hr, representing a 25% increase in energy expenditure.

Thermoregulation

Energy Expenditures and Heart Rates

Energy expenditures and heart rates of moose cows while standing varied with ambient temperature during winter and summer (Fig. V.5). During winter, two-phase regression analysis indicated that ambient temperatures above -5.1°C stimulated metabolic rate. A similar upper critical temperature for winter heart rates was calculated at -2.2°C, which corresponds to the point when these animals started thermal panting (see below).

The corresponding upper critical temperature of moose in summer hair coat was between 14°C and 20°C. Above these temperatures, metabolic rates increased at a rate of 0.7 KJ/kg BW$^{0.75}$/hr/°C and heart rate at a rate of 0.9 beats/min/°C.

Thermal environments were not sufficiently cold to define lower critical temperatures. Although piloerection was observed at winter temperatures of -25°C to -30°C, metabolic rate and heart rate remained relatively constant below the upper critical temperature at means of 18.8 ± 2.6 kJ/kg BW$^{0.75}$/hr and 46.4 ± 6.2 beats/min, respectively.

Fig. V.4. Effect of fasting on mean (±SE) metabolic rates of two moose cows in November, March and April at the Ministik Wildlife Research Station, Alberta.

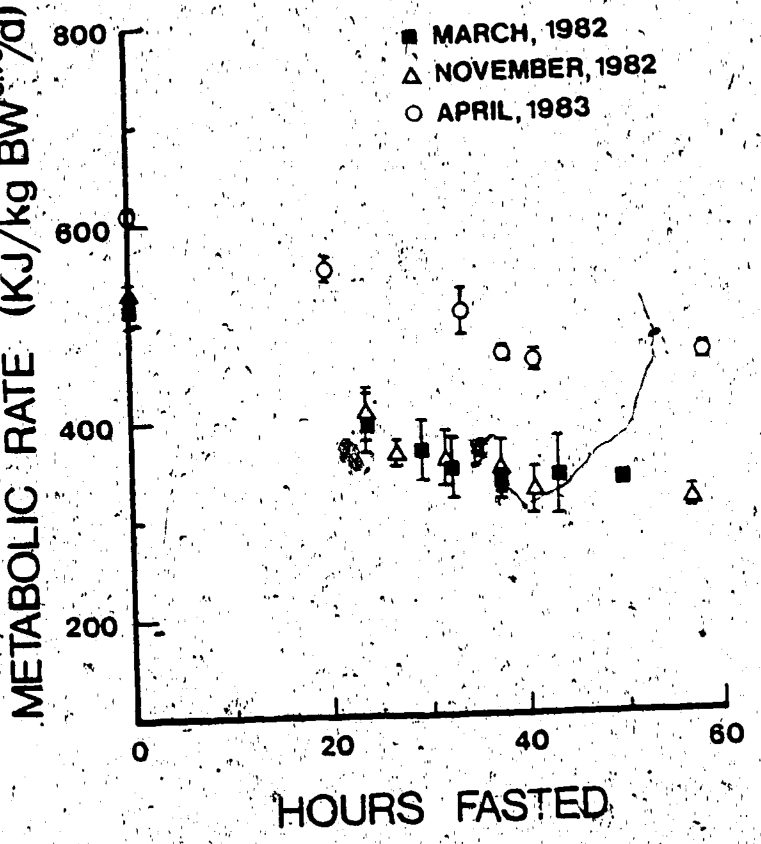
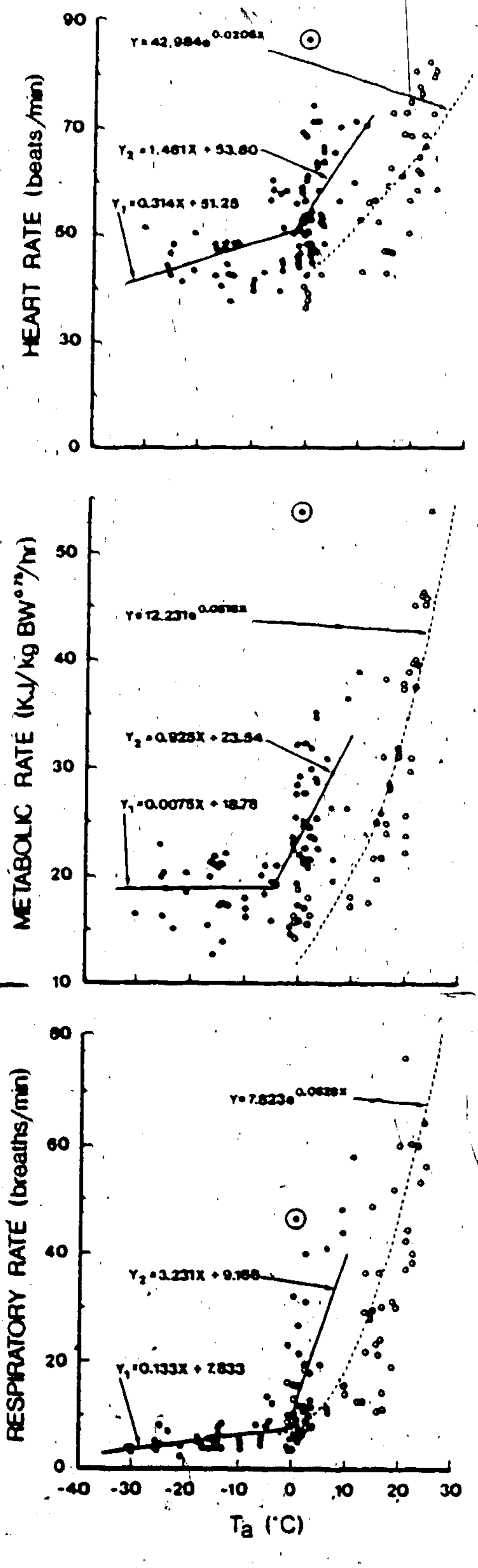

METABOLIC RATE (KJ/kg BW$^{0.75}$/d)
800
600
400
200
0
20
40
60
HOURS FASTED
■ MARCH, 1982
△ NOVEMBER, 1982
○ APRIL, 1983

Fig. V.5. Effect of ambient temperature (Ta) on respiratory rate, energy expenditure and heart rate of two moose cows during winter, (December to April) and summer (June to September) at the Ministik Wildlife Research Station, Alberta. Closed circles represent winter values and small open circles summer values. Winter symbols enclosed by large open circles represent data for an extreme chinook condition in early winter and were not included in the regressions.


HEART RATE (beats/min)
90
70
50
30
0
Y = 42.984e^0.0206x
Y₂ = 1.461X + 53.80
Y₁ = 0.314X + 51.28
METABOLIC RATE (KJ/kg BW^0.75/hr)
50
40
30
20
10
Y = 12.231e^0.0616x
Y₂ = 0.928X + 23.54
Y₁ = 0.0076X + 18.78
RESPIRATORY RATE (breaths/min)
80
60
40
20
0
Y = 7.823e^0.0638x
Y₂ = 3.231X + 9.168
Y₁ = 0.133X + 7.833
-40
-30
-20
-10
0
10
20
30
Ta (°C)

Respiratory Response

Panting is a major cooling mechanism in larger ruminants. Respiratory responses to ambient temperature differed markedly between winter and summer (Fig. V.5).

During winter, respiratory rates ranged from 3 to 58 breaths/min. Two-phase regression analysis indicated that, below -0.4°C, respiratory frequency remained relatively constant at 6.1±0.2 breaths/min. Above this winter critical temperature, respiratory rate increased rapidly (3.2 breaths/min/°C) to over 40 breaths/min at 11°C during chinook conditions. Because of the rapid rise in temperature during chinooks, which apparently exaggerate thermoregulatory responses, the extreme value circled in Fig. V.5 was not included in two-phase regression analysis of slopes and intercepts.

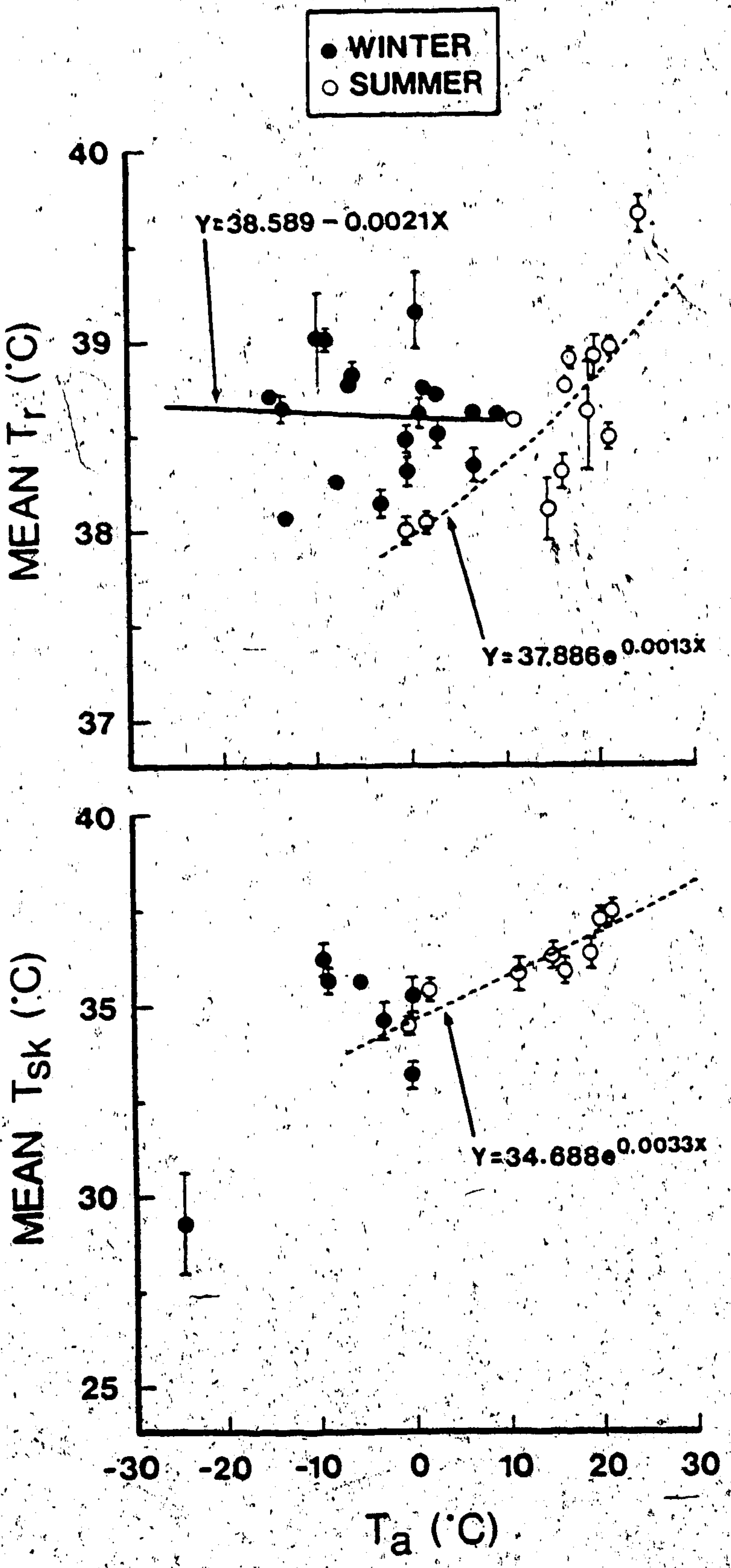
The upper critical temperature for moose was higher during summer. Respiratory rate increased exponentially ($r=0.79$, $P<0.001$) between -1.0°C and 25°C. Thermal panting occurred above 14°C, while open-mouthed panting (60±7 breaths/min) occurred at ambient temperatures above 20°C.

Rectal and Skin Temperatures

Rectal temperatures ranged from 38.0°C to 39.7°C with an overall mean of 38.6±0.1°C. During winter, there was no significant relationship between rectal temperature and ambient temperature, but during summer a significant correlation ($r=0.77$, $P<0.01$) existed between these parameters (Fig. V.6).

Skin temperatures ranged from 27.8°C in winter to 38.3°C in summer. Generally, lower temperatures were recorded on mid thigh during late winter when wind speeds were over 18 m/sec. Skin temperature increased ($r=0.89$, $P<0.001$) with ambient summer temperatures (Fig. V.6), while no apparent pattern was observed in winter except that mean skin temperatures recorded at -25°C were significantly lower ($P<0.05$) than at warmer temperatures.

Fig. V.6. Effect of ambient temperature (Ta) on mean (±SE) skin (Tsk) and mean rectal (Tr) temperature of two moose cows during winter, (December to April) and summer (June to September) at the Ministik Wildlife Research Station, Alberta.


● WINTER
○ SUMMER
Y=38.589 – 0.0021X
Y=37.886e$^{0.0013X}$
MEAN T_r (°C)
40
39
38
37
40
35
30
25
MEAN T_{sk} (°C)
Y=34.688e$^{0.0033X}$
-30
-20
-10
0
10
20
30
T_a (°C)

E. Discussion

Seasonal Metabolic Rates

Resting metabolic rates of 430 kJ/kg BW$^{0.75}$/d in winter and 940 kJ/kg BW$^{0.75}$/d in summer diverge more widely than comparable measurements of 552 and 904 kJ/kg BW$^{0.75}$/d, respectively, made by Regelin et al. (1985) on Alaskan moose. Since not all data used for these estimates were made under thermoneutral conditions and since cycles for our moose tended to differ in the two years of study, this slight difference probably does not represent subspecific or latitudinal adaptation. It is possible to generalize that the amplitude of the resting metabolic cycle of moose is high among wild ruminants. Since both roe deer (Weiner 1977) and bison (Christopherson et al. 1979) exhibit much smaller contrasts between resting metabolic rates during summer and winter, it appears that neither body size nor digestive adaptation (browser vs grazer) is a simple determinant of the metabolic cycles in ruminants. The problem with interspecies comparisons is that measurements are not standardized in terms of calorimetric techniques, feeding regimes and diet quality.

Resting metabolic rates include the heat increment of digestion and nutrient metabolism. Therefore, resting metabolic cycles are expected to have greater amplitudes than fasting metabolic cycles and more closely follow seasonal changes in feed intake. Since fasting trials were not conducted at the extreme points in the annual cycle, it is not possible to make direct comparisons with data for a wider spectrum of species (Hudson and Christopherson 1985). However, an impression of the magnitude of the feeding increment was gained. Fasting metabolic rates were 6 to 9 kJ/kg BW$^{0.75}$/hr lower than resting metabolic rates and were similar to declines of 7.8 KJ/kg BW$^{0.75}$/hr determined for moose calves (L. A. Renecker unpublished data). Regelin et al. (1985) detected a narrower difference of 4 to 5 kJ/kg BW$^{0.75}$/hr between fed and fasted Alaskan moose on the same pelleted ration. Differences are probably related to feeding levels.

Since the heat increment of feeding makes such an important contribution to energy expenditures, seasonal and inter-specific comparisons are usually made on the basis of measurements taken after a 72 hr fast. But, according to strict definition, this should follow a 3 week period of maintenance feeding to remove the effects of prior nutrition (Hudson and Christopherson 1985). This procedure is seldom followed in wildlife studies so reported values are not highly standardized. Nevertheless, fasted metabolic rates in winter, when animals are experiencing weight stasis, should approach conditions consistent with the conventional definition of fasting metabolic rate. In this study, fasting metabolic rates of adult moose in November and March were 340 kJ/kg $BW^{0.75}$/d, close to the accepted interspecies mean of 293 kJ/kg $BW^{0.75}$/d. (Hudson and Christopherson 1985) when corrected for the apparently high energy increment associated with standing. Regelin et al. (1985) measured fasting metabolic rates of 356 kJ/kg $BW^{0.75}$/d for recumbent adult Alaskan moose.

In general, circannual metabolic rhythms of northern ungulates seem linked to fluctuations in forage quality, growth rate, endocrine activity and photoperiod (Sadler 1973, McEwan 1975). An intrinsic metabolic cycle entrained by photoperiod appears to be exacerbated by a superimposed cycle of forage intake and perhaps smoothed by elevation of metabolic rate with chronic cold exposure (Webster et al. 1969, Young 1975, Chappel and Hudson 1978). The decline in energy expenditures during winter may be either a cause or consequence of reduced energy intake.

Beyond the question of regulation is one of adaptive significance. Explanations often relate to the reduction of energy requirements in winter when forage supplies are limited. However, compared with the interspecies mean, winter metabolism is not depressed, rather summer metabolic rates are high. Perhaps the purpose of cycles is better explained by the need to grow and fatten rapidly during the brief pulse of plant production in the short northern summer.

Cost of Standing

Like many other wild ruminants, energy costs of standing in moose is high compared with the accepted value of 10% over basal metabolism (Blaxter 1962) for domestic livestock. Our results suggest an increment of 25% for adults (this study) and 35% for calves (Renecker et al. 1978) of resting metabolism. Regelin et al. (1981) measured increments for adult moose which ranged from 25% to 69% of fasting metabolism depending on the level of alertness and movement. Estimates for other species include 18%-25% of resting metabolic rate for wapiti (Gates and Hudson 1978, Pauls et al. 1981, Parker et al. 1984), 18% of resting metabolism for bighorn sheep (Chappel and Hudson 1979) and 61% to 150% of resting metabolism for white-tailed deer (Mattfeld 1974, Mautz and Fair 1980), mule deer and black-tailed deer (Kautz et al. 1982, Mautz et al. 1985). Although differences may have an anatomical basis, the role of alertness must be considered. Measurements on wild ruminants are almost always made opportunistically, and experimental animals are more likely to bed when they are relaxed. Hence standing measurements often include effects of arousal as well as posture.

Thermal Tolerance

Adult moose are extremely tolerant of cold but are susceptible to heat stress in both summer and winter. Temperatures as low as -30°C failed to stimulate metabolic rate although piloerection occurred. Well-fed moose calves are almost as tolerant (Renecker et al. 1978). As expected, moose are less sensitive to cold than smaller ungulates such as bighorn sheep (Chappel and Hudson 1978) and deer (Freddy 1984, Parker and Robbins 1984, Mautz et al. 1985).

The winter upper critical temperature (-5 to 0°C) of adult moose cows is similar to that determined for moose calves (Renecker et al. 1978) and mule deer (Parker and Robbins 1984), but lower than estimates for bison (Christopherson et al. 1979), reindeer (Segal 1980), wapiti (Parker and Robbins 1984) and white-tailed deer (Holter et al. 1975).

In summer, upper thermal limits are 14 to 20°C. Similar results have been obtained for moose calves which initiated polypnea at temperatures above 17°C (Chermnykh and Mochalov 1987). Upper critical temperatures for mule deer and wapiti are 10°C to 15°C higher (Parker and Robbins 1984). Thermal panting in smaller wild ungulates generally commences at higher ambient temperatures than determined for moose (Jacobsen 1973, Holter et al. 1975, Parker and Robbins 1984).

Compared with work on other wild ungulates (Parker and Robbins 1984), mean skin temperatures of moose appear high when ambient temperatures are low. Species differences in insulative value of hair coats may account for this difference. Christopherson et al. (1978) found that the winter coat of bison provides more external insulation relative to its depth than pelages from either yak (*Bos grunniens*) or cattle, while the thermal insulation of the winter hair coat of bighorn sheep ranks between bison and cattle (Chappel and Hudson 1978). The long winter guard hairs (9-10 cm) and dense undercoat may greatly increase the external insulation of moose.

Ecological Implications

Factors limiting the biogeographical distributions of moose have been identified as food supply, climate and habitat composition (Kelsall and Telfer 1974). The results of this study emphasize the importance of climate. Although moose are superbly adapted to cold, they are intolerant of heat and alter daily patterns of behavior and habitat utilization in an attempt to seek shade and water (Flook 1955, Knorre 1959, Kelsall and Telfer 1974). In this study, moose remained bedded on snow in shaded areas with their legs extended during warm winter days. The impact of heat stress extends beyond the mere alteration of activity budgets and habitat selection. In this study, food intake and body condition declined during hot summer periods. The southerly distribution of moose may well be defined by summer operative temperatures.

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PART C. COMPARATIVE DIGESTIVE PHYSIOLOGY

VI. COMPARATIVE DIGESTIBILITY OF FORAGES AND PARTICLE SIZE DISTRIBUTION IN FECES OF MOOSE, WAPITI AND CATTLE

A. Introduction

Digesta is removed from the rumen through the competitive processes of digestion and passage, the rates of which largely depend on plant composition. Forbs and browse often have higher proportions of lignin or cell solubles to cell wall fiber than grasses, resulting in more rapid degradation but lower asymptotic digestibility (Mertens 1973, Uden 1978). Rates of particle size reduction also differ among forage classes as do the shapes and densities of particles which are able to pass the reticulo-omasal ostium.

Ruminants show a variety of anatomical digestive adaptations to diet. On this basis, they have been classified as concentrate selectors, intermediate or mixed feeders and roughage grazers. Selective feeders have relatively small and simple digestive tracts while grazers have large rumens and various structures which slow rate of passage (Hofmann 1973).

Although anatomical differences have been thotoughly documented and functional inferences made (Hofmann 1973, 1984, 1985), definitive tests of these predictions have received attention only recently. Consistent with anatomical design, concentrate selectors seem to propel digesta rapidly through the digestive tract fermenting mainly soluble carbohydrates. Roughage grazers retain food particles in the ruminoreticulum to allow time for more complete digestion of fiber. Mixed feeders adopt an intermediate strategy and often display marked seasonal adaptation. However, interactions between forage characteristics and season have not been fully evaluated.

This study was conducted to explore these interactions in moose, wapiti and cattle as representative large browsers, mixed feeders and grazers, respectively. The specific objective was to distinguish the relative roles of fermentation capacity and passage rate in dietary adaptation. This chapter compares rumen fermentation and passage rates of grass (timothy-brome hay), forbs (alfalfa), and browse (aspen foliage and twigs) during winter and summer. Size distributions of feed particles in feces were also examined to test the prediction that grazers delay passage by retaining particles of smaller dimensions.

B. Methods and Materials

Animals, Diets and Periods

One adult moose cow, two adult wapiti steers and two adult Charolais-cross steers fitted with ruminal cannulae (Renecker et al. 1982) were maintained in outdoor pens during trials conducted from January to April and July to September, 1982. Weights of the moose, wapiti and cattle ranged from 265-303, 302-347 and 611-738 kg, respectively.

Dietary ingredients were selected to represent major forage classes; grasses [timothy (*Phleum pratense*)-brome (*Bromus inermis*) hay], forbs [alfalfa (*Medicago sativa*)], and browse [aspen (*Populus tremuloides*)]. However, since moose are unable to subsist on pure diets of grass and cattle are unable to subsist on browse, the following three mixed diets were composed: (a) a 1:1 mixture of alfalfa and timothy-brome hay, (b) 100% alfalfa and (c) a 1:1 combination of alfalfa and either aspen twigs or foliage during winter and summer, respectively.

Alfalfa and timothy-brome hay were chopped, prior to feeding, in approximately 10 cm lengths with a New Holland Tub Grinder. Aspen twigs, consisting of the current annual growth from saplings cut during late winter, were chopped into 2-3 cm lengths, whereas aspen foliage offered during summer consisted of leaves "stripped" by hand from mature trees. The chemical composition of these diets is given in Table VI.1. Animals were fed *ad libitum* twice daily at 0800-1000 and 1700-1900 hours. Level of feeding was adjusted to 90% of the daily voluntary dry matter intake during the 12 d trial period.

Species interactions were studied only with grass hay and alfalfa diets. Since moose rarely consume woody stems during summer, foliage was the appropriate diet to test during this time period. Further, it would be difficult to preserve volumes of fresh vegetation for several

Table VI.1. Chemical composition of forages used [illegible]inter and summer trials 1982.

Feedstuff	Dry Matter (%)	% of DM					
		Crude Protein (%)	Cell Solubles (%)	Hemi-Cellulose (%)	Cellulose (%)	Lignin (%)	Ash (%)
Timothy-Brome Hay	97.5	9.3	41.2	25.9	27.6	4.8	0.5
Alfalfa (Winter)	94.4	16.2	51.3	13.6	25.1	9.5	0.5
Alfalfa (Summer)	94.5	16.6	52.3	13.3	26.4	7.5	0.5
Trembling Aspen Twigs	55.0	6.5	56.7	12.2	15.5	15.0	0.5
Trembling Aspen Foliage	44.4	13.9	63.0	13.4	12.5	11.5	0.6

months in a study of this scope. However, comparisons were made between seasons and rations using orthogonal sets of comparisons (Steele and Torrie 1980) and the "contrast" subcommand in one-way procedures of SPSS (Anon. 1983).

Rumen Dry-Matter Disappearance

The rate and completeness of forage digestion can be determined most directly by suspending nylon bags containing forage samples into the rumen of a fistulated animal (Playne et al. 1978). Potential sources of error arising from bag features, sample characteristics, rations, incubation procedures, time effects, washout methods and replication can be minimized if these variations in procedure are recognized (Mehrez and Orskov 1977, Uden 1978, McBride 1980, Orskov et al. 1980, Hawley 1981, Setälä 1983).

Bags containing forage samples were made of Nitex monofilament nylon bolting cloth (B. & S.H. Thompson and Co., Ltd.) with external dimensions of 10 X 15 cm and a porosity of 10 µm. Dried forages were ground through a 3 mm screen of a Christy-Norris laboratory mill. Approximately 3 g were weighed into each bag, tied with a drawstring (Orskov et al. 1980) to a 250 ml sample bottle filled with sand and then placed in the ventral sac of the rumen. Bags were incubated in duplicate for 0, 3, 6, 12, 24, 36, 48 and 72 hr. Rumen pH was measured when nylon bags were placed in the rumen. Upon removal, bags were washed and oven-dried at 60°C to constant weight according to the procedures of Orskov et al. (1980). Dry matter digestibility was calculated as the percent change in the dry weight of the bag contents. The procedure was conducted in duplicate for the moose since only one animal was available. Microscopy was used to examine pore size of each bag after each incubation and discarded if deviation from 10 µm was observed.

Dry matter disappearance was calculated as the percent change in dry weight of the bag contents. An iterative least squares curvilinear regression procedure (Jennrich 1981) was used to calculate asymptotic digestibility (A, maximum potential digestibility %), rate of degradation (k, %/hr) and intercepts (B) on the digestibility axis which represent the component of dry matter degraded rapidly. Asymptotes, rate constants and intercepts were compared by analysis of variance using SPSS procedures (Anon. 1983) and Duncan's Multiple Range Test (Steele and Torrie 1980).

Potentially digestible neutral detergent fiber (NDF) was determined for each forage (except timothy-brome hay during summer) from the bags removed at 72 hr. Dry matter residue remaining in each bag after incubation was analyzed for NDF content (Goering and Van Soest 1970). Samples of forages were also analyzed for NDF, acid detergent fiber and acid detergent lignin according to Goering and Van Soest (1970). The relationship of potentially digestible NDF to lignin content was explored by least squares linear regression.

Particle Turnover Time

Samples of either timothy-brome hay, alfalfa, trembling aspen twigs (not for wapiti) in winter and alfalfa and trembling aspen foliage in summer were ground through a 3 mm screen, made into a slurry with distilled water and fractionated using the wet sieving technique (Kennedy 1985). The 1-2 mm size fraction of each forage was mordanted with trivalent chromium (Cr) using the method described by Uden et al. (1980). Initially, 11.2 g of the of the Cr-mordanted fiber were placed in a paper bag and then introduced into the gastrointestinal tract via the ruminal cannula.

Rectal grab samples of fresh feces were taken every 3 hr for the first 36 hr, then every 6 hr for 1 d and then once every day until 120 hr. Subsamples of fecal collections were oven-dried at 60°C for 48 hr and ground through a 20 mesh screen of a Wiley mill. Subsamples were dry ashed, digested in concentrated HNO_3, redissolved in 1.0 N HNO_3, centrifuged and the supernatant solution removed (Murthy et al. 1971). Concentration of Cr in aliquots was measured using Atomic Absorption Spectrophotometry (Model 4000, Perkin Elmer).

Passage of the Cr-labelled particles from the ruminoreticulum was determined by least squares regression of the natural log of concentration of the marker on time after the marker was administered. The resulting slope was the rate constant (k_1). Rumen turnover time (RTT) was calculated as the reciprocal of k_1 (Hungate 1966).

Particle Size Distributions

Reduction of feed particles to a size eligible for leaving the rumen is an important factor influencing voluntary intake, digestibility and retention time of feeds in ruminants (Weston and Kennedy 1984). Passage of particles can be expressed in terms of critical sizes which pass into the lower tract (Poppi et.al. 1981) or, alternatively, in terms of distributions described by various mathematical functions (Mertens et al., 1984) particularly the lognormal distribution (Waldo et al. 1971) used in this study.

Particle size distributions of fecal samples frozen at -20°C were obtained by a manual wet sieving technique (Dixon and Milligan 1985, Kennedy 1985). Thawed fecal samples of 15 g from moose and wapiti and 25 g from cattle were made into a slurry with 2 l of saline solution. The mixture was sieved using a logarithmic series of screen opening sizes (7.4, 4.0, 3.35, 2.0, 1.0, 0.71, 0.50 and 0.25 mm). Material retained on each sieve was oven-dried at 60°C to determine dry matter. Particulate material which passed through the smallest screen aperature was subsampled (4 replicates), weighed, centrifuged at 13,000 g for 10 min, washed with distilled water and recentifuged and then oven-dried at 60°C in order to obtain the weight of small paticles.

The log-normal distribution was fitted to the cumulative weight of particles over the size of screen aperature and the sieve opening sizes as described by Waldo et al. (1971). Particle size distibutions were expressed in terms of log10 mean (±SD) particle size (MPS) in um. Also, the cumulative percentage of dry matter retained on screens was reported as large particle size (LPS) (>3.35 mm), 1-3.35 mm and <1.0 mm. Analysis of variance (Steele and Torrie 1980) and orthogonal comparisons (Anon. 1983) were applied to MPS data.

The potential effects of freezing fecal samples were examined at the beginning of the winter trials. Four replicate samples of cattle feces which were either frozen at -20°C and then thawed or only refrigerated were sieved through the series of screens using the procedures above. Analysis of variance was used to test significance between treatments.

C. Results

Potential Digestibility

Patterns of dry matter disappearance are summarized in Fig. VI.1. Parameters computed for dry matter disappearance curves are presented in Table VI.2. Potential (asymptotic) digestibilities (A) did not vary significantl among ruminant species ($P > 0.77$). Although diets were significantly different ($P < 0.001$), no difference between seasons ($P > 0.06$) or in the diet x season interaction ($P > 0.92$) was observed for grass hay or alfalfa. Potential digestibility of aspen foliage was consistently higher ($P < 0.001$) than for twigs. Alfalfa and aspen foliage were similar while aspen twigs showed the lowest potential digestibility, significantly less than alfalfa ($P < 0.02$). Grass hay varied significantly from both aspen twigs ($P < 0.001$) and foliage ($P < 0.002$).

Potential digestibility of plant cell wall (NDF) increased inversely with lignin content ($P < 0.001$), a relationship which differed little among ruminant species (Fig. VI.2). The potential digestibility of timothy-brome hay was higher than that of the other forages while lower levels of digestible NDF were measured for woody stems from trembling aspen.

Readily Fermentable Dry Matter

The Y-intercept of asymptotic regression provides an estimate of the proportion of forage dry matter which is rapidly attacked and solubilized by rumen microbes. It is calculated as the difference between the constants A and B of the regression equation (Table VI.2). Differences in computed intercepts (A-B) were not detected among ruminant species ($P > 0.15$). For grasses and alfalfa, differences were detected between diets ($P < 0.01$) and in the diet x season interaction ($P < 0.002$). Both aspen twigs and foliage had similar high content of readily-fermented dry matter while grass hay contained the lowest. These Y-intercepts for

Fig. VI.1. Dry matter disappearance of four forages from nylon bags incubated in moose, wapiti and cattle during winter and summer and fitted asymptotic curves.

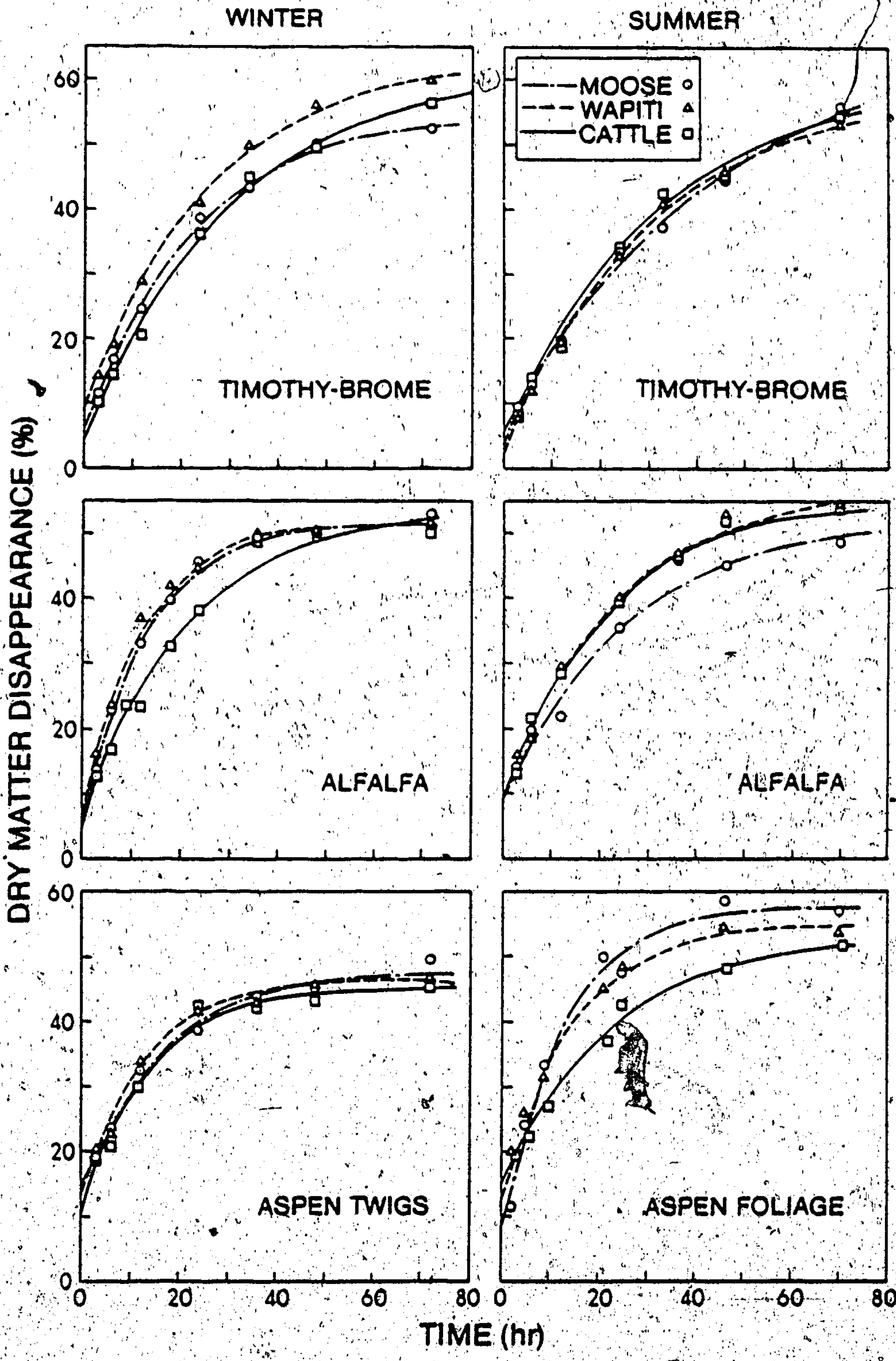

WINTER
SUMMER
MOOSE ○
WAPITI △
CATTLE □
TIMOTHY-BROME
TIMOTHY-BROME
ALFALFA
ALFALFA
ASPEN TWIGS
ASPEN FOLIAGE
DRY MATTER DISAPPEARANCE (%)
TIME (hr)
0
20
40
60
0
20
40
60
80

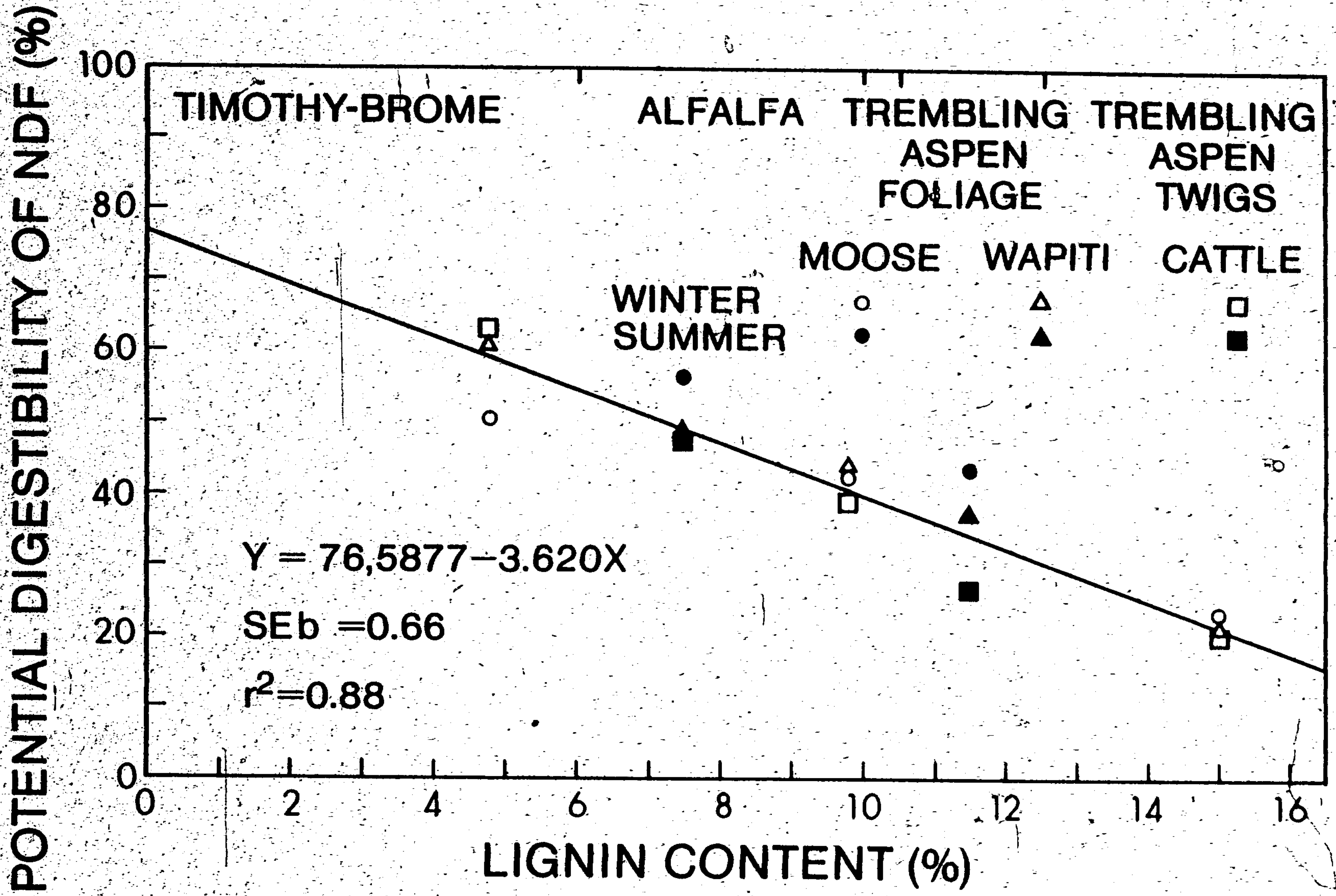
Table VI.2. Regression[1] of dry matter loss of feed from nylon bags on time that bags were incubated in the rumen of moose, wapiti and cattle during winter and summer 1982.

Species	Asymptotic Digestibility (±SE)	B	Relative Digestion Rate (k, %/hr±SE)	r^2
Winter				
Timothy-Brome Hay				
Moose	55.0±0.9	50.1±0.3	4.46±0.96	1.00 ***
Wapiti	64.2±4.9	56.3±2.6	3.86±0.80	1.00 ***
Cattle	62.1±2.3	58.3±2.3	3.31±1.60	1.00 ***
Mean	60.9	54.9	3.89	
Alfalfa				
Moose	51.9±0.0	47.6±1.0	7.79±0.90	1.00 ***
Wapiti	51.5±0.5	46.4±0.4	8.81±1.10	1.00 ***
Cattle	53.9±0.5	49.3±0.7	4.76±2.42	0.98 ***
Mean	52.4	47.8	7.11	
Aspen Twigs				
Moose	48.1±0.4	34.3±0.9	5.90±1.10	0.99 ***
Wapiti	46.2±0.7	34.1±0.8	8.03±1.49	0.99 ***
Cattle	45.3±1.2	35.5±1.5	7.47±1.94	0.98 ***
Mean	46.6	34.6	7.30	
Summer				
Timothy-Brome Hay				
Moose	67.9±4.8	62.6±4.1	2.26±1.88	0.99 ***
Wapiti	58.8±0.7	56.8±0.1	3.27±0.91	1.00 ***
Cattle	60.8±5.3	54.5±3.8	3.13±2.06	0.99 ***
Mean	64.0	58.0	2.88	
Alfalfa				
Moose	52.4±2.7	44.0±1.0	4.08±2.81	0.98 ***
Wapiti	57.7±0.1	48.6±2.8	4.33±1.54	0.99 ***
Cattle	55.1±0.3	46.7±1.5	4.70±0.17	1.00 ***
Mean	55.3	46.4	4.35	
Aspen Foliage				
Moose	57.7±2.8	50.8±0.0	7.98±2.23	0.97 ***
Wapiti	54.7±0.1	42.9±2.2	7.24±1.14	1.00 ***
Cattle	52.9±4.3	38.8±3.4	4.63±1.04	1.00 ***
Mean	56.3	44.1	6.61	

[1] Variables fit an equation where $y = A - Be^{-kt}$

*** Significant at $P < 0.001$.

Fig. VI.2. Regression of potential digestibility of cell wall (NDF) on lignin content of forages.


POTENTIAL DIGESTIBILITY OF NDF (%)
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
LIGNIN CONTENT (%)
TIMOTHY-BROME
ALFALFA
TREMBLING ASPEN FOLIAGE
TREMBLING ASPEN TWIGS
MOOSE
WAPITI
CATTLE
WINTER ○ △ □
SUMMER ● ▲ ■
Y = 76,5877−3.620X
SEb =0.66
r2=0.88

aspen twigs and foliage were significantly higher than either grass hay or alfalfa ($P<0.04$). Intercepts of asymptotic regressions were correlated ($P<0.001$, $r=0.74$) with cell soluble content of the feed.

Dry Matter Disappearance Rates

The slope (k) of the relation between dry matter disappearance and incubation time estimates the rate of disappearance of potentially-digestible dry matter. These rates (%/hr) did not differ significantly among ruminant species ($P>0.23$). Differences were evident between grass hay and alfalfa ($P<0.04$) and in the diet x season interaction ($P<0.05$) of these feeds. Rates of dry matter disappearance were similar ($P<0.40$) for aspen twigs and foliage. Highest mean rates of dry matter disappearance were observed for aspen twigs which had significantly higher rates of fermentation than winter grasses ($P<0.003$) but were similar to alfalfa. In summer, rate of disappearance of foliage was significantly higher than grass hay ($P<0.05$) or alfalfa ($P<0.04$). The pH of rumen contents of moose, wapiti and cattle was similar and averaged 6.76±0.06 in summer and 6.96±0.03 in winter.

Because of the slower rate at which potentially degradable grass hay was broken down, the half-life for the material which could be degraded was 16 to 31 hr. The time of incubation at which one half the potentially digestible dry matter disappeared ranged between 9 and 15 hr for aspen twigs and leaves and 8 and 17 hr for alfalfa.

Rates of Particulate Passage

Rumen turnover times of 1-2 mm particles are given in Table VI.3. In the winter trial, the moose retained alfalfa longer than either timothy-brome hay or aspen twigs. In summer, turnover times of alfalfa were surprisingly short. Aspen foliage was also propelled rapidly through the rumen with a retention time of only 16 hrs. Ruminal turnover times of wapiti were independent of season and diet. Generally, passage rates of wapiti were higher than those of moose in winter and lower in summer. Ruminal turnover times of cattle remained relatively

Table VI.3. Rumen turnover time (RTT) of 1-2 mm particles from several Cr-mordanted forages given to moose, wapiti and cattle during winter and summer 1982.

	RTT (hr)			
Species	Timothy-Brome Hay	Alfalfa	Aspen Twigs	Aspen Foliage
Winter				
Moose	30.7	36.9	27.9	--
Wapiti	22.6	21.4	--	--
Cattle	27.5	29.2	35.6	--
Summer				
Moose	--	19.2	--	16.4
Wapiti	--	25.0	--	20.5
Cattle	--	26.3	--	20.6

constant between seasons. Cattle retained food particles longer than wapiti for all rations, however flow rates were considerably lower than those of moose on aspen twigs and foliage diets.

Fecal Particle-Size Distributions

Mean particle size of fecal samples for each diet, species and season are presented in Table VI.4 as means of 4 samples. No species differences in MPS ($P>0.12$) or %LPS ($P>0.08$) of fecal residues were observed. Differences in MPS due to diet ($P<0.009$) and diet x season interaction ($P<0.003$) were apparent for grass hay and alfalfa. No difference was detected between MPS of feces for aspen twigs or leaves ($P>0.11$), but MPS was markedly larger when animals were fed aspen twigs or foliage in comparison to grass hay ($P<0.01$). Mean particle size of frozen and refrigerated fecal samples from cattle were similar ($P>0.05$).

There was a tendency for the MPS of fecal particles to be larger in all animals fed rations containing aspen leaves or twigs, but was markedly higher in moose. Particles of fragmented aspen leaves collected in the LPS fraction of moose measured 12.6 x 7.6 mm in size. Large fecal residues up to 13.7 mm long were collected from moose fed the grass hay/alfalfa ration, however these particles were only 1.1 mm in width. Moose appeared to pass a larger proportion of particles in the LPS and 1-3.35 mm pools when fed aspen/alfalfa diets. However, percentage of particles passing through the 1 mm screen decreased. Wapiti passed a relatively constant proportion of particles in the 1-3.35 mm fraction on all diets except for winter alfalfa. Large cylindrical particles measuring 23.6 x 2.1 mm, were collected in the LPS fraction of feces from wapiti fed 100% alfalfa. With cattle fed grass hay/alfalfa, a larger percentage of forage residues were passed as <1 mm in size which is related to the low MPS. However, when cattle were placed on a ration of aspen/alfalfa, the distribution of larger particles tended to increase concurrently with MPS.

Based on the critical particle size theory of Poppi et al. (1980), different threshold ranges (<5% of fecal particles oversize) were observed for moose and wapiti. Critical particle

Table VI.4. Particle size distribution of feces from moose, wapiti and cattle fed four diets during winter and summer 1982.

Item	Winter			Summer		
	Moose[1]	Wapiti	Cattle	Moose[1]	Wapiti	Cattle
Grass/Alfalfa						
Slope	-2.005	-2.338	-1.923	-1.869	-2.088	-1.984
Intercept	10.665	11.916	10.310	10.231	11.059	10.533
Log um	2.825	2.959	2.762	2.799	2.902	2.790
Log SD	0.499	0.428	0.097	0.535	0.479	0.504
r^2	0.96	0.95	0.97	0.96	0.96	0.97
MPS (um)	668	909	578	630	797	616
%LPS (>3.35 mm)	6.41	6.68	5.59	8.05	7.71	5.92
% 1-3.35 mm	40.43	53.92	34.94	36.92	47.66	36.16
% <1 mm	53.16	39.42	59.44	55.04	44.64	57.97
Alfalfa						
Slope	-1.798	-1.828	-1.841	-1.860	-2.130	-2.162
Intercept	10.078	9.751	9.751	10.123	11.119	11.150
Log um	2.824	2.600	2.678	2.754	2.873	2.845
Log SD	0.566	0.547	0.543	0.538	0.470	0.463
r^2	0.99	0.97	0.98	0.98	0.96	0.97
MPS (um)	667	398	476	568	746	700
%LPS (>3.35 mm)	9.72	4.21	5.79	6.05	6.49	5.52
% 1-3.35 mm	34.79	24.51	27.85	33.48	44.79	42.59
% <1 mm	55.42	71.29	66.05	60.49	48.77	51.90
Aspen Twigs/Alfalfa						
Slope	-2.104	-2.418	-2.083	--	--	--
Intercept	11.229	12.053	11.129	--	--	--
Log um	2.961	2.917	2.943	--	--	--
Log SD	0.475	0.414	0.480	--	--	--
r^2	0.98	0.96	0.98	--	--	--
MPS (um)	915	827	876	--	--	--
%LPS (>3.35 mm)	9.62	4.96	9.12	--	--	--
% 1-3.35 mm	46.21	52.01	45.09	--	--	--
% <1 mm	44.20	43.09	45.82	--	--	--

Table VI-4. Particle size distribution of feces from moose, wapiti and cattle fed four diets during winter and summer 1982.

Aspen Foliage/Alfalfa						
Slope	..	..	..	-1.921	-2.270	-1.999
Intercept	..	..	..	10.732	11.505	10.592
Log um	..	..	..	2.984	-2.874	2.797
Log SD	..	..	..	0.521	0.441	0.500
r^2	..	..	..	0.96	0.96	0.97
MPS (um)	..	..	..	963	748	627
%LPS (>3.35 mm)	..	..	..	15.27	4.81	5.76
% 1-3.35 mm	..	..	..	42.06	46.25	38.15
% <1 mm	..	..	..	42.73	49.02	56.15

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[1] Values indicate mean of 4 samples x 2 replicates from a single animal.

[2] MPS = mean particle size.

[3] %LPS = percent of fraction which includes the large particle size.

size for escape from the ruminoreticulum and passage through the lower gastrointestinal tract was highest for moose ranging from 4.4 to 6.9 mm with the probability of passage increasing for high lignin rations. In wapiti, critical size was lower, ranging between 3.2 and 4.8 mm.

D. Discussion

Although ruminants differ in their ability to use various forage classes, it is not clear how this is accomplished. This study attempted to distinguish differences related to microbial fermentation and retention by offering a concentrate feeder (moose), roughage feeder (cattle) and mixed feeder (wapiti) rations consumed by the other types. Fermentation capacity of these ruminants was compared on the basis of dry matter digestion from *in situ* incubations of browse, grass and forbs in nylon bags. Differences in the sorting process of the reticulo-omasal orifice and its tolerance of large particulate residues or retention for further comminution were determined from inspection of particle size distributions of feces and passage of a specific particulate fraction.

Concentrate selectors would be expected to have a low capacity for digestion of diets rich in fiber (Van Soest 1982) since they have adapted to faster passage rates (Huston 1978). On the other hand, roughage feeders with capacious rumens are usually non-selective feeders adapted for retention of fermentable cell wall material (Hofmann 1973). Mixed feeders would be expected to have a greater capacity to digest fiber than concentrate selectors (Mould and Robbins 1982, Baker and Hansen 1985) while maintaining digestive plasticity for efficient utilization of browse diets higher in cell contents.

If these ruminants were fed forages to which they were poorly adapted, differences in digestive capacity, particle size breakdown and passage rate would be expected. Large particles of grass diets high in cell wall content have a greater resistance to removal from the rumen than highly lignified legumes which fracture more easily during mastication (Poppi et al 1980, Chai et al. 1984, 1985) and should be retained longer in cattle and elk than in moose. Longer rumination times required by grass forages would presumably impose restrictions on the flow of digesta in the browser with a tube-like gut. Consequences of this plan would be more profound if chewing efficiency of browsers was lower than grazers when fragmenting long grass fibers. If such differences did exist, then one would expect the browser (moose) to have difficulty maintaining a high level of intake. Because browsers rely on rapid passage rates (Van Hoven and Boomker 1985), moose would probably become bulk limited on grasses. In contrast, highly lignified cell walls in browse forages prevent extensive degradation by cattle.

In this study, fermentative capacities of moose, wapiti and cattle given equal opportunities for digestive adaptation were not significantly different. This suggests that digestive adaptations are primarily related to regulating the flow of feed particles and changing absorptive surfaces. With the exception of diet selection, ruminants seem unable to adjust the rumen environment sufficiently to select different microbial populations. Passage rates did vary seasonally and this seemed to be achieved by passing larger particles during summer. However, it was not possible to simply rank species accordingly to typical passage rates since this varied widely with diet.

Fermentation Capacity

The nylon-bag technique allows the effects of passage rate and particle size reduction by rumination to be controlled. When this is done, microbes found in the rumens of different species seem to digest fiber with equal efficiency. Similar results have been reported for *in situ* comparisons of sheep and cattle (Prigge et al. 1984) and *in vitro* comparisons of wapiti and mule deer (Baker and Hansen 1985).

There was a major difference in asymptotic digestibility between forages and seasons which probably reflected the chemical constituents of the plant material. In general, grass diets are higher in slowly digesting cell wall fractions, but contain less lignin which would reduce the potential digestibility of dry matter (Weston and Hogan 1968, Minson 1971, Van Soest 1982). Richards (1976) has speculated that lignin may inhibit digestion by either preventing attachment of microbes to substrate or by inhibition of enzyme attack on cell wall linkages

(Morris 1984). The present study has confirmed this aspect and shown that digestibility of NDF decreases with cell wall lignin. Although, the lignin content of the leaves and twigs from shrubs is higher compared to grasses and alfalfa (Oldemeyer et al. 1977, Milchunas et al. 1978, Hjeljord et al. 1982), browse provides a higher percentage of cell solubles (Chapter III) which largely disappear in the rumen (Morris 1984). Browsers, mixed feeders and grazers do not differ in these respects.

Differences between mean asymptotic digestibility by ration largely reflected the marked differences in digestible cell wall material. These differences are largely attributed to the influence of lignin which forms complex cross-linkages with other cell wall fibers. Nevertheless, lignin reduced its influence on dietary fiber of aspen leaves accounting for higher cell wall digestion.

Progressively higher rates of digestion were observed with higher proportion of readily fermentable cell solubles. Since cell contents are 98% digestible (Robbins 1973), peak fermentation occurs shortly after feeding (Van Soest 1982). Grasses have a lower proportion of cell solubles, a higher amount of dietary fiber and lower rates of fermentation than browse. Moose clearly retain grasses longer than browse, however, browsers are nutritionally unable to adhere to the constraints of long retention and extensive cell wall digestion since they lack the capacious rumens of grazers.

Computed intercepts suggested a slower initial rate of fermentation with some forages (Table VI.2). Factors affecting initial fermentation rate could be related to hydration and physical alteration of the fiber (Mertens 1977) or time required for bacterial attachment to feed particles (Alkin and Amos 1975, Mertens 1977). Inadequacy of the microbes to handle substrates at the same initial rate, could be related to level of intake. Intake may directly affect fermentation by furnishing more fibrous components than bacteria can accomodate. Further, at pH levels above 7.5 or below 5.5, fiber and organic matter digestion can become depressed (Hoover et al. 1984), however these extremes were not evident in this study. It is also possible that more fermentable cell solubles, which occur in alfalfa and aspen, accelerated initial rates as suggested by Van Soest (1982).

Kinetics of Particulate Breakdown and Passage

Hofmann (1973,1984) generalized that passage rates should be highest in browsers and lowest in grazers. This study confirmed this hypothesis but pointed out an additional complexity related to differences between diets. Moose (browsers) were consistent with Hofmann's (1973, 1984) prediction. Grass rations required a greater time for particle size reduction before residues escaped from the rumen of moose, whereas passage rates tended to decrease with lignin content in cattle (grazers). These patterns indicate the penalty of diet fibrosity in a browser, which only holds a distinct advantage in rate of passage over other ruminant types when consuming browse.

Rates of particulate passage are regulated by rates of particle-size reduction. Species exhibiting highest rates of passage should pass larger particles. Particle size reduction in ruminants can occur by microbial digestion, chewing during eating and rumination and ruminoreticular contractions. However, chewing during eating and rumination of feed particles is predominantly the most important means for reduction to a size suitable for passage (Ulyatt 1983, Ulyatt et al. 1986). Since there is little postruminal change in particle size distributions of digesta (Grenet 1970, Poppi et al. 1980), particle size distributions in feces collected in this study should be representative of particles escaping the rumen.

Although the rumen pool consists of both small and large particles with variable probabilities for escape (Egan and Doyle 1984), it is meaningful to speak of critical sizes for passage to the lower tract. Studies have indicated that such critical dimensions are between 1 and 2 mm in sheep (Poppi et al. 1980) and 2 and 4 mm in cattle (Ulyatt et al. 1986). This study has added information on browsers and mixed feeders.

Hofmann (1984) has speculated that the differences in critical particle size in feces of browsers could reflect seasonal fluctuations in the size of the reticulo-omasal orifice and close association of liquid and solid pools in moose (Chapter VII). Another profound factor may be the absence, in the rumen of moose, of a fiber mat which has been associated with filtration and sorting in cattle (Van Soest 1982) and, when eliminated, may allow larger particles to escape than for grazers. Smaller limits for escape can only imply a greater need for fragmentation.

Each ruminant used each diet differently. For grass hay/alfalfa rations high in cell wall material, moose and cattle passed particles of a similar size, however turnover time of the Cr-mordanted grass particles was longer in moose suggesting a restriction in flow. This pattern indicated that variation in the particle size distributions is most likely a function of fragility of the diet, efficiency of chewing and passage rate. Values of the log mean particle size of cattle in this study are consistent with data from other investigations with cattle fed a grass hay or legume diet (Murphy and Nicoletti 1984, Kennedy 1985), but higher than data presented by Jaster and Murphy (1983). However, little information exists on studies with wild ungulates offered browse diets. Ulyatt (1983) indicated that cattle are less efficient in the reduction of ingesta particles than sheep. Hofmann (1973) also hypothesized that cattle passed smaller feed particles than browsing ruminants as a result of a smaller reticulo-omasal orifice and the need for more complete fiber digestion. Further, the concentrate browser may offer a certain plasticity in the size of this opening in relation to fiber type (Hofmann 1984).

Fecal particles of aspen leaves from moose passed at a faster rate and had a larger LPS pool than recorded in the other ruminants. The large square dimensions of the aspen leaves (thin in depth) and rectangular shapes of woody twigs may reflect the effect of fiber lignin on fragmentation (Troelson and Campbell 1968, Mertens 1973). Grass hay was fragmented into residues of long cylindrical particles often with fine curled edges in "S" and "Y" shapes which could adhere to the reticulo-omasal orifice and restrict particle passage. The smaller cuboidal particles of alfalfa accompany a decrease in flow rate of particulate fractions and an increased need for rumination.

E. Conclusions

From the results of this study, we can conclude that a browsing ruminant such as moose relies on rapid fermentation of diets high in cell solubles. The ability of this ungulate to extract adequate energy from foods with low asymptotic digestibility is dependent on RTT. This is related to their ability to propel larger particles through the rumen and not become bulk-limited by grass diets which require long RTT before reaching maximum digestibilities. Despite the similarity in retention times and particle distributions of the 1-2 mm fractions of wapiti fed different rations, it is probable that their ability to adjust chewing rates may be the controlling step. The outcome of this study would suggest that further comparative information about chewing behavior and particle size reduction in ruminants with different digestive strategies is required before a more comprehensive understanding can be achieved.

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VII. RATE OF PASSAGE AND TURNOVER TIME OF DIGESTA IN MOOSE, WAPITI AND CATTLE

A. Introduction

Ruminants have radiated in considerable variety since their appearance in the Eocene. Differences in their feeding strategies are reflected in morphological changes of their digestive tract. On this basis, Hofmann (1973) classified African ruminants, and more recently, numerous European and North American *Cervidae* (Hofmann 1984, 1985) into three categories: (1) browsers (concentrate selectors), (2) grazers (grass or roughage eaters) and (3) intermediate or mixed feeders.

Gastrointestinal structures in ruminants delay passage of dietary fiber to variable degrees. Rumens of selective feeders are relatively small with few physical barriers, but well papillated for utilizing diets with rapidly fermenting cell solubles (Hofmann 1973, Langer 1984). There is no advantage in retaining lignified diets once fermentable nutrients are extracted, so browsers propel digesta through the rumen rapidly (Van Soest 1982). Presumably, faster rates of passage result from a less selective but variable reticulo-omasal orifice (Owen-Smith 1980, Hofmann 1984). Roughage feeders generally have a highly developed and capacious rumen with numerous pillars and narrow ostia (Kay et al. 1980). These compartments are filled to near capacity during feeding in bulk feeders whereas rumen fill is somewhat less in browsing ruminants (Van Hoven and Boomker 1985). Grazing ruminants can ingest forage with a higher cell wall content since the constraints of rapid passage are relaxed. Between these two extremes, mixed feeders have rumens of transitional size and they are capable of selecting and digesting grasses, forbs and browse depending on seasonal availability and quality (Hofmann 1973).

[illegible] the past, comparative investigations on digestive function have lacked standardization. Comparisons made from animals in different studies with dissimilar rations or feeds have lacked consistency. More recently, studies have compared retention times of poor quality and milled diets in sheep and red deer and found shorter residency times of solids in red deer (Kay and Goodall 1976). Valtonen et al. (1983) found that retention time of residues in the ruminoreticulum of reindeer was shorter than in sheep. Comparisons among grazers have shown that a mixture of alfalfa and grass hay have longer retention times in bison and yak than cattle (Schaefer et al. 1978). Rumen turnover times of liquids have been compared between muskox (*Ovibos moschatus*) and reindeer fed pelleted rations in Alaska (White et al. 1984), while Baker (1983) compared digestive capacity and flow kinetics of a small browser, the mule deer, and a mixed feeder, the wapiti, fed several rations. Foose (1982) studied trophic strategies of numerous captive exotic ruminants. However, there are few critical comparisons of the digestive kinetics of browsers, grazers and mixed feeders offered browse, grass and mixed diets.

Material is removed from the digestive tract by the processes of digestion and passage. In Chapter VI, digestibility of forages and particle size distributions of fecal residues in moose (browser), cattle (grazer) and wapiti (mixed feeder) were investigated. Objectives of this experiment were to determine the kinetics of particulate and liquid passage in these three species fed diets representative of those normally selected by each and to determine if fibrous grass hay particles will pass more slowly than lignified browse. Trials were conducted in winter and summer to evaluate possible seasonal adaptation.

B. Methods and Materials

Comparative rate of passage trials were carried out during winter (January-April) and summer (July-September) with three rations which covered the dietary range encountered by moose, wapiti or cattle. A grass hay/alfalfa ration, high in cell wall content and lignin, represented diets eaten by bulk feeders. An aspen/alfalfa ration, high in both cell solubles and lignin, was chosen to represent the typical diet of a concentrate selector. A homogeneous alfalfa ration represented a diet intermediate in chemical composition and physical characteristics.

Animals and Diets

One adult moose cow, two adult wapiti castrate males and two adult Charolais-cross steers were fitted with ruminal cannulae (Renecker et al. 1982). Body weights (BW) of the moose, wapiti and cattle ranged between 265-303, 302-347 and 611-738 kg, respectively. During winter, animals were exposed to temperatures which ranged from -31°C to 10°C. In summer, ambient temperatures were markedly higher and ranged from -2°C to 28°C.

Pure diets of grass hay and browse were not offered because of the potential difficulty in maintaining adequate intake. The three chopped diets consisted of a 1:1 mixture of alfalfa with: (a) timothy-brome hay, (b) 100% alfalfa or (c) either trembling aspen twigs or foliage during winter and summer trials, respectively. Alfalfa and timothy-brome hay were mechanically chopped into approximately 10 cm lengths. Aspen twigs consisted of current annual growth from saplings during late winter and were chopped into 2-3 cm lengths. Foliage included leaves stripped from mature aspen in early summer. Animals were fed twice daily between 0800-1000 and 1700-1900 hours *ad libitum* for three weeks to determine voluntary intake. Voluntary intakes of moose, wapiti and cattle were compared on the basis of g dry matter (DM) ingested/ kg BW, since intra-specific changes in rumen capacity scales isometrically with body weight (Van Soest 1982). Feed offered was adjusted to 90% of the determined dry matter consumption rate during the 12 day trial period in an attempt to eliminate uneaten portions.

Analytical Methods

Flow rate of the particulate pool was estimated by administering a pulse dose of the Dysprosium (Dy)-labelled timothy-brome hay in diet (a), alfalfa in diet (b) and either trembling aspen twigs or leaves in diet (c). Forages were labelled by immersing 675 g of ration into a solution of distilled water and 10.1 g (28 mM) of Dy chloride crystal ($DyCl_3 . 6H_2O$) for a period of 24 hours. Labelled feed was rinsed with distilled water for 6 hours and then oven-dried at 60°C (Ellis et al. 1982). A known quantity of Dy-labelled forage, enclosed in a paper bag, was administered through the ruminal cannula on day 1 of each trial. The mass of Dy bound to labelled feedstuffs ranged from 5.3 to 8.4 mg Dy/g DM, with higher values associated with the alfalfa diet.

A solution of Cobalt EDTA (CoEDTA) (15 g) and distilled water was introduced into the rumen on day 1 for estimation of rumen liquid volume and turnover time. The water soluble marker was prepared as a sodium salt according to the method of Uden et al. (1980).

Rectal grab samples of feces were collected every 3 hr for the first 36 hr, every 6 hr for 1 day, and then once each day until 120 hours. Samples of rumen solids were collected from three sites of the middle stratum following the schedule described for fecal grab samples. Volumes (20 ml) of ruminal fluid were collected every 3 hr for the first 24 hr and then every 6 hr until 72 hr. Fecal and rumen particulate samples were oven-dried at 60°C for 48 hr and ground through a 20 mesh screen of a Wiley mill. Subsamples were weighed into irradiation vials; the remaining volume of each vial was filled with sugar to immobilize the sample and heat sealed. Oven-dried feed samples were ground through a 20 mesh screen of a Wiley Mill and dry-ashed in a muffle furnace by ignition at 550°C for 4 hours. A quantity of 6 M HCl was required to dissolve the precipitate and the resulting solution was diluted to 100 ml with distilled deionized water. An aliquot (0.25 ml) was dried on filter paper and heat sealed in an irradiation vial. Feed and fecal samples were analyzed in the University of Alberta SLOWPOKE reactor facility, using the Dy INAA scheme (Kennelly et al. 1980).

Samples of ruminal fluid were centrifuged at 12,000 rpm for 15 min. An aliquot (1-5 ml) of the supernatant was diluted with 0.3 M HCl to a volume of 50 ml. Samples were analyzed for Co concentration by atomic absorption spectroscopy.

Calculations

Disappearance of water soluble and particulate markers from the ruminoreticulum was determined by least-squares regression of the natural log of marker concentration in rumen contents against time post-administration. The resulting slope was the rate constant (k_1) and its intercept estimated marker dilution at time zero. Rumen volume was calculated from the estimated zero-time marker concentration in the rumen and the initial dose of water soluble marker. Rumen turnover time (RTT) was calculated from the reciprocal of k_1 (Hungate 1966).

C. Results

Dry Matter Intake

Mean (±SE) feed consumption of moose and wapiti varied markedly between seasons, increasing significantly ($P<0.05$) by 36±6% and 63±6%, respectively, from winter to summer trials (Table VII.1). In contrast, cattle maintained a relatively constant level of intake when fed grass hay/alfalfa and 100% alfalfa rations but invariably reduced dry matter consumption by an average of 62% and 15%, when fed rations containing aspen twigs or foliage, respectively. Intakes were remarkably similar among ruminant species in summer trials. There was a trend for the difference in voluntary intake between cattle and the two wild ungulates to be greater in winter when fed rations of grass hay and alfalfa.

Rumen Volumes

Ruminal fluid volumes varied between diets and season (Table VII.2). In winter, volumes were greater for grass hay in moose and for alfalfa in cattle but remained relatively constant for all diets in wapiti. In summer, solute space in the rumen for the aspen foliage diet in moose increased from winter levels. Fluid volumes were smallest ~~in summer~~ for the grass hay diet in both moose and wapiti. In general, liquid volumes were similar for all diets offered cattle during summer trials.

Estimations of total rumen dry matter for each species varied with intake and season. During winter, dry matter contents were greatest for the aspen twig ration. For all ruminant species, the alfalfa ration resulted in more dry matter bulk in the reticulorumen. Weight of dry matter contents was lowest for the aspen foliage ration for moose, however, the dry matter

Table VII.1. Mean dry matter intake (DMI) and body weight (BW) of moose, wapiti and cattle fed four diets *ad libitum* during winter and summer 1982.

	Winter			Summer		
Item	Moose	Wapiti	Cattle	Moose	Wapiti	Cattle
Grass Hay/Alfalfa						
BW (kg)	265	316	622	303	336	716
DMI (g/d)	4,155	3,886	13,902	6,774	7,161	15,861
DMI (g/kg BW)	15.7	12.3	22.4	22.4	21.3	22.2
DMI (g/kg $BW^{0.75}$)	63.3	51.8	111.7	93.3	91.3	114.9
Alfalfa						
BW (kg)	271	336	642	294	337	700
DMI (g/d)	4,324	4,394	14,269	5,797	6,693	14,963
DMI(g/kg BW)	16.0	13.1	22.2	19.7	19.9	21.4
DMI(g/kg $BW^{0.75}$)	64.7	56.0	112.0	92.7	84.1	110.0
Aspen Twigs/Alfalfa						
BW (kg)	271	336	626	..	..	..
DMI (g/d)	3,929	3,866	5,301	..	..	..
DMI (g/kg BW)	14.5	11.5	8.5	..	..	..
DMI (g/kg $BW^{0.75}$)	58.8	49.3	46.4	..	..	..
Aspen Foliage/Alfalfa						
BW (kg)	..	..	..	288	328	699
DMI(g/d)	..	..	..	5,795	6,160	12,652
DMI(g/kg BW)	..	..	..	20.1	18.8	18.1
DMI(g/kg $BW^{0.75}$)	..	..	..	82.9	80.0	93.2

Table VII.2. Rumen liquid volumes (Vol) and dry matter (DM) pool of particulates in the rumen of moose, wapiti and cattle fed four diets during winter and summer 1982.

Item	Winter			Summer		
	Moose	Wapiti	Cattle	Moose	Wapiti	Cattle
Grass Hay/Alfalfa						
Vol(l)	56.1	29.4	87.5	33.3	25.9	91.3
DM(kg)	2.09	1.20	5.53	3.58	3.06	7.53
DM(%)	15.2	15.7	17.6	14.2	17.4	17.3
DM/BW (%)	0.79	0.38	0.89	1.18	0.91	1.05
Alfalfa						
Vol(l)	49.9	28.5	114.5	48.1	54.1	98.3
DM(kg)	3.00	1.92	6.73	3.85	5.80	11.30
DM(%)	15.0	15.5	18.6	16.4	16.4	18.3
DM/BW (%)	1.1	0.57	1.05	1.31	1.72	1.61
Aspen Twigs/Alfalfa						
Vol(l)	40.3	23.3	101.0	--	--	--
DM(kg)	3.69	2.84	6.76	--	--	--
DM(%)	14.8	16.6	17.0	--	--	--
DM/BW (%)	1.36	0.85	1.08	--	--	--
Aspen Foliage/Alfalfa						
Vol(l)	--	--	--	50.8	33.9	94.5
DM(kg)	--	--	--	3.22	3.38	7.87
DM(%)	--	--	--	15.0	16.7	17.5
&BC> DM/BW (%)	--	--	--	1.11	1.03	1.13

pool tended to be lowest for the grass hay/alfalfa ration in both wapiti and cattle.

Stratification of particulate matter was most striking within the rumen of cattle. As a result, they had the highest DM content among the three species. In contrast, no layering of rumen solids was observed in moose which had the lowest mean dry matter content of 15.1 ± 0.3%. Wapiti appeared intermediate with a somewhat drier surface on the rumen mass.

Inter-specific differences in rumen liquid volumes and wet and dry weight of rumen contents were partly related to body weight (Fig. VII.1). However, in spite of similarity of body weight, moose had larger ruminal pools than wapiti on certain diets.

Rate of Passage of Particulates

Disappearance of Dy-labelled feedstuffs from the ruminoreticulum of all animals was logarithmic (Fig. VII.2). Moose retained Dy-labelled timothy-brome hay and alfalfa particles 11 to 15 hr (40 to 86%) longer in the rumen than either wapiti or cattle (Table VII.3). With the labelled alfalfa ration, all ruminant species decreased RTT between 0.4 and 4.5 hr from that of grass hay. The shortest retention times for both moose and wapiti were obtained for chopped aspen twigs. Cattle retained aspen twig fragments longer than other labelled fractions and showed a marked reduction in dry matter intake.

Similar trends were observed in RTT of diets fed during summer. Overall, the slowest flow rates were observed for labelled alfalfa, however, only the moose showed a marked reduction in RTT of cured grass hay and alfalfa from winter estimations. Passage was most rapid in all animals for aspen foliage.

Liquid Pool

Wapiti had higher rate constants for flow of liquids than moose or cattle especially on the aspen/alfalfa mixture. For both cattle and moose, passage rate constants of liquids in winter were lower for alfalfa than grass hay/alfalfa (Table VII.4). In summer, rate constants for flow of water leaving the rumen were marginally lower for alfalfa in moose, however, rate

Fig. VII.1. Logarithmic relationship between body weight and estimated weight of wet rumen contents of moose, wapiti and cattle fed four diets during winter and summer. Solid line is logarithmic relationship between these variables, as computed by Parra (1978), for ruminant species.

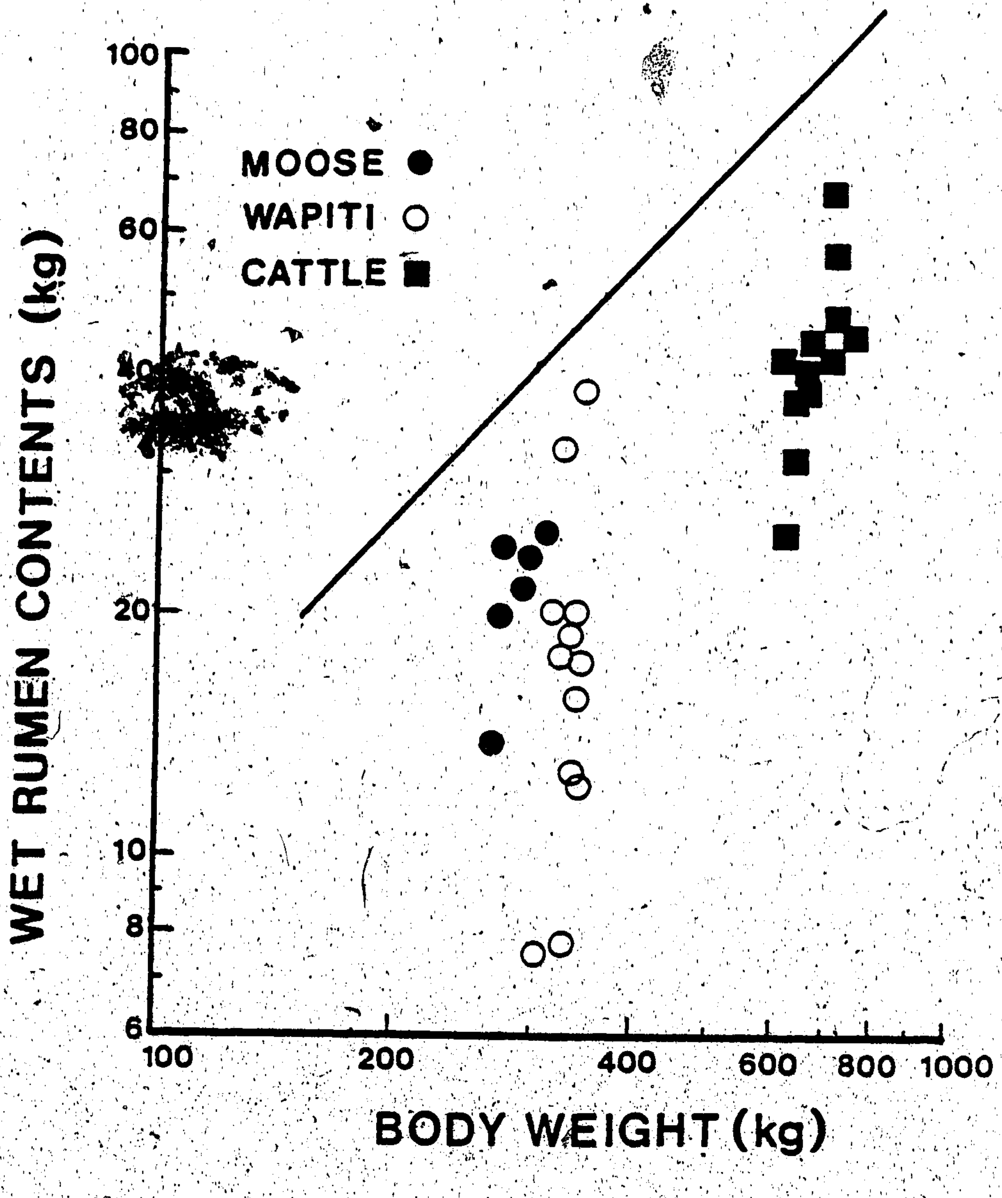
100
80
60
40
20
10
8
6
WET RUMEN CONTENTS (kg)
MOOSE ●
WAPITI ○
CATTLE ■
100
200
400
600
800
1000
BODY WEIGHT (kg)

Fig. VII.2. Decrease in rumen Dysprosium (Dy) concentration with time following administration of pulse doses of four Dy-labelled feeds in moose, wapiti and cattle during winter and summer 1982.

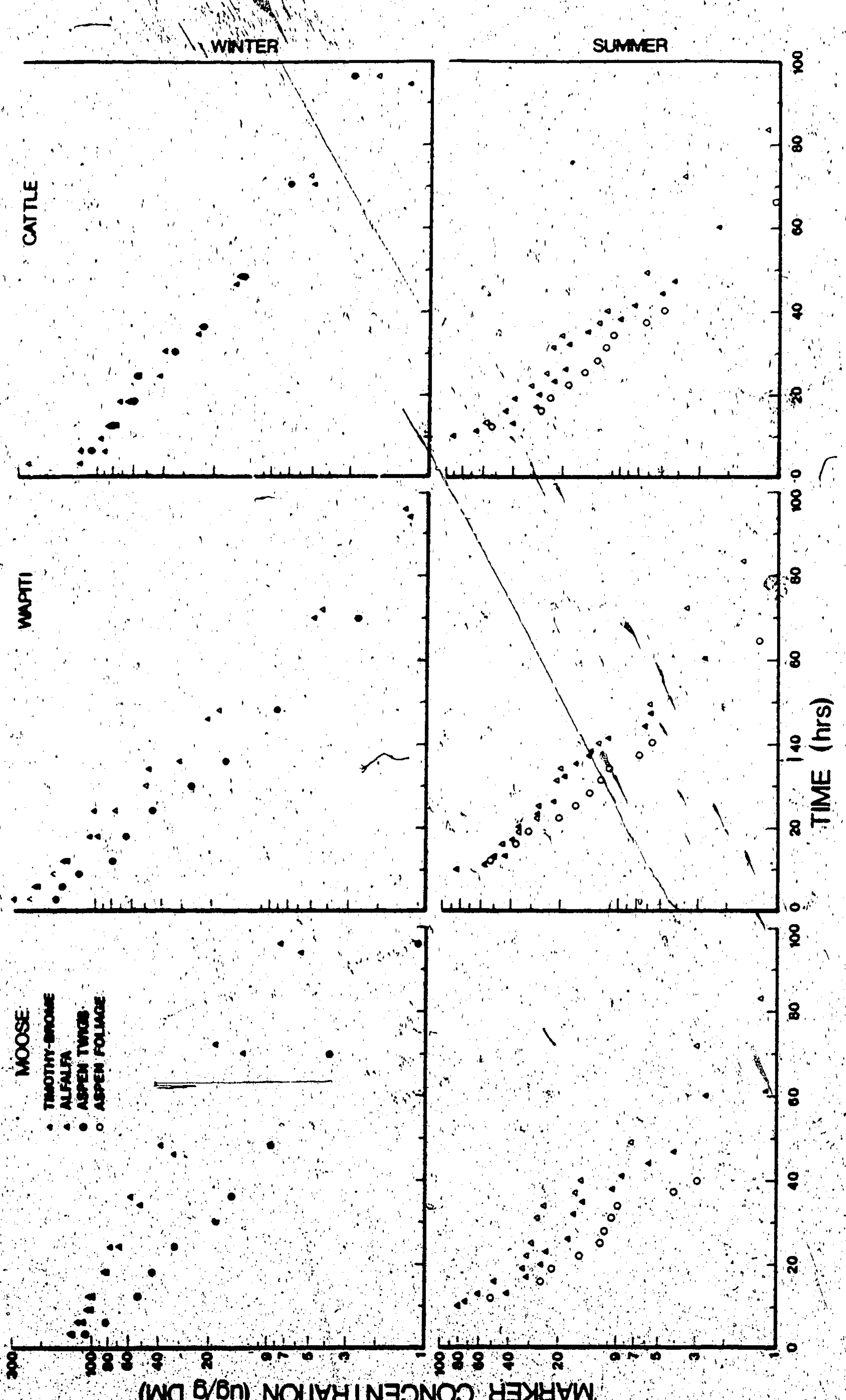
WINTER
SUMMER
CATTLE
WAPITI
MOOSE
▴ TIMOTHY-BROME
▲ ALFALFA
● ASPEN TWIGS
○ ASPEN FOLIAGE
MARKER CONCENTRATION (ug/g DM)
200
100
80
60
40
20
10
7
5
3
1
TIME (hrs)
0
20
40
60
80
100

Table VII.3. Passage rate constants and rumen turnover times (RTT) of particulates in the rumens of moose, wapiti and cattle given four Dy-labelled forages during winter and summer 1982.

Item	Winter			Summer		
	Moose	Wapiti	Cattle	Moose	Wapiti	Cattle
Grass Hay						
Passage Rate Constant (hr^{-1})	0.0354	0.0585	0.0483	0.0554	0.0600	0.0569
RTT (hr)	28.2	17.2	20.7	18.1	16.8	17.6
Alfalfa						
Passage Rate Constant (hr^{-1})	0.0306	0.0570	0.0474	0.0523	0.0479	0.0470
RTT (hr)	32.7	17.6	21.1	19.1	20.9	21.4
Aspen Twigs						
Passage Rate Constant (hr^{-1})	0.0518	0.0586	0.0421	--	--	--
RTT (hr)	19.3	17.2	23.8	--	--	--
Aspen Foliage						
Passage Rate Constant (hr^{-1})	--	--	--	8.09	7.13	6.80
RTT (hr)	--	--	--	12.4	14.0	14.6

Table VII.4. Passage rate constants and rumen turnover times (RTT) of rumen liquids in moose, wapiti and cattle fed four diets during winter and summer 1982.

	Winter			Summer		
Item	Moose	Wapiti	Cattle	Moose	Wapiti	Cattle
Grass Hay/Alfalfa						
Passage Rate Constant (hr^{-1})	0.0426	0.8630	0.1148	0.0697	0.0982	0.08
RTT (hr)	23.5	11.6	8.8	14.4	10.2	12.3
Alfalfa						
Passage Rate Constant (hr^{-1})	0.0433	0.0959	0.0857	0.0594	0.0893	0.0942
RTT (hr)	23.1	10.6	11.7	16.8	11.5	10.7
Aspen Twigs/Alfalfa						
Passage Rate Constant (hr^{-1})	0.0530	0.1023	0.0760	--		
RTT (hr)	18.9	9.8	13.5	--	--	--
Aspen Foliage/Alfalfa						
Passage Rate Constant (hr^{-1})	--	--	--	0.1027	0.1003	0.0851
RTT (hr)	--	--	--	9.7	10.0	11.8

constants tended to be similar for wapiti and cattle. Highest rates of passage for liquids in moose were with the aspen foliage/alfalfa ration.

Rate constants for flow of particulates were highly correlated to rate constants for the liquid pool in moose ($P<0.01$) (Table VII.5). A similar but weaker relationship ($P>0.05$) was obtained for wapiti. Passage rates of solids and liquids were not significantly ($P>0.05$) related in cattle.

D. Discussion

Wild ruminants are faced with the choice of forages varying widely in nutrient content and physical structure. Grasses are high in digestible energy but their linear fiber shape delays passage and increases mastication requirements (Chai et al. 1984, 1985). Although lignin may reduce digestibility, in some cases, lignin can increase brittleness enhancing reduction during mastication and producing particle shapes more optimal for passage (Smith 1968, Mertens 1973, Milchunas et al. 1978). In contrast, browse is low in digestible energy concentration but high in lignin. As a result, fiber particles should break down rapidly into particle sizes optimal for passage; therefore not restricting intake.

Since the success of herbivores is related to daily digested organic matter intake, ruminants should attempt to optimize the trade-off between passage rate and completeness of digestion (Foose 1982). Their ability to do this depends on digestive morphology and function. Large browsers (eg. moose) are expected to propel highly lignified browse residues through the ruminoreticulum while becoming bulk-limited on more fibrous grass diets. In contrast, grazers should detain food in the rumen for extensive digestion, with flow decelerating with indigestibility of the cell wall. Mixed feeders (eg. wapiti) normally feed on a wide variety of forages which vary makedly in chemical composition and would be expected to control passage rate similarly which would account for their ability to exploit a variety of habitats.

Although it is easy to see how anatomical differences reflect adaptation to specific food types, it is more difficult to predict how divergent diets would behave in a browser, grazer and

Table VII.5. Regression of passage rate constants (hr^{-1}) of particulates on rate constants (hr^{-1}) for flow of liquids from the rumen in moose and wapiti.

Species	a	b	SEb	r
Moose	0.0041	0.761	0.209	0.96
Wapiti	0.0055	0.679	0.871	0.62

mixed feeder. Mertens (1973) argued that although grasses contained less lignin, shapes of masticated particles were less optimal for escape, thereby delaying passage. Characteristics of fibrous diets probably dictate slower passage because of greater requirements for comminution. On the other hand, several authors have speculated that lignin in certain cases increases brittleness of forage particles enhancing reduction during mastication and producing particle shapes more optimal for passage (Smith 1968, Mertens 1973, Milchunas et al. 1978). Extensive use of highly lignified forages by browsers invokes the need for rapid passage to propel large undigested residues rapidly through the digestive tract. Resistance of linear fiber shapes of grasses to physical breakdown (Chai et al. 1984, 1985) establishes an expectation for a slower rate of passage because of greater mastication requirements. Unlike browsers, which depend on rapid turnover of undegradable fiber, grazers (cattle) are adapted for longer retention times and maximal digestibilities of high cell wall diets. I would expect that when grazers were fed highly lignified browse, the additional delaying structures would reduce passage rates and thereby maximize digestion.

I would expect the absence of particulate stratification in the rumen of browsers. The raft of feed particles in capacious rumens of grazing ruminants acts largely as a sieving mechanism for high cell wall forages (Ulyatt et al. 1985), whereas the need to pass large particles would probably prevent layering of solids in the rumen of browsers.

The effects of food types on RTT reported here, support the hypothesis that fiber particles of grass hay will pass more slowly than lignified browse, but this conclusion cannot be extended to a mixed feeder, the wapiti. For those feeds tested, fibrousness of the diet did not have a clear influence on particulate flow rates in wapiti. This was probably achieved by a compensatory change in chewing efficiency. High flow rates of browse fragments in moose may be achieved if solids could be closely associated with the liquid phase. Residues of digesta would be flushed from the reticulo-rumen with the flow of water. However, this association was only weakly detectable in wapiti and unrelated in cattle. In cattle, passage rates showed only slight variation and this seemed to be largely explained by forages with higher lignin content passing more slowly. For lignified aspen foliage, results obtained in this study did not support this trend in cattle.

Dry Matter Intake

In ruminants, voluntary intake is limited by the fibrous nature of the feed and physical distention of the rumino-reticulum (Balch and Campling 1962, Baumgardt 1970). Forages with low nutritive value may limit intake before energy requirements are met. Under these circumstances, further consumption can only occur within the constraints of comminution and passage. Many authors have argued that forage intake should be scaled isometrically to body weight since rumen fill would probably limit intake on fibrous diets (Poppi et al. 1980, Van Soest 1982, Baker and Hansen 1985). In this experiment, intake in summer was remarkably similar among all species when expressed on the basis of body weight (BW).

Another factor shown to influence voluntary intake of wild ungulates has been photoperiod (Ozoga and Verme 1970, Milne et al. 1978, Westra and Hudson 1981, Suttie et al. 1983). In this experiment, moose and wapiti, but not cattle showed a pronounced reduction in food intake during winter. Similar forage intakes to those obtained in the present study were previously obtained during late winter with mule deer and wapiti fed grass diets (Baker and Hansen 1985). Whether this reflects trophic adaptation of wild ungulates is not certain. Although domestic sheep show these traits (Kay 1985), large wild bovids such as bison do not have well developed seasonal cycles (Richmond et al. 1977).

Rumen Capacity

Interspecies regressions between body size and gut capacity (Hofmann 1973, Parra 1978, Demment and Van Soest 1985) predict greater volumes than observed in this study. The linear increase in rumen capacity with body weight reflects the need of larger grazing ruminants to accomodate a larger mass of fibrous food in order to acquire adequate energy (Parra 1978).

Rumen contents estimated here were less than predicted by Parra (1978) for ruminants of similar body size. These differences may reflect an underestimation by the particulate marker or perhaps the wide range of capacities for digestion in the rumen. As discussed by Demment (1982), fill weights (obtained by weighing rumen contents) of the rumen tend to underestimate rumen capacity in concentrate feeders whereas fill volumes (obtained by filling ligated rumino-reticulums) overestimate these capacities. When feeding on forage with a high cell content, browsers seldom use more than 60% of the rumino-reticular space (Van Hoven and Boomker 1985) because this highly nutritious food is digested and propelled rapidly through the gastrointestinal tract (Demment 1982), whereas slowly digesting grasses occupy more rumen volume. This study supports this idea and has shown similar trends in moose, wapiti and cattle with changes in forage type.

Particulate Flow

Within the constraints of rumen capacity, forage intake is determined largely by passage rate. Although it is easy to see how anatomical differences may impart different rates, it is more difficult to determine how this will affect relative passage of different forage types.

Species Comparison

Grazers (cattle) are adapted for longer retention times and more complete digestion of diets high in cell walls. When grazers are fed highly lignified browse, well-developed delaying structures cause ruminal accumulation of indigestible material.

Browsers have less well-developed ostia than grazers (Hofmann 1973) and pass larger fecal particles (Chapter VI). However, these results suggest that the reticulo-omasal orifice may be selective for size and shape, restricting passage of long fibrous particles but allowing larger cuboidal browse particles to pass. Smith (1968) reported that while lignin depressed cell wall digestion, its greater shattering ability made particles more optimal in shape for passage (Mertens 1973). Similar findings were reported for deer (browser) which passed highly lignified *Vaccinium* faster than grass (Milchunas et al. 1978).

Seasonal and Dietary Adaptation

Passage rates may change seasonally even on the same diet (Schwartz et al. 1987). These differences could be related either to changes in the digestive anatomy/function (particularly of the reticulo-omasal ostium), or to changes in comminution during feeding and ruminating. Evidence of the former explanation comes from studies on African ruminants by Hofmann (1984). More recently, studies by Hofmann (pers. comm.) on moose in Scandinavia suggests that the size of reticulo-omasal opening changes seasonally with diet quality.

Although passage rates could also be improved by increased rumination efficiency, this question was not addressed in this study. This mechanism was studied in cattle (Balch and Campling 1962), sheep (Welch and Smith 1970, Poppi et al. 1980) and reindeer (White et al. 1984). Browsers may be more responsive to tactile stimulation from highly lignified browse diets than fibrous grass (Milchunas et al. 1978) and thereby increase rumination and mastication times to accelerate passage rates. Because mixed feeders show seasonal shifts in diet selection (Nietfeld 1983), they may also show a plasticity in their efficiency of comminution which may result in similar turnover times for all feeds.

Mixed feeders are opportunistic and have the flexibility to exploit both grass and browse resources. Comparative studies have indicated that intermediate feeders may be better adapted for fiber digestion than browsers partly because of a larger body size and development of structures to delay particulate flow. There was, however, no evidence of difference in turnover times of labelled forages in wapiti between seasons.

Turnover of Liquids

Seasonal effects appeared to influence flow rates of moose. Longer retention times of liquids is often associated with lower levels of digestible dry matter intake (White et al. 1984). As quality and cell soluble content of forage increases, flow of liquids from the rumen would also accelerate, thereby increasing the amount of protein escaping to the lower digestive tract.

This would ultimately increase efficiency of nutrient utilization (Christiansen et al. 1964, Bergen and Yokoyama 1977). This adaptation may be extremely important to a browser which must rapidly replenish body stores during a relatively brief period of quality forage.

The ability of browsers (moose) to propel highly lignified forages rapidly through the digestive tract may be explained by a close association between the flow of solid and liquid phases from the rumen. Similar findings have already been observed in Alaskan moose fed pelleted diets (Schwartz et al. 1987). Since no stratified layers of solids were found in the rumen of moose, particulates may be flushed through the reticulo-omasal orifice by larger volumes of liquids.

The raft of feed particles in capacious rumens of grazing ruminants acts largely as a seiving mechanism (Ulyatt et al. 1986). Consequently, no relationship between these pools is expected. The intermediate strategy of mixed feeders is to utilize different forage classes in relation to quality and availability. For those feeds tested, fibrousness of the diet did not have a clear influence on particulate flow rates in wapiti and particle passage was only weakly related to liquid flow.

The potential for marker migration between feed particles (Faichney 1980, White et al. 1984) cannot be dismissed. If labelled feeds are carefully prepared and washed (Ellis et al. 1982, Allen 1982) then movement of weakly-bound marker should be reduced. Teeter (1981) and Ellis et al. (1982) inferred that uptake or binding of EDTS-markers by ruminal bacteria could result in insoluble marker-metabolite complexes which could alter estimates of ruminal volumes.

E. Conclusions

Browsing ruminants are adapted for highly lignified plant material with an abundance of cell solubles. If turnover time is short, intake would be less limited by rumen fill and presumably more efficient use of nutrients could be made in the lower digestive tract. Consumption of forage high in cell wall content results in detained passage and potentially greater chewing requirements. Furthermore, seasonal enlargement of the rumino-reticulum would allow a concentrate selector to benefit from high quality summer forage.

Cattle (grazers) utilize grasses which require long retention times to maximize digestibilities. Thus, capacious rumens and delay mechanisms for digesta would be advantageous for this forage type but not for browse which would accumulate in the rumen.

Mixed feeders (wapiti) appear to be more flexible without compromising their ability to use either grass or browse. Although they are highly selective for succulent green growth, this species shifts diet selection to grasses or browse when biomass or quality declines. This placticity in turnover time perhaps explains, in part, their ability to effectively exploit numerous habitat types. However, it remains unclear how exactly these adjustments in flow rates are accomplished. A closer examination of rumination efficiency and fibrousness of the diet is warranted.

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PART D. RESOURCE-USE BEHAVIOR

VIII. ESTIMATION OF DRY MATTER INTAKE OF FREE-RANGING MOOSE[1]

A. Introduction

Seasonal variations in forage intake by free-ranging ungulates express the interactions of animal requirements and wide fluctuations in diet quality and availability. Schwartz et al. (1981) showed that penned ~~Alaska~~ moose fed a pelleted diet reached peak intake during summer and low points during the breeding season and late winter. Miquelle (1979) reported dry matter intakes of young moose on Isle Royale during summer from pen trials with clipped browse and of free-ranging moose using the bite-count technique. Crête and Bédard (1975) and Nyström (1980) estimated browse consumption for moose in Quebec and Sweden, respectively, using modified versions of the twig-count technique. Approximate calculations of daily food consumption by moose were made by Gasaway and Coady (1974) based on seasonal differences in rumen fill. However, few empirical data are available on seasonal forage intake by free-ranging moose.

Several methods for determining forage intake of free-ranging animals have been published. Among these, ratio and bite-count methods are most practical for studies on wild ruminants. The *ratio technique* (fecal excretion/indigestibility of the diet) appears most reliable for estimations of intake by grazing livestock (Cordova et al. 1978). Measures of fecal output are usually combined with an *in vitro* estimate of diet digestibility from esophageal samples (Allison et al. 1982, Holechek and Vavra 1982). However, fecal output also can be determined indirectly using external markers (indigestible indicators attached to diet particles) and digestibility can be estimated with indigestible internal markers such as lignin or silica (Langlands 1975, Engdahl 1976). The *bite-count technique*, a useful alternative for less tractable animals, has been used to estimate feeding rates and daily intake by wapiti (Collins 1977, Hobbs 1979, Nietfeld 1983, Wickstrom 1983), mule deer (Wickstrom 1983) and moose

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[1] A version of this chapter has been published. Renecker, L.A. and R.J. Hudson. 1985. J. Wildl. Manage. 49: 785-792.

(Miquelle 1979). Accurate measurement of bite rate, simulated bite size and total foraging time are required for a reliable prediction of voluntary intake.

The objective of this study was to determine seasonal changes in dry matter consumption by free-ranging moose using both ratio and bite-count methods simultaneously.

B. Methods

Two hand-reared, non-pregnant, non-lactating moose cows were maintained in a 2 ha pasture on a pelleted aspen-concentrate ration (Schwartz et al. 1980) supplemented with hand-cut browse. The moose were 2.5 years old at the commencement of the study and were habituated to human presence.

Every 6-8 weeks from December, 1982 to January, 1984, they were released into a 65 ha enclosure to evaluate feeding activity and forage intake by the ratio and bite-count techniques. An average adjustment period of 4 weeks allowed the animals and their digestive microbes time to adjust to natural forage.

Feeding Activity

Foraging activities of each individual were recorded by continuous time-sampling during 24-hour observation periods. Activities were classified as grazing (forbs or graminoids), feeding on leaf litter, browsing low (below the brisket level), browsing middle (between brisket and topline of the moose), browsing high (above topline) and feeding on bark ("stripping"). Plant species, plant part selected and feeding time were recorded within each of these categories.

Ratio Technique

Samples of plant material were selected to simulate the portion consumed by each moose. Clipped forages were oven-dried at 60°C for 48 hours and ground through a 20 mesh screen with a Wiley Mill. Ground samples of each plant species were combined to yield a 3 g composite sample reflecting dietary proportions. Four replicates of the combined diet samples were weighed into nylon bags and placed in the ventral sac of the rumen of a ruminally-fistulated moose (Renecker et al. 1982) maintained on the pelleted ration, chopped alfalfa and fresh browse (species consumed during trial periods). The bags were removed after 48 hours, washed and oven-dried at 60°C to constant weight. Dry matter digestibility was calculated as the percent change in the dry weight of the bag contents.

Total fecal collections were obtained from each moose during each 24-hour observation period. Feces were oven-dried at 60°C for 48 hours and weighed to determine dry matter (DM) content. Dry matter intake (DMI, g) was calculated from total fecal output and *in situ* nylon bag digestibility with the equation:

$$\text{DMI} = (\text{FDM} \times 100)/(100 - \text{NBD\%})$$

where,

FDM is daily fecal dry matter excretion

NBD% is diet digestibility determined by the nylon bag technique.

Daily consumption was expressed as a function of metabolic body weight (g/kg $BW^{0.75}$) to identify intraspecies intake requirements.

Bite-Count Technique

Bite rates were determined from the number of bites taken for several 1-15 min sample periods. Bite rate was expressed as cropping bites per minute of foraging time. Results were aggregated for each foraging category.

Bite sizes of each forage type were estimated from (10-80) simulated bites taken in close proximity to each moose during 24-hour observation periods. These samples were oven-dried at 60°C for 48 hr.

Daily DMI of each food item selected by an animal was calculated as the product of bite rate, bite size and foraging time. Values were summed for forage species within and across bouts and expressed in g/kg BW$^{0.75}$ for each moose.

Chemical Composition

Composite forage and fecal samples were analyzed in duplicate for crude protein (CP) by the macrokjeldahl technique according to A.O.A.C. (1965). Fecal samples were taken from total collections. Neutral detergent fiber (NDF) was determined for the simulated diets according to the method of Goering and Van Soest (1970).

C. Results and Discussion

Dry Matter Intake

Estimates of voluntary intake, for each season, were similar using both techniques (Fig. VIII.1). Generally, the bite-count method overestimated intake determined by the ratio technique by 1.0% to 6.0%. There was no significant difference ($P>0.05$) in the estimation of DMI when technique effects were tested against the mean square for error (Table VIII.1) by an analysis of variance (Steele and Torrie 1980). The difference among months ($P<0.025$) was significant.

The mean size of simulated bites (±SD) of the two moose cows increased from 0.60 (±0.11) g DM/bite in December, 1982 to an average weight of 1.0 (±0.24) g DM/bite in April, 1983. The smallest average bites of 0.54 (±0.04) g DM/bite were estimated during late May when moose "stripped" leaves with low dry matter content from selected plant species. The largest bites (1.22 ±0.21 g DM/bite) during July were associated with the higher DM content of mature leaves and the consumption of cattails. Bite size declined to 0.68 (±0.18) g DM/bite during October and then rose to 0.76 (±0.17) g DM/bite in early winter as woody stems became the main food.

Fig. VIII.1. Dry matter intake (g/kg $BW^{0.75}$) of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta. Estimates based on ratio and bite-count techniques.

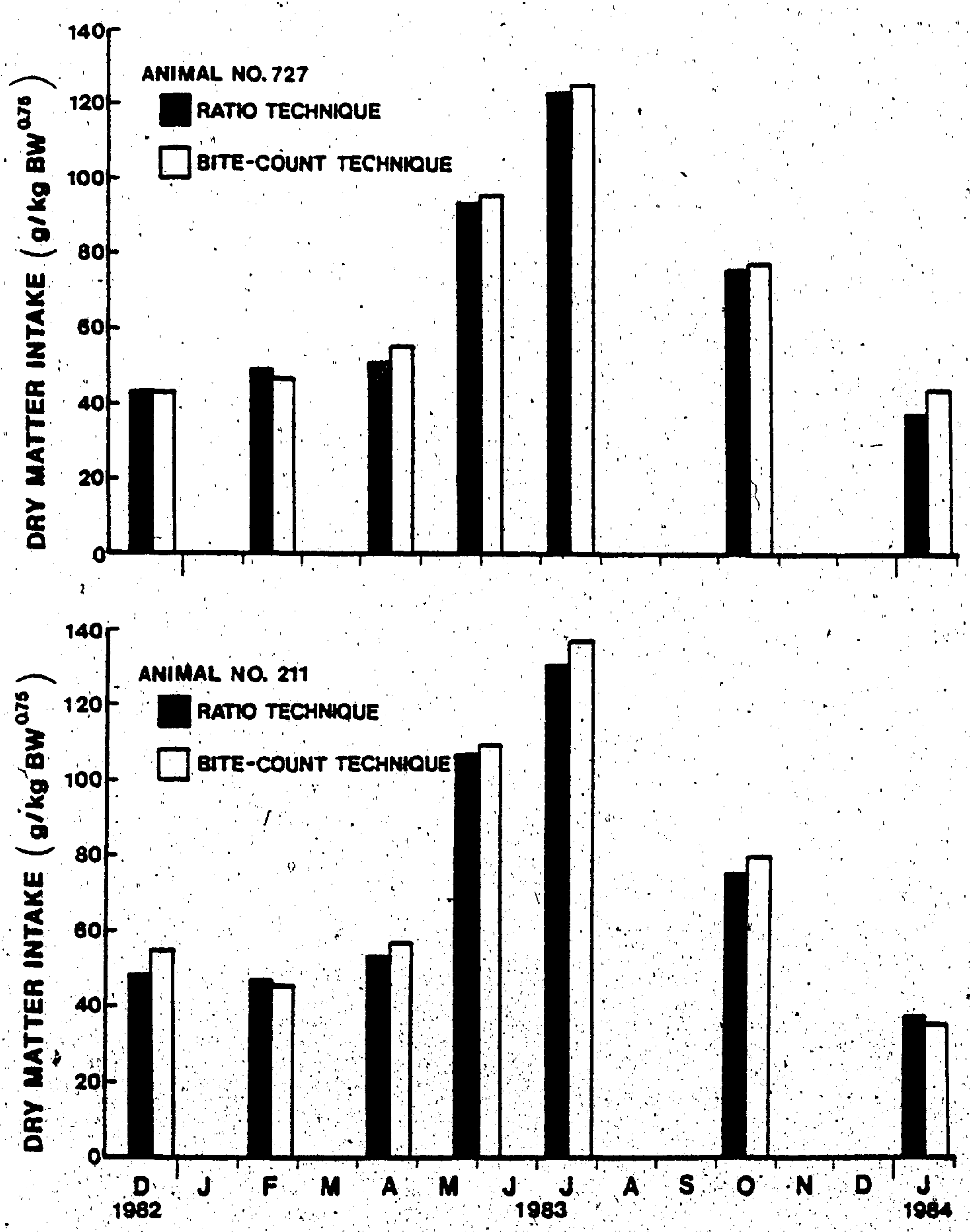

ANIMAL NO. 727
RATIO TECHNIQUE
BITE-COUNT TECHNIQUE
DRY MATTER INTAKE $(g/kg\ BW^{0.75})$
0
20
40
60
80
100
120
140
ANIMAL NO. 211
RATIO TECHNIQUE
BITE-COUNT TECHNIQUE
DRY MATTER INTAKE $(g/kg\ BW^{0.75})$
0
20
40
60
80
100
120
140
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1982
1983
1984

Table VIII.1. Analysis of variance for techniques used to determine dry matter intake of two free-ranging moose cows between December 1982 and January 1984 at the Ministik Wildlife Research Station, Alberta.

Source of variance	df	MS	F
Month	6	4,506.90	170.91 ***
Technique	1	40.95	1.55 NS
Month x technique	6	3.65	0.14 NS
Error	13	26.37	
Total	26		

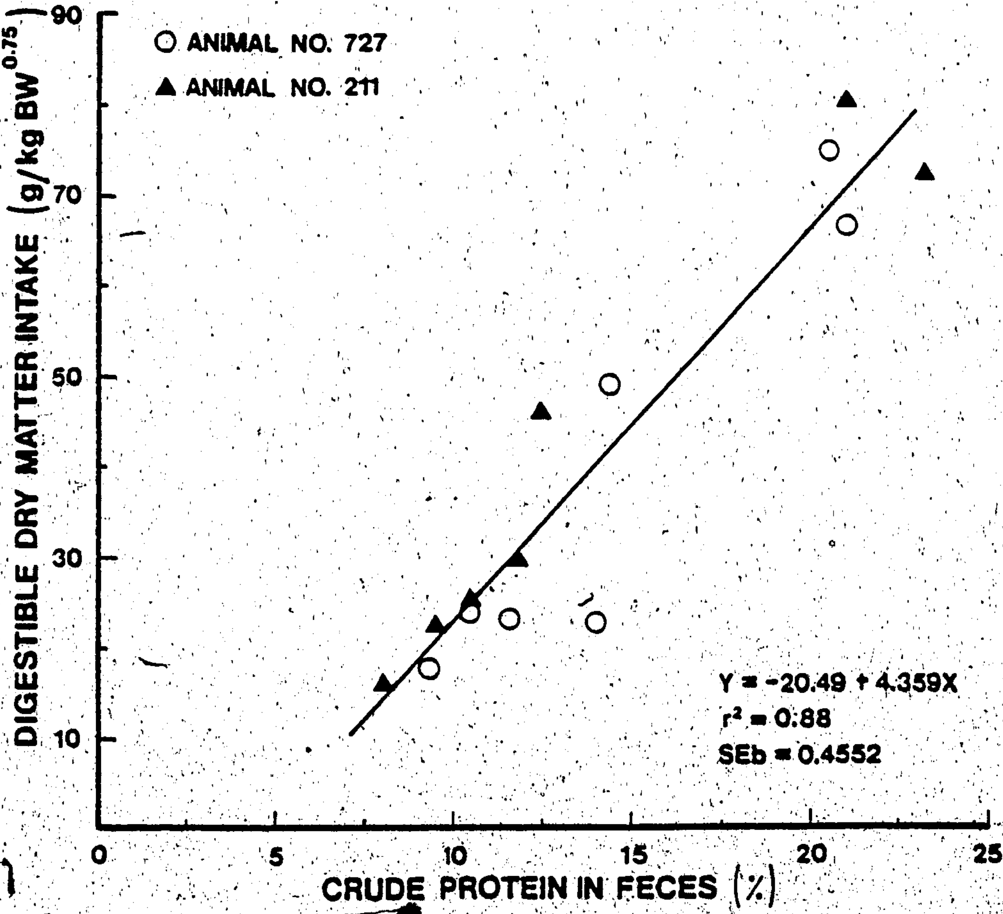
NS Not significant at the 0.10 level.
*** Significant at the 0.005 level.

Daily intakes of dry matter of the two free-ranging moose varied from over 129 g/kg $BW^{0.75}$ in mid summer to about 38 g/kg $BW^{0.75}$ in mid winter. The initial rise in daily consumption during April preceded the spring bud break by almost four weeks. During this period, animals allocated 39% of their foraging time to consuming bark from trembling aspen and balsam poplar. Mean daily consumption (±SD) rose to 9,938 (±836) g/d by mid July as foliage became the most important dietary item. This value falls between those reported for penned moose by Schwartz et al. (1981) and Miquelle (1979), and computed estimates by Gasaway and Coady (1974). During autumn, intake declined with the maturation of available forage although moose selected many items such as Canada thistle, red raspberry and Western snowberry which remained green. Dry matter intakes during January 1984 were lower than in December and February of the previous winter. Repeated melt-freeze cycles during the second winter period resulted in a snow crust which probably prevented moose from forming craters with their muzzles for leaf litter. As a result, moose spent more time searching for forage. An increase in the dietary proportion of woody stems accompanied the decline in leaf litter.

Fecal CP concentrations ranged from 7.8% to 23.1% and were significantly correlated ($P<0.05$) with digestible dry matter intake (DDMI) (Fig. VIII.2). Although fecal CP has been assessed as a better indicator of digestibility than DDMI (Cordova 1977), fecal CP in this study was a better predictor of seasonal intake than were levels of chemical constituents in plants. Each relationship represents a specific set of conditions and separate equations may be required for each application.

The use of this fecal index is based on the assumption that metabolic fecal nitrogen is primarily of body origin and variation in metabolic fecal nitrogen (MFN) is proportional to DDMI (Blaxter and Mitchell 1948, Arnold and Dudzinski 1963). The validity of this assumption is also a function of dietary nitrogen in that fecal nitrogen content will increase proportionally to that of forage nitrogen. Excretion of MFN is generally related to dry matter intake, diet digestibility and fecal dry matter (Robbins 1983). Because MFN represents a nitrogen cost of digestion (Smuts 1935), an increase in its excretion could reflect an additional

Fig. VIII.2. The relationship between fecal concentrations of crude protein (%) and digestible dry matter intake (g/kg $BW^{0.75}$) of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.


○ ANIMAL NO. 727
▲ ANIMAL NO. 211
DIGESTIBLE DRY MATTER INTAKE (g/kg BW^0.75)
90
70
50
30
10
0
5
10
15
20
25
CRUDE PROTEIN IN FECES (%)
Y = -20.49 + 4.359X
r² = 0.88
SEb = 0.4552

requirement of the animal as well as the quality of its food supply (Hobbs et al. 1982). However, secondary plant compounds such as phenols and tannins found in deciduous trees and shrubs can form cross-linked complexes which may precipitate dietary and microbial protein and thereby reduce protein digestibility (Choo et al 1981). These secondary metabolites increase with the higher fiber content of mature leaves (Choo et al. 1981) and especially in twigs during winter (Mould and Robbins 1981, Palo 1984). As a result, diets high in tannins and phenolic compounds could increase total fecal nitrogen and MFN (Van de Veen 1979, Mould and Robbins 1981).

Total nitrogen content of moose feces was correlated ($P < 0.001$) with nitrogen content of experimental diets (Fig. VIII.3). This regression coefficient was greater by a factor of two than was reported in previous investigations with wapiti fed grass and alfalfa (Mould and Robbins 1981). The higher slope for a browser, such as a moose, could reflect higher MFN values. Browsing herbivores may excrete higher levels of total fecal nitrogen and MFN than grazing ungulates which consume a high proportion of grass.

Diet Quality

Digestibility of diet dry matter ranged from 44.5% in mid winter to 68.9% in late May (Fig. VIII.4). Lowest values obtained in January 1984 reflected heavy use of woody stems. In December and February of the first winter, slightly higher digestibilities corresponded with greater use of leaf litter. Digestibility increased only marginally during April as bark became more important in the diet. However, trembling aspen and balsam poplar bark had a dry matter digestibility of 65.4%. This may have resulted from a relatively high level of soluble nutrients being transported through the bark cambium to expanding buds in preparation for spring growth (Chapin 1980). Concomitantly, growth of meristematic tissue within the bark may have lowered the concentration of secondary compounds and increased its palatability (Bryant et al. 1983). High digestibility during late May reflects the quality of forage during leaf flush (Stewart et al. 1977) and the selectivity of moose observed "stripping" leaves from browse

Fig. VIII.3. Relationship between nitrogen content (%) of experimental diets and fecal nitrogen levels (%) of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

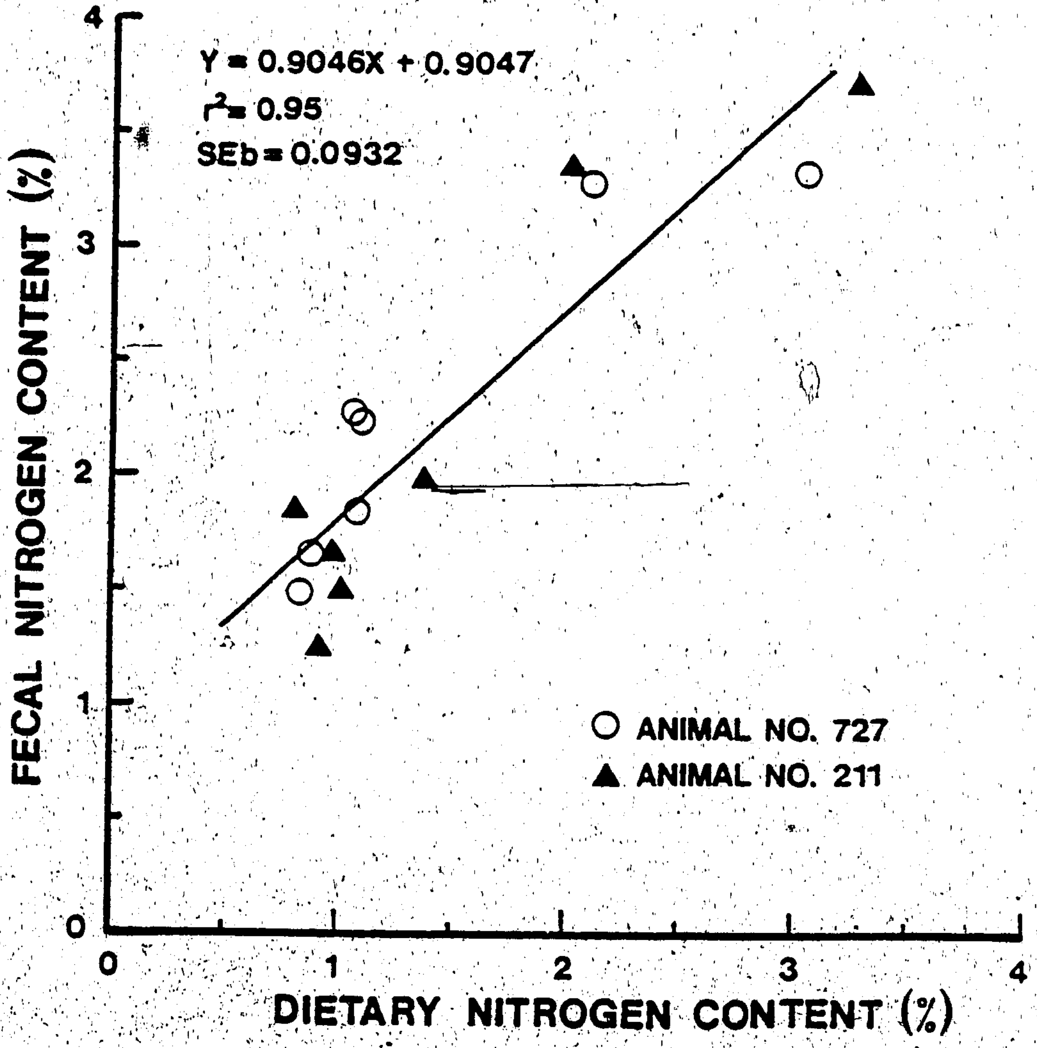
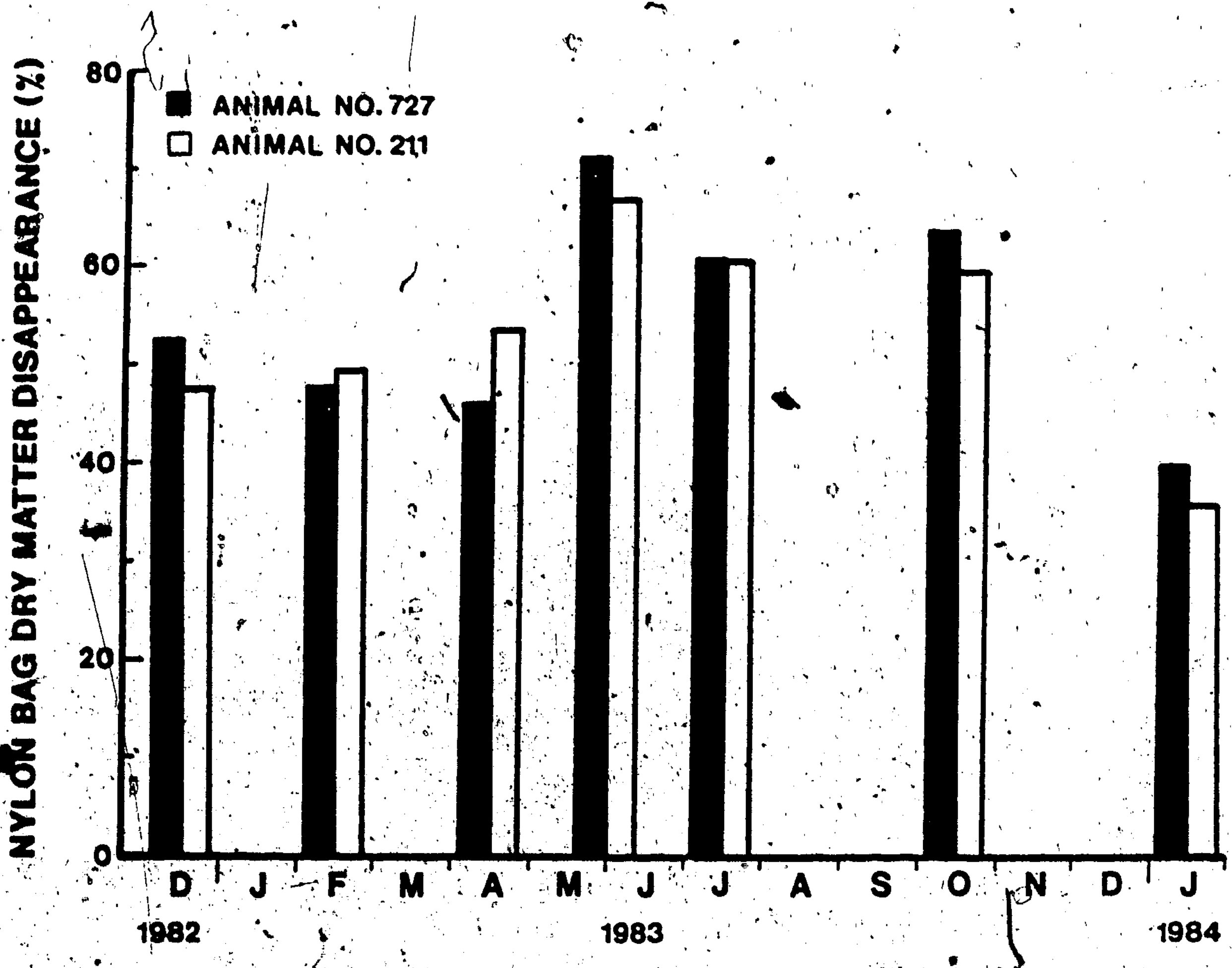

Y = 0.9046X + 0.9047
r² = 0.95
SEb = 0.0932
FECAL NITROGEN CONTENT (%)
DIETARY NITROGEN CONTENT (%)
0
1
2
3
4
0
1
2
3
4
○ ANIMAL NO. 727
▲ ANIMAL NO. 211

Fig. VIII.4. The seasonal change in nylon bag dry matter disappearance (%) for composite diets of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.


NYLON BAG DRY MATTER DISAPPEARANCE (%)
80
60
40
20
0
■ ANIMAL NO. 727
☐ ANIMAL NO. 211
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1982
1983
1984

species. After leaf drop, use of forbs and low shrubs maintained digestibilities which were as high as during mid summer although intake declined.

The annual change in chemical content of composite diets (Table VIII.2) appeared to predict NBD%. Diet digestibility was weakly correlated with forage parameters such as DM, CP and NDF (Table VIII.3). A decrease in DM and NDF content during spring, summer and fall probably resulted in greater concentrations of cell solubles which would produce higher rates of digestion and passage of digesta than if moose consumed a bulk-limiting grass diet (Mertens 1973, Short et al. 1974). High levels of dietary CP would complement ruminal microbial populations and ultimately enhance the energy balance of free-ranging moose. Greater proportions of cell wall constituents require longer retention times to achieve maximum digestibility. However, moose can not afford to be restricted by low quality grass forage during the winter nadir as a result of the reduced rumen turnover time characteristic of grazing ruminants. The shattering characteristics of highly lignified browse forages may actually enhance particle breakdown through rumination and produce more optimally shaped particles for passage (Mertens 1973). Schwartz et al. (1987) suggested that an increase in dietary lignin would decrease the rate of particle passage through the rumen of moose. However, moose probably increase their rumination time and intensity when highly lignified browse and shrubs are consumed in order to try to reduce digesta particles to shapes which pass rapidly through the gastrointestinal tract.

Weight Changes

Although energy requirements are likely seasonal, pooled data relating weight change (Table VIII.4) to DDMI provide an estimate of average annual maintenance requirements (Fig. VIII.5). The intercept of the regression line and zero gain or loss in body weight gives an estimated maintenance requirement for DDMI of 37.4 g/kg $BW^{0.75}$. If 20.08 KJ/g DM is assumed as the calorific value for moose browse (Hjeljord et al. 1982), then the digestible energy (DE) intake at weight stasis should be 751 KJ/kg $BW^{0.75}$. The percent of DE that is

Table VIII.2. Seasonal change in quality of composite diets consumed by two free-ranging moose cows between December 1982 and January 1984 at the Ministik Wildlife Research Station, Alberta.

Month and Animal Number	Composite Diet		
	Dry Matter (%)	Crude Protein (%)	Neutral Detergent Fiber (%)
1982			
Dec			
727	62.5	6.9	51.7
211	56.1	6.1	51.6
1983			
Feb			
727	61.2	6.9	50.6
211	56.1	6.4	48.9
Apr			
727	52.0	5.5	52.0
211	50.0	5.1	50.0
May			
727	25.5	19.1	31.1
211	26.7	20.5	34.2
July			
727	33.6	13.2	42.7
211	27.7	12.6	35.4
Oct			
727	46.3	6.7	37.8
211	54.5	8.7	41.5
1984			
Jan			
727	59.6	5.2	52.6
211	58.8	5.8	51.1

Table VIII.3: Relationship between digestibility and composition of composite diets consumed by two free-ranging moose cows between December 1982 and January 1984 at the Ministik Wildlife Research Station, Alberta.

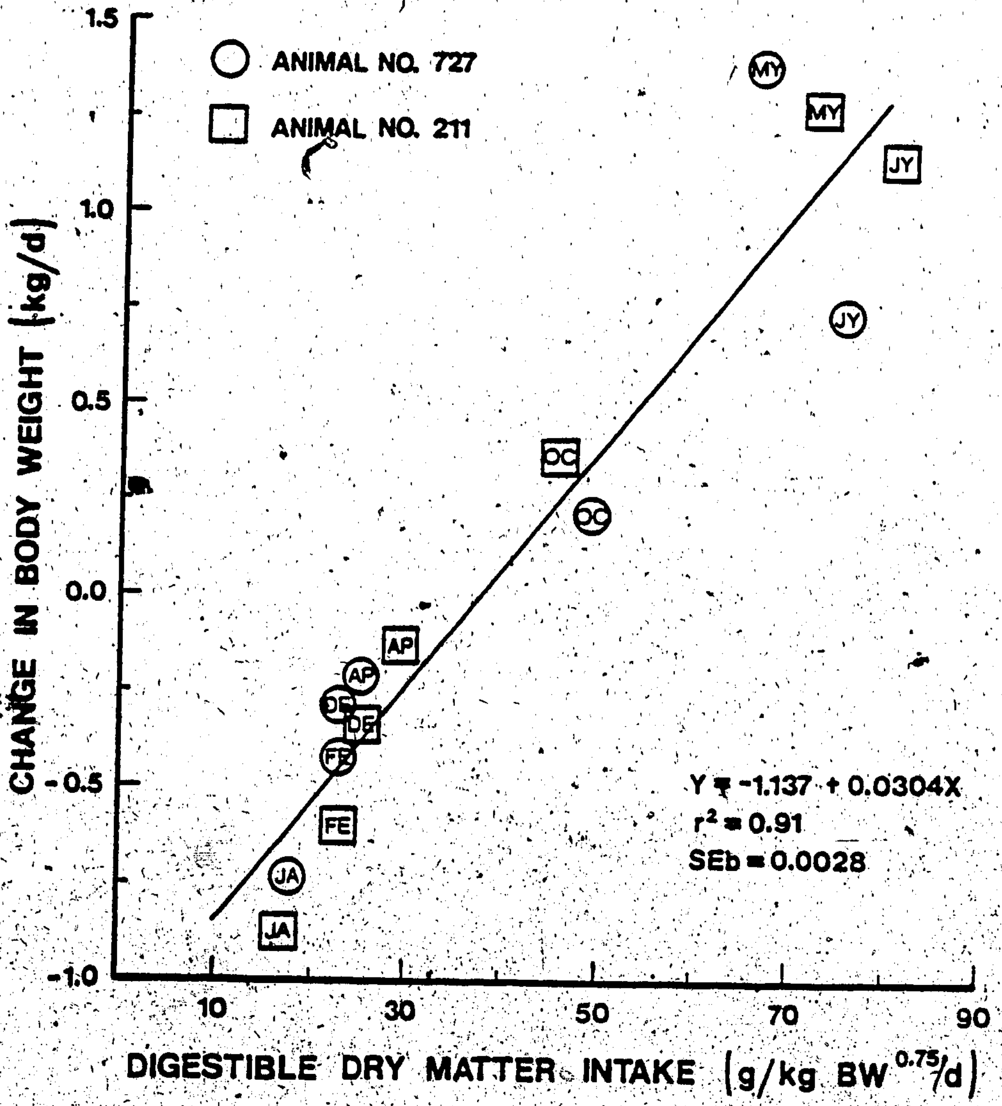
Regression	N	a	b	SEb	r^2
Diet digestibility (%) vs.					
Dry matter (%)	14	80.16	-0.5010	0.0902	0.73 •••
Crude protein (%)	14	41.78	1.4140	0.2766	0.69 •••
Neutral detergent fiber (%)	14	103.50	-1.0800	0.1043	0.90 •••

••• Significant at the 0.001 level.

Table VIII.4. Seasonal changes in body weight of two free-ranging moose cows between December 1982 and January 1984 at the Ministik Wildlife Research Station, Alberta.

Month and animal number	Body weight (kg)		Period between measurements (days)	Change in body weight (g/day)
	Beginning of period	End of period		
1982				
Dec				
727	322	318	14	-290
211	330	322	24	-330
1983				
Feb				
727	328	314	33	-420
211	350	335	25	-600
Apr				
727	303	295	35	-230
211	292	290	14	-140
May				
727	267	289	14	1,380
211	264	284	14	1,250
July				
727	306	328	30	730
211	338	355	15	1,130
Oct				
727	342	345	14	210
211	365	373	22	360
1984				
Jan				
727	340	307	44	-730
211	360	321	44	-890

Fig. VIII.5. Relationship between digestible dry matter intake (g/kg $BW^{0.75}$/d) and body weight change (kg) of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.


○ ANIMAL NO. 727
□ ANIMAL NO. 211
CHANGE IN BODY WEIGHT (kg/d)
1.5
1.0
0.5
0.0
-0.5
-1.0
10
30
50
70
90
DIGESTIBLE DRY MATTER INTAKE (g/kg BW^0.75/d)
MY
MY
JY
JY
OC
OC
AP
AP
DE
DE
FE
FE
JA
JA
Y = -1.137 + 0.0304X
r² = 0.91
SEb = 0.0028

metabolizable has been estimated to be 77.9% for moose on a browse diet (Regelin et al. 1981), which calibrates as a metabolizable energy (ME) maintenance requirement of 585 KJ/kg $BW^{0.75}$. The efficiency with which increments of ME are used for maintenance in moose has been estimated at 68.2% (Regelin et al. 1981). Therefore, the net energy requirement for maintenance of free-ranging moose cows can be computed to approximate 400 KJ/kg $BW^{0.75}$. Hudson and Christopherson (1985) reviewed the metabolizable energy requirements for maintenance of several wild and domestic ruminants. Comparison with this range of values (from 466 KJ/kg $BW^{0.75}$ for adult beef cattle (ARC, 1980), to 529 KJ/kg $BW^{0.75}$ for adult red deer (Brockway and Maloiy 1968)) indicated that maintenance requirements for moose may be somewhat lower than other wild Cervids.

The regression equation computed between DDMI and change in body weight was linear (Fig. VIII-5). However, the efficiency with which ME is used for maintenance and gain is usually considered curvilinear, decreasing at higher levels of feeding (ARC 1980). In agreement, moose appeared to utilize increments of DDMI more efficiently during periods of weight loss than during gain. Similar findings have been observed for domestic ruminants (Blaxter 1962, Webster et al. 1974), mule deer (Baker et al. 1979), white-tailed deer (Ullrey et al. 1970) and moose (Hjeldjord et al. 1982). Deviation is slight, and the linear fit provides an indication of average maintenance requirements for free-ranging moose.

Energy content of the gain is dependent on the type of tissue deposited by the body, rumen fill and water. Changes in water and fat content of body tissues can vary extensively with changes in body weight, age or season (Reid and Robb 1971, Holter et al. 1979) and can influence the amount of energy retained in the body. Weight gain, therefore, provides only a crude index of net energy balance.

Compensatory growth appeared to replace catabolized tissue when diet quality and innate metabolic cycles increased during spring and summer (Suttie et al. 1983). White-tailed deer have demonstrated a propensity to deposit body protein for growth rather than fat at lower levels of DE intake during summer (Holter et al. 1979). Because tissue protein is associated with more water than is fat (ARC 1980), the greater change in body weight of moose cows recorded during late May (Fig. VIII.5) may reflect some hydration of body tissue. Lower increments in body weight during July which occurred concurrently with a peak in DDMI may reflect a lower metabolizability of diets due to a greater concentration of secondary metabolites in forage plants (Bryant et al. 1983), or alternatively may reflect deposition of tissues with higher fat content.

D. Conclusions

Voluntary intake by free-ranging moose appears to be influenced by the interaction of metabolic rhythms, forage availability and forage quality. The importance of forage quality was evident in a strong relationship between DDMI and fecal protein concentration. Moose extended weight gains into the autumn season by selectively foraging for green, digestible species. During winter, in aspen boreal habitats, moose depended heavily on leaf litter and decreased intake as it became unavailable. Although energy requirements are expected to change seasonally, on an annual basis, weight stasis was achieved on a DDMI of slightly over 37 g/kg $BW^{0.75}$ which corresponds to a net energy maintenance requirement of 400 KJ/kg $BW^{0.75}$.

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IX. SEASONAL FORAGING RATES OF FREE-RANGING MOOSE[7]

A. Introduction

Changes with season, in the quality and availability of forage, potentially limit daily food intake by moose throughout much of their biogeographical range. The ultimate constraint on daily intake of dry matter for ruminants is capacity of the rumen and hence rates of digestion and passage which are strongly influenced by physico-chemical properties of forage. At another level, biomass and structure of vegetation influence rate of food capture and impose an additional constraint to ingesting adequate amounts of forage; particularly for large herbivores feeding in sparse or clumped habitats. Longer foraging times, higher biting rates or greater bite sizes are tactics which herbivores can employ to meet their daily forage requirements (Wickstrom et al. 1984). Total time devoted to feeding can be limited by search times and the need to ruminate while compensatory limits on bite rates and sizes are often dictated by vegetation characteristics.

Following pioneering work on domestic animals (Allden and Whittaker 1970, Chacon and Stobbs 1976), a growing number of studies have investigated the intensity with which wild ungulates harvest food. The earliest of these considered feeding rates in relation to [illegible] type (Collins and Urness 1983). This was followed by studies designed to determine how forage biomass and structure influenced feeding behavior of such species as reindeer (Trudell and White 1981), mule deer (Wickstrom et al. 1984) and wapiti (Nietfeld 1983, Wickstrom et al. 1984, Hudson and Nietfeld 1985).

Comparable studies have not been conducted on large browsers such as moose. Vivas (1987) measured winter consumption rates of woody stems by moose in Norway and Renecker and Hudson (1985) documented seasonal changes in dry matter intake by moose in central Alberta, but these measures have not been related to seasonal forage supplies. This chapter

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[7] A version of this chapter has been publishe[illegible] Renecker, L.A. and R.J. Hudson. 1986. J. Wildl. Manage. 50:143-147

examines the logistics of foraging by moose in the aspen boreal environment and provides data on how seasonal changes in biomass of selected forages influence feeding rates.

B. Methods

Two hand-reared moose cows habituated to human presence were maintained in a 2 ha pen on a pelleted aspen-concentrate ration (Schwartz et al. 1985). Their weights ranged between 306 and 373 kg during the study. They were released into a 65 ha enclosure during July and October, 1983 and January, 1984 for an average of 4 weeks prior to sampling to allow for digestive adjustment and stabilization of selection patterns.

Each moose was observed once for a continuous 24 hr period during selected months. Estimates of cropping bite rates and size of bites were obtained from 1 to 15 min observation periods during feeding periods in various habitats, and from 10 to 80 portions of plants taken by the observer to closely duplicate plant species and parts used by moose (Renecker and Hudson 1985). Simulated bites were oven-dried at 60°C for 48 hr and weighed.

Movements while feeding (steps/min) as well as feeding rates (bites/min) were noted by an observer usually situated within 3-5 m of the animal. Consumption rate (g/min) was calculated as the product of cropping rate (bites/min) and bite size (g/bite). Results were grouped according to species, habitat type and season.

Forage biomass was determined for each habitat selected by moose during the 24 hr scans using five randomly located 1 x 2 m sample plots. Each plot was clipped to estimate total and usable biomass (kg/ha). Usable biomass was defined as the total mass of those forage species used by moose during each observation period. Samples were oven-dried at 60°C for 48 hr to obtain dry weights.

C. Results and Discussion

Available Biomass

Total vegetation biomass (x ± SE) in habitat types used by moose averaged 2,779 ± 468 kg/ha during July and October declining to 536 ± 293 kg/ha during January (Table IX.1). Biomass of usable forage showed no significant ($P > 0.05$) decrease from summer to autumn and averaged 1,567 ± 186 kg/ha. In autumn, maturation and fall of foliage from deciduous trees and shrubs contributed largely to the reduction in biomass of browse in upland aspen forest. Fallen leaves represented a potentially important food source exceeding 3,200 kg/ha in some habitat types. Early winter snowfalls and repeated freeze-thaw cycles significantly ($P < 0.05$) reduced total and selected forage biomass to 536 ± 293 and 518 ± 219 kg/ha, respectively. During January, moose were unable to muzzle through snow crusts for leaf litter except in habitats where fallen branches and penetrating sunlight reduced or eliminated the dense snow cover.

Consumption Rate

Moose increased their rate of dry matter (DM) intake (g DM/min) in a significant ($P < 0.001$) curvilinear manner as available biomass increased during summer, autumn and winter (Fig. IX.1) with almost identical responses in each animal. The intercept of the asymptotic equation was close to zero in October but slightly positive in both July and January. This suggests that moose selected a greater proportion of total herbage than I estimated to be usable. Although it is possible to fit the curve through zero, this would incorrectly increase slopes. Ignoring these differences, the pattern can be summarized in terms of the asymptote (theoretical maximum foraging rate) and slope (instantaneous relative consumption rate).

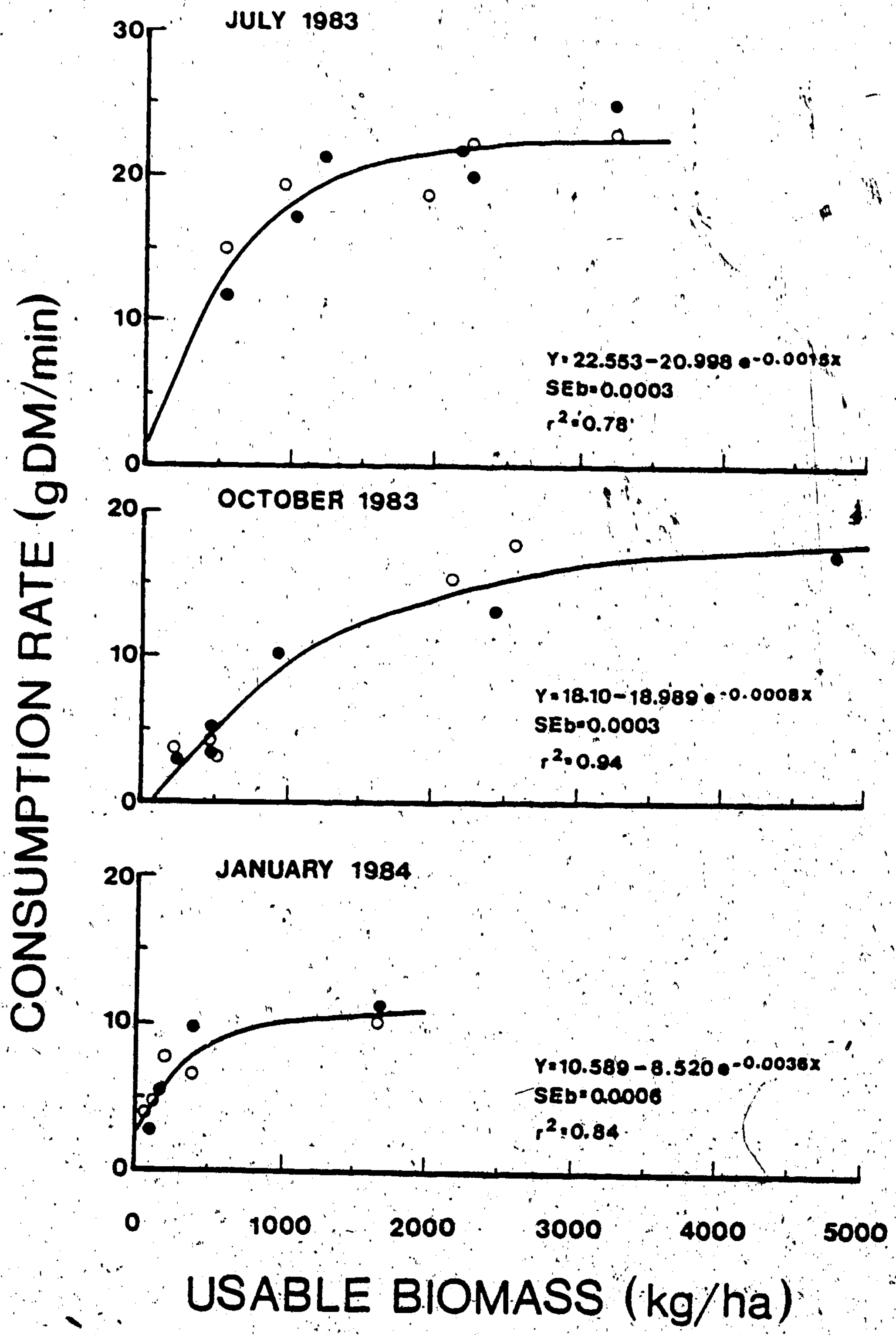
~~Predicted maximum fo~~raging rates fell from 23 g DM/min in July and 18 g DM/min in October to 11 g DM/min in January. Since this expression accounts for biomass, differences must be related ultimately to forage quality, forage structure or perhaps animal factors such as appetite and selectivity. The summer asymptote was higher than comparable summer feeding

Table IX.1. Average available biomass of forage in habitat types utilized by moose during summer, autumn and winter at the Ministik Wildlife Research Station, Alberta.

Habitat	Biomass of Forage Class (kg/ha)					
	Forbs	Grass	Sedge	Browse	Leaf Litter[1]	Total
Summer						
Upland Aspen Forest	62	9	0	856	0	927
Steep Incline-Aspen Forest	233	6	0	697	0	936
Forest Edge	224	160	0	1,948	0	2,332
Willow Scrub	678	102	35	2,232	0	3,047
Willow-Sedge Meadow	13	7	2,545	530	0	3,095
Cattail-Sedge Meadow	3,225	0	299	0	0	3,524
Autumn						
Upland Aspen Forest	62	100	0	60	2,428	2,650
Scrub Poplar-Grassland	332	3,353	0	185	0	3,870
Willow Scrub	123	24	0	53	289	489
Willow-Sedge Meadow	2,695	0	3,093	42	41	5,871
Sedge Meadow	0	0	4,187	0	690	5,097
Grassland-Snowberry	78	1,289	0	188	249	1,804
Winter						
Upland Aspen Forest	2	3	0	97	1	103
Forest Edge	2	7	0	54	1,603	1,666
Poplar Lowland	10	130	0	17	345	502
Willow Scrub	180	16	43	105	0	344
Old Field Succession	5	13	0	45	0	33

[1] Leaf litter was composed primarily of fallen leaves from trembling aspen, balsam poplar, beaked hazel and willow.

Fig. IX.1. Relationship between usable forage biomass and consumption rate (g DM/min) of two free-ranging moose during summer, autumn and winter at the Ministik Wildlife Research Station, Alberta. Open circles represent data from moose no. 211 and closed circles from moose no. 727.


JULY 1983
Y=22.553−20.998 e^{-0.0016x}
SEb=0.0003
r²=0.78
OCTOBER 1983
Y=18.10−18.989 e^{-0.0008x}
SEb=0.0003
r²=0.94
JANUARY 1984
Y=10.589−8.520 e^{-0.0036x}
SEb=0.0006
r²=0.84
30
20
10
0
20
10
0
20
10
0
0
1000
2000
3000
4000
5000
CONSUMPTION RATE (gDM/min)
USABLE BIOMASS (kg/ha)

rates for both mule deer (Deschamp et al. 1979, Collins and Urness 1983, Wickstom et al. 1984) and wapiti (Collins and Urness 1983, Wickstrom et al. 1984, Nietfeld 1983) as might be expected for a larger animal (Clutton-Brock and Harvey 1983).

The slope of the asymptotic regression was highest during winter when animals appeared to forage quite indiscriminantly. With an abundance of available forage in summer, the slope was intermediate. The lowest slope occurred in October when animals were most selective, seeking green foliage and berries from snowberry and gooseberry with a bite size as low as 60 mg. Although specialized, moose have relatively large mouth parts which may constrain their effectiveness when prehending single food items in comparison to smaller selective feeders such as deer.

An alternative expression of the response of animals to changing food availability is the biomass at which intake is reduced to 50% of the asymptotic value. This critical biomass was 500 kg/ha in July, 950 kg/ha in October and 150 kg/ha in January. Values for other browsing herbivores are 244 kg/ha for wapiti selecting mixed diets and perhaps one half this for mule deer (Wickstrom et al. 1984). Better information is available for herbivores using grassland forages. Wapiti reduce consumption rates by 50% at a biomass of between 542 kg/ha (Wickstrom et al. 1984) and 1,200 kg/ha (Hudson and Nietfeld 1985) while mule deer maintain feeding rates on sparse pastures which provide less than 100 kg/ha (Wickstrom et al. 1984).

Bite Rate, Bite Size and Searching Effort

Consumption rates result from the complex interaction of several components. Mean cropping rate, bite size and rate of movement of foraging moose (Table IX.2) varied significantly ($P<0.05$) among seasons as determined by paired t-tests (Steele and Torrie 1980).

Generally, the highest bite rates were observed during summer. Maximum cropping rates of 40 bites/min were recorded while moose fed on hazel foliage in aspen forests. This is somewhat lower than maxima of 50-60 bites/min recorded for other ruminants using grassland forages but similar to their cropping rates in forested and mixed habitats (Wickstrom et al.

Table IX.2. Seasonal changes in mean (±SE) bite rate, bite size and number of steps/bite of free-ranging moose in several selected habitat types from July 1983 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Habitat	Bite Rate (bites/min)	Bite Size (g DM/bite)	Search Effort (steps/bite)
July			
Upland Aspen Forest	24.4 ± 2.0	0.83 ± 0.05	0.17 ± 0.05
Forest Edge	16.3 ± 2.1	1.19 ± 0.07	0.22 ± 0.22
Willow Scrub	17.1 ± 2.5	1.18 ± 0.09	0.13 ± 0.05
Willow-Sedge Meadow	13.8 ± 2.0	1.43 ± 0.27	0.20 ± 0.04
October			
Upland Aspen Forest	12.2 ± 1.0	1.34 ± 0.42	0.26 ± 0.06
Grassland-Snowberry	14.3 ± 1.0	1.12 ± 0.72	0.28 ± 0.08
Willow Scrub	8.8 ± 0.7	0.99 ± 0.57	0.37 ± 0.09
Willow-Sedge Meadow	8.1 ± 0.8	0.46 ± 0.02	0.44 ± 0.11
January			
Upland Aspen Forest	8.3 ± 1.2	0.95 ± 0.05	0.31 ± 0.06
Willow Scrub	8.6 ± 1.1	0.78 ± 0.02	0.32 ± 0.15
Old Field Succession	9.7 ± 1.1	0.54 ± 0.07	0.77 ± 1.12

1984, Hudson and Nietfeld 1985).

Bite sizes ranged from 0.06 g DM/bite for gooseberry leaves during autumn to 4.56 g DM/bite for cattail during summer with a pooled mean of 1.02 ±0.12 g DM/bite. This mean is high in relation to bite sizes of other ruminants but falls within the range of 0.54 -1.74 g DM/bite reported for wapiti consuming browse (Wickstrom et al. 1984).

Rates of movement (search effort) during feeding bouts increased from an average of 3.3±0.4 steps/min during July to 4.3±0.6 steps/min during winter. Extreme rates of travel (15 steps/min) were observed during winter when moose foraged on widely spaced sprout growth, Canada thistle and yarrow (*Achillea millefolium*) in the old field successional sites.

Handling vs Search Components of Foraging

Foraging is often partitioned into search and handling times. Inter-relationships of these variables were explored to determine which may be the most important determinant of feeding rates. In the absence of more direct measurements, we used bite size as a correlate of handling time while steps/bite served as a proxy for search effort.

During July, but not other trials, a significant compensatory relationship ($P<0.001$; $r=-0.75$) existed between bite rates and bite sizes similar to findings for other ruminants (Allden and Whittaker 1970, Collins et al. 1978, Trudell and White 1981, Wickstrom et al. 1984). This relationship was obscured perhaps by changing forage quality and the emerging dominance of the search component when results for all trials were pooled.

On an annual basis (data pooled for all trials), search effort appeared to be a more important component since mean bite rates decreased in a significant ($P<0.01$; $r=-0.80$) curvilinear pattern with increasing search effort (steps/bite). Moose reacted to the seasonal decline in foraging opportunities by moving farther between feeding stations. There are two possible ways to view this relationship. Greater search times may reduce feeding or, low feeding rates may encourage movement of the moose between feeding stations.

D. Conclusions

Compared with smaller herbivores, moose exhibit high consumption rates which are achieved mainly by taking larger bites. Bite rates are comparatively low. Nevertheless, in the face of seasonal changes in forage biomass, structure and homogeneity, moose display considerable adaptability.

In summer, forage was highly digestible and homogeneous, requiring moose to be only moderately selective to achieve an acceptable nutrient intake. During this period, consumption rates were high even when forage biomass fell below 1,000 kg/ha. Moose responded to autumn senescence by feeding more selectively which enabled them to maintain a diet digestibility similar to that of summer (Renecker and Hudson 1985). However, they required relatively high forage biomass to maintain intake rates. During winter, diets were comprised mainly of highly lignified woody stems and leaf litter (see Chapter XI) which offered few opportunities to feed selectively. Although maximum intake rates were low, they were maintained even when forage biomass fell to 500 kg/ha

During summer, free-ranging moose in the aspen boreal forest have little difficulty in meeting their daily forage requirements in <10 hours of foraging. Plant dormancy imposes logistic constraints on foraging behavior. Moose can increase foraging time and feed more selectively as a compensatory strategy during autumn. However, during winter as opportunities for selection decrease and time required for rumination increases, moose must abandon this tactic.

Comparison of the foraging parameters of species that have been studied indicates that, at an equivalent biomass, herbivores generally can forage faster in forested habitats. Large herbivores consume forage faster than smaller ones but require greater forage biomass densities to do so. To meet daily food requirements, larger herbivores must either occupy richer habitats (or at least those with dense forage patches) or reduce selectivity so that a greater proportion of available forage is selected as food.

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X. HABITAT AND FORAGE SELECTION OF FREE-RANGING MOOSE

A. Introduction

Moose utilize areas with a variety of vegetation types in North America (Krefting 1974a, Telfer 1978, Coady 1983). Patterns of habitat use have been described for populations of moose in eastern North America (Chamberlain 1972, Brassard et al. 1974, Krefting 1974b), Minnesota (Berg and Phillips 1974), Riding Mountain National Park in Manitoba (Trottier et al. 1983), montane areas of western North America (Edwards and Ritcey 1956, Houston 1968, Peek 1974, Pierce and Peek 1984) and Alaska (Le Resche et al. 1974). In Alberta, few detailed studies have been conducted which quantify habitat selection and food choice. Barrett (1972) briefly discussed the food habits of moose in the Cypress Hills of Alberta by examination of undigested rumen contents. Nowlin (1978) and Mytton and Keith (1981) reported on the fall to spring habitat selection and/or food habits of moose in north-central Alberta. Cairns (1976) documented seasonal distribution and food habits of moose in Elk Island National Park. However, none of these studies provided detailed information based on direct observation of moose in the aspen-dominated boreal forest zone.

The objectives of this study were to determine the seasonal food habits and habitat use patterns of two free-ranging moose.

B. Methods

The two adult moose used in this study were hand-reared and maintained on a pelleted aspen-concentrate ration (Schwartz et al. 1985) in a 2 ha pasture at the Ministik Wildlife Research Station. The animals were 2.5 years old at the beginning of the study and habituated to human presence.

The animals were released into a 65 ha enclosure every 6-8 weeks from December, 1982 to January, 1984. An average of 4 weeks was allocated for animal adjustment (Chapter VIII, Renecker and Hudson 1985) before observation periods commenced.

Food choice was recorded by an observer during each 24 h observation period. The relative use of each forage species was calculated on the dry weight basis using the bite-count technique described in Chapter VIII. Intake of each food species was presented as a percentage of the daily aggregate intake (Chapter VIII, Renecker and Hudson 1985). The diameters at the point of browsing of several woody species were measured with calipers to the nearest 0.1 mm while observing the moose browsing the plant during winter, spring and autumn.

Habitat use patterns of each moose were determined by continuous time-sampling during single 24-h observation periods. Relative use of habitats occupied by each moose was calculated as a percentage of the aggregate 24-h day. The key habitat types in the 65 ha enclosure, determined by Gates (1980) and Nietfeld (1983), were used in this study.

C. Results

Food Habits

Moose used the 5 major forage categories (Fig. X.1) with shrubs and leaf litter contributing the largest proportion of seasonal diets. Use of forbs was highest during summer and autumn. Willow, balsam poplar, beaked hazel and leaf litter comprised an average of 95±2% of the intake on an annual basis (Tables X.1 and X.2). Use of trembling aspen was highest during January, 1984 comprising over 42% of the dry matter intake. Heavy winter use (>10%[illegible]as also recorded for willow, balsam poplar, beaked hazel and aspen bark.

Diameter at the point of browsing of selected foods increased as winter progressed (Table X.3) to a peak in April. Twigs of balsam poplar and willow measured during January, 1984 were markedly larger than recorded the previous winter as animals reverted to large sprout growth in old field succession sites because of the dense snow crust.

Leaf flush did not occur until early May. Moose began stripping bark from trembling aspen in early April. Consumption of other plants consumed was essentially the same as during winter with leaf litter the main component of the diet. Light snowfalls and minimal crusting

Fig. X.1. Relative use of 5 forage categories by two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

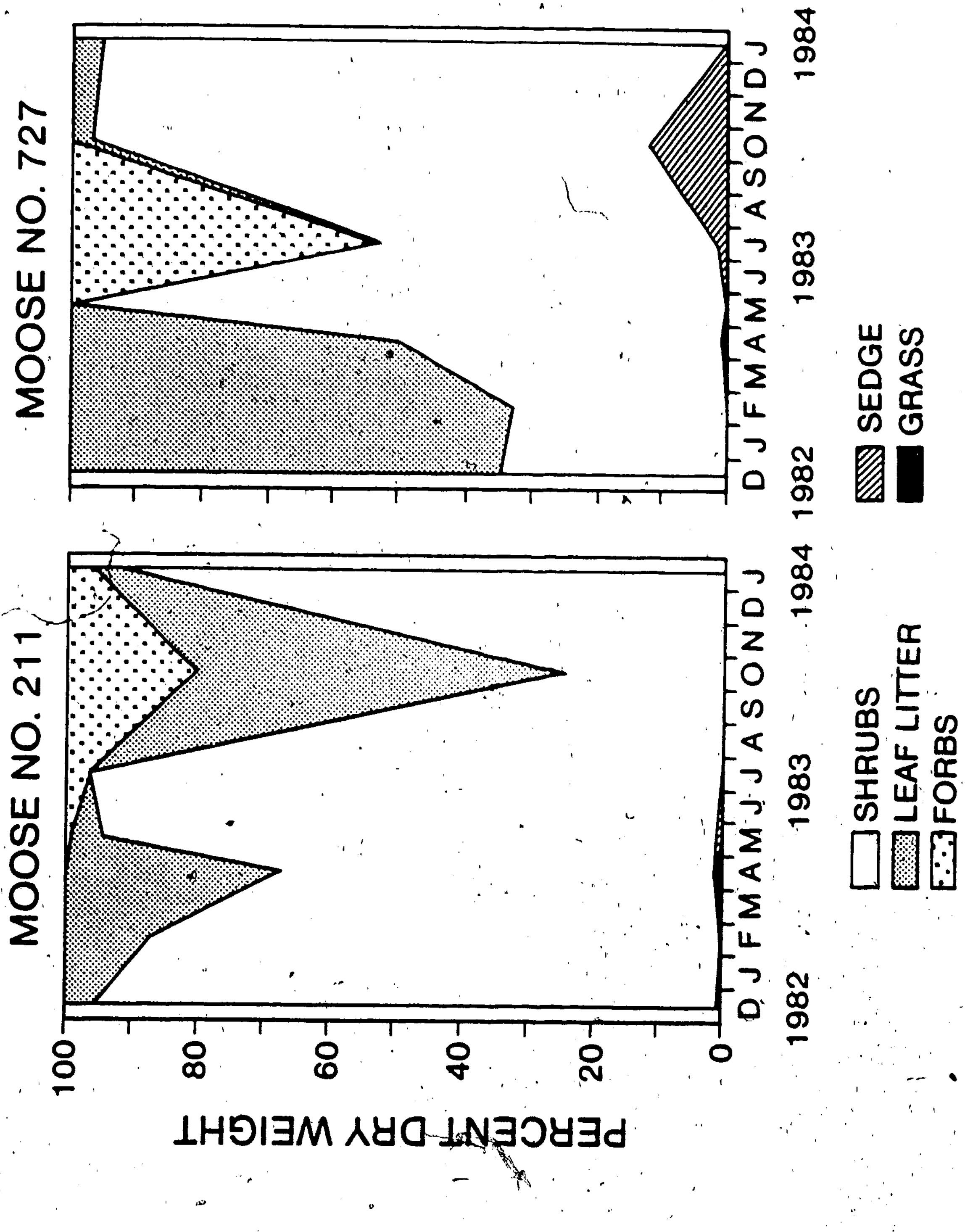

MOOSE NO. 211
MOOSE NO. 727
PERCENT DRY WEIGHT
100
80
60
40
20
0
D J F M A M J J A S O N D J
1982
1983
1984
SHRUBS
LEAF LITTER
FORBS
SEDGE
GRASS

Table X.1. Seasonal variation in the mean percentage, by dry weight, of foods in the diet of free-ranging moose no. 727 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Plant Species	Percentage[1]						
	Dec	Feb	Apr	May	July	Oct	Jan
Shrubs							
Willow	6.9	11.1		1.0	12.0	2.2	3.8
Balsam Poplar	19.5	20.0	7.1	4.8	11.4		6.6
Trembling Aspen	6.1	0.6	0.5	3.1	6.6		42.9
Beaked Hazel	1.6		3.2	68.5	8.8	0.2	14.8
Red-Osier Dogwood		0.6			0.1	0.2	
Rose				2.4	1.2	0.4	
Western Snowberry				15.5	4.8	77.3	
Saskatoon				0.2		0.8	
Chokecherry				3.4			
Soapberry				0.8			
Red Raspberry					1.1	0.9	
Bracted Honeysuckle					1.1	1.1	
White Birch					0.6		
Low Bush Cranberry						1.6	
Gooseberry						0.3	
"Stripped" Bark			38.6		0.2		27.0
Leaf Litter	65.8	67.8	49.8			2.7	4.9
Forbs							
Cattails					46.7		
Stinging Nettle					0.1		
Canada Thistle						0.3	
Sedge				0.1	1.2	11.9	
Grass			0.8			—	

---

[1] Percentage values less than 0.1% were omitted. Percentages calculated as percent of dry weight of forage intake estimated by bite-count technique (Renecker and Hudson 1985).

Table X.2. Seasonal variation in the mean percentage, by dry weight, of foods in the diet of free-ranging moose no. 211 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

	Percentage[1]						
Plant Species	Dec	Feb	Apr	May	July	Oct	Jan
Shrubs							
Willow		58.5		11.1	56.7	8.8	12.7
Balsam Poplar	19.5	26.1	28.2	14.3	14.0	13.0	22.0
Trembling Aspen	5.9			2.1	1.8		53.3
Beaked Hazel	67.8			39.2	18.3		
Red-Osier Dogwood	0.3				0.2	0.2	
Rose				0.8	0.2	0.1	0.1
Western Snowberry				0.3		4.2	0.7
Saskatoon	0.8			1.5	0.7		
Chokecherry				0.6			
Soapberry	0.4	2.6			0.1		
Red Raspberry				12.3	1.8	8.9	0.1
Bracted Honeysuckle				9.4	0.9	0.4	
Twinning Honeysuckel				0.3			
White Birch				0.8	1.3		
Low Bush Cranberry				1.9			
Gooseberry				3.8		1.0	
"Stripped" Bark			38.5				
Leaf Litter	4.3	12.8	32.2			55.6	7.1
Forbs							
Pea Vine				0.6			
[illegible]tails					3.1		
[illegible]e Clover					0.2		
Canada Thistle						19.8	3.0
Yarrow							1.1
Sedge				0.8	0.2		
Grass	0.8		1.1				

[1] Percentage values less than 0.1% were omitted. Percentages calculated as percent of dry weight of forage intake estimated by bite-count technique (Renecker and Hudson 1985).

Table X.3. Mean diameter (±SE) at point of browsing for several browse species consumed by free-ranging moose from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Plant Species	Mean Diameter±SE (mm)				
	Dec	Feb	Apr	Oct	Jan
Balsam Poplar	2.86±0.06	3.09±0.07	3.67±0.08	2.78±0.11	3.42±0.13
Trembling Aspen	2.50±0.13				3.03±0.10
Willow	2.23±0.08	2.44±0.07	3.15±0.18	2.18±0.06	2.75±0.14
Beaked Hazel	2.13±0.04		2.31±0.05	2.10±0.08	2.20±0.09
Saskatoon	2.10±0.09			1.57±0.11	
Red-Osier Dogwood	2.13±0.12	2.17±0.17		1.64±0.08	
Western Snowberry				1.17±0.06	
Low Bush Cranberry				2.43±0.49	
Red Raspberry					2.00±0.03
Soapberry	1.74±0.08	2.55±0.19		1.64±0.12	
Bracted Honeysuckle				2.22±0.21	

permitted moose to crater for fallen leaves.

Foliage was dominant in diets during late spring; beaked hazel accounted for 39-69% of the diet, although willow, balsam poplar and western snowberry were also frequently used. Red raspberry leaves were selected exclusively by moose no. 211 at a level exceeding 19% of the daily intake. The remaining shrub species constituted between 10-11% of the late spring diet. Sedge and grass did not exceed 10% use and the only forb consumed was pea vine.

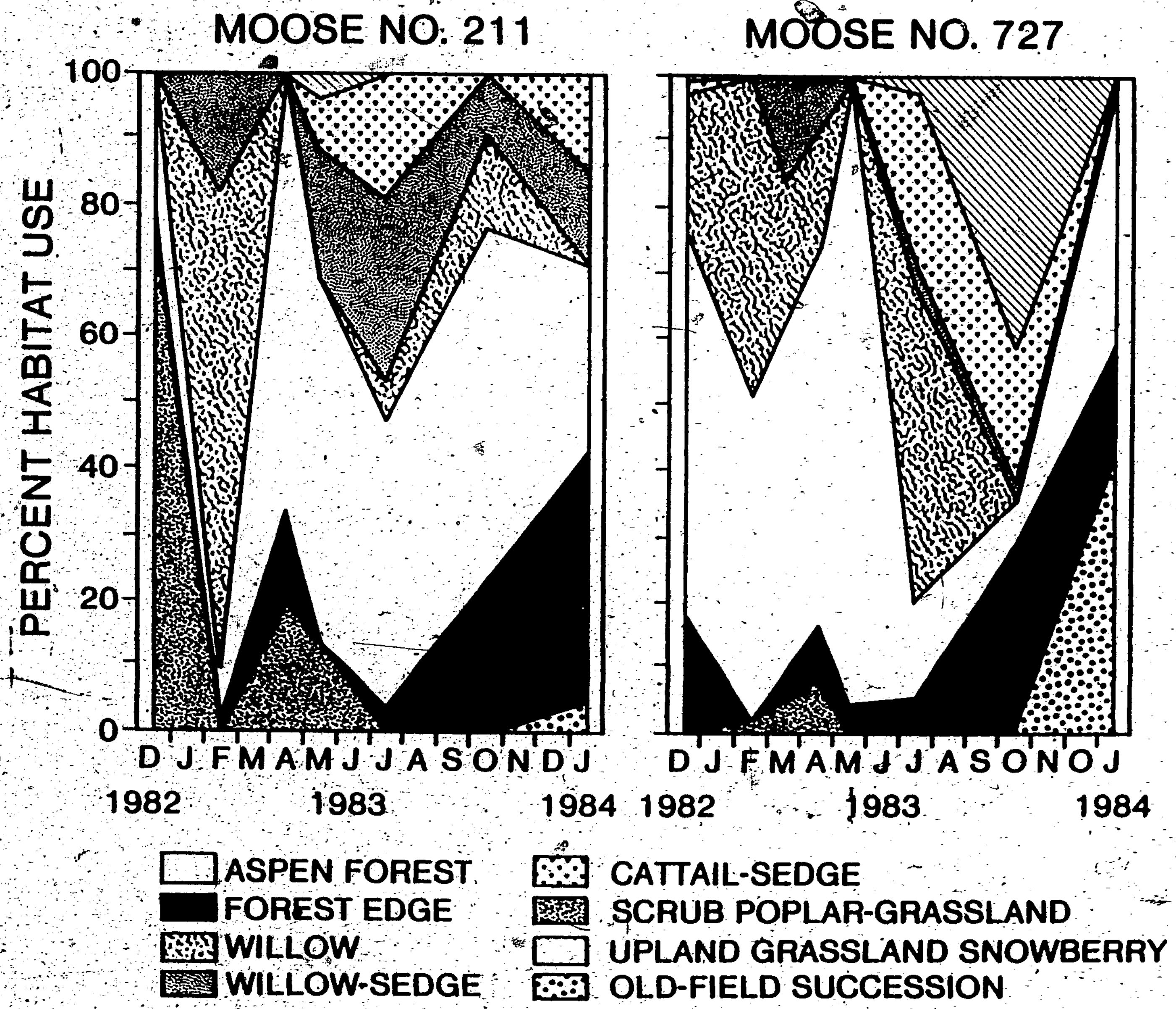
By mid July, willow, balsam poplar and beaked hazel accounted for 9-57% of the diet. Cattails were consumed by breaking the stalk above the root and then slowly consuming the entire plant. On other occasions, animals would only feed on the thickened white portion of the stem below the water level. Sedge (*Carex* spp.) accounted for 0.2-1.2% of the use of this habitat. Stinging nettle (*Urtica gracilis*) and alsike clover (*Trifolium hybridum*) were eaten occasionally.

During autumn, moose foraged selectively on available green plant material. Western snowberry and Canada thistle maintained green growth and were favored by moose. In several cases, moose were observed stripping fruits from snowberry when green leaves were not present. Leaf litter was a dominant food component for animal no. 211 accounting for over 55% of the diet. Fallen leaves during early autumn that remained partially green, had not been subject to leaching and were in high abundance (Chapter VIII and IX, Renecker and Hudson 1985, 1986a). Along with fallen leaves, moose no. 211 selected stems of willow and balsam poplar which amounted to 32.7% of its diet. Sedge was consumed during one feeding bout in an area which supported green plant material.

Habitat Selection

During winter, moose selected habitats which provided canopy cover or were in close proximity to nearby tall shrubs (Fig. X.2). In the second winter, they spent more time in open habitats and the forest edge. A large proportion of this time was allocated to food consumption before bedding under wooded cover. Frequent melt-freeze cycles hardened snow and restricted

Fig. X.2. Relative use of habitats by two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.


MOOSE NO. 211
MOOSE NO. 727
PERCENT HABITAT USE
100
80
60
40
20
0
D J F M A M J J A S O N D J
1982
1983
1984
D J F M A M J J A S O N O J
1982
1983
1984
ASPEN FOREST
FOREST EDGE
WILLOW
WILLOW-SEDGE
CATTAIL-SEDGE
SCRUB POPLAR-GRASSLAND
UPLAND GRASSLAND SNOWBERRY
OLD-FIELD SUCCESSION

access to leaf litter except near dead fall and the base of trees. This probably forced moose into open areas in search of food.

Aspen forest remained the most frequently used habitat during early spring. A striking trend was observed in the high use of open areas such as willow sedge, forest edge and scrub-poplar grassland habitats from mid-winter to April. However, animals returned to the aspen forest to bed.

Use of the aspen forest increased markedly during late spring as animals stripped leaves from shrubs. Utilization of cattail-sedge communities increased into late May. Relative use of cattail-sedge and willow habitats continued to increase into summer. Animals foraged on cattails during the daylight periods when black-globe temperatures exceeded 29°C and insect activity was extreme. These wet meadows were often used as bedding sites since they provided water and higher wind velocities which provided relief from possible heat stress and insect harassment. Variation in habitat selection between individuals was greatest during autumn. Moose no. 211 spent 52% of the time in aspen forest selecting Canada thistle and red raspberry which had not senesced whereas animal no. 727 spent 41% of the day in more open habitat consuming green leaves and fruits of western snowberry. There was also a notable shift to the forest edge and willow areas where woody stems and fallen leaves were consumed.

D. Discussion

Moose exhibited a high preference for use of forested and willow habitats throughout the year. Plant communities most often utilized by moose provided both food and cover. The shrub forage class was most often exploited by moose for available browse throughout the year.

Several studies have identified the contribution of browse to the winter diets of moose in Elk Island National Park in Alberta (Cairns 1976) and Riding Mountain National Park in southwestern Manitoba (Trottier 1981, Trottier et al. 1983). Other studies have reported similar usage patterns of cover types (Telfer 1970, Berg and Phillips 1974, Peek et al. 1976, Eastman 1977, Nowlin 1978, Pierce and Peek 1984) but, relative selection of these areas varies markedly with environmental conditions (Cairns 1976, Peek et al. 1982), availability of food (Telfer 1967) and individual animals (Fig. X-2).

Browse plant species commonly utilized throughout the year are balsam poplar, beaked hazel, trembling aspen and willow. Animals consumed woody stems during winter but, diet expansion and selectivity increased with the presence of leaf growth in late spring and autumn. Trottier (1981) noted the importance of beaked hazel to foraging moose in aspen boreal habitats and it has been identified as a major food item of moose during the winter in Minnesota when forage biomass is reduced (Peek et al. 1976, Trottier et al. 1983). In central North America, Berg and Phillips (1974), Krefting (1974b), Peek (1974) and Zach et al (1982) reported that balsam poplar, trembling aspen and willow are important foods of moose. Although twigs and/or foliage of browse were eaten by moose in each season, diets occasionally comprised a relatively large portion of bark stripped from aspen, balsam poplar and willow, fallen leaves and forbs. Contrary to these findings, Murie (1934) concluded that stripping bark from trees by moose is an indicator of low forage availability. Other studies have noted the seasonal use of bark (Peterson 1981, D. Miquelle pers. comm., K. Risenhoover pers. comm.) which may be more closely related to diet quality (Chapter VIII, Renecker and Hudson 1985). Often studies have not reported extensive use of leaf litter by moose during autumn, winter and spring.

Extreme heat and insect harasssment encouraged animals to feed in open, aquatic habitat types. Under these circumstances, moose probably discriminate between resources on the basis of forage availability and quality, insect activity and high ambient temperatures.

Food Availability

Plant availability is undoubtedly one of the most important factors affecting forage selectivity. Snow is of paramount importance in the winter distribution of moose (Formosov 1946, Telfer 1970, Kelsall and Prescott 1971) and greatly reduces the availability of forage biomass (Telfer and Scotter 1975). Large selective feeders, such as moose, have mouth parts suited for acquisition of concentrated sources of nutrients.

However, leaf abscission and snow accumulations reduce forage biomass (Chapter IX, Renecker and Hudson 1986a) and result in less selection of food. Investigations have demonstrated the importance of leaf litter as seasonal forage for wapiti (Gates 1980, Nietfeld 1983) and quantified the large biomass it provides during autumn and winter (Chapter IX, Renecker and Hudson 1986a). Therefore, it is not unexpected that moose may attempt to utilize this resource to meet daily nutrient requirements.

Telfer (1967) regarded the presence of moose in aspen forest and willow habitat as a response to availability of food. Several studies in central Alberta have also reported heavy use of poplar and mixed poplar cover types for both feeding and non-feeding activities (Nowlin 1976, Penner 1981). Autumn, winter and spring diets of moose were composed of a large percentage of fallen leaves obtained under aspen and poplar forests. Feeding activities and habitat use patterns only changed when melt-freeze cycles formed snow crusts (Chapter VIII, Renecker and Hudson 1985) reducing accessiblity of leaf litter biomass (Chapter IX, Renecker and Hudson 1986a). Distances travelled by moose during feeding bouts were markedly reduced when animals ate this material (Chapter XI). Although the crude protein content of fallen leaves decreased with the occurrence of leaching from autumn precipitation and spring thaws, digestibility remained higher than for woody stems (Renecker and Hudson 1985). Moose cratered readily through powdery snow 25cm deep to consume leaf litter. Thus, the importance of fallen leaves in the autumn and winter diet of moose may be noteworthy because the availability of this material may provide more digestible nutrients than woody twigs, while reducing travel costs between food patches.

Plant Quality

Forage selection is likely related to seasonal changes in quality of the food supply. Moose showed seasonal patterns in selection for food items such as bark, leaf litter and forbs. Other studies have indicated that, during the spring nutrient flush, the digestibility of bark was extremely high (Chapter VIII, Renecker and Hudson 1985) probably as a result of cell solubles throughout the bark cambium (Chapin 1980). Similarly, in central British Columbia, Cowan et al. (1950) reported higher levels of crude protein in the bark of trembling aspen than in woody twigs. These facts help explain the high percentage of bark in the diet and indicate that it may improve diet quality prior to leaf flush because of high levels of digestible nutrients.

Quality of forage is also an important factor in the choice of autumn foods by moose. Areas protected from early frost supported green, succulent forage such as western snowberry, Canada thistle, red raspberry and gooseberry. Hanley (1982) reported that cell solubles are the most valuable nutrient source of herbivores. The ability of moose to exercise selective feeding and diet diversity, during autumn, indicates the efficiency of the animal to choose more digestible material (Trottier et al. 1983). Dietary mixing of fallen leaves, highly digestible green growth and twigs from selective foraging in combination with lower autumn energy expenditures would enable moose to maintain a higher intake of nutrients (Chapter VIII; Renecker and Hudson 1985) and extend the period of tissue anabolism.

Effect of Insect Activity and Heat on Diet and Habitat

Use of open wetland communities coincided with extreme heat and insect activity. Low tolerance levels of moose to high ambient temperatures is paramount in seasonal energy budgets (Chapter XII), as it can result in refusal of feed and static body weights (Chapter V, Renecker and Hudson 1986b). Standing or lying in sedge meadows or cattail stands probably reduced thermal stress (Chapter XII) and annoyance due to large numbers of mosquitoes (*Culicidae* spp.). This choice of wetland habitats as a temperature control mechanism in moose has been reported previously by Flook (1959) and Kelsall and Telfer (1974). Wapiti have demonstrated similar behavior during the summer season (Gates and Hudson 1981). Moose are highly susceptible to heat stress at relatively low ambient temperatures in contrast to many ungulates (Chapter V, Renecker and Hudson 1986b) which may explain the close association reported between wetland communities and moose in previous studies.

Consumption of cattails in wetland habitats probably reflects a response by the animals to maintain rumen fill while ameliorating the effects of extreme heat and insect harassment during summer. Although cattails were lower in digestibility and crude protein and higher in dietary fiber content than leaves of shrubs during summer (Chapter III), the thermal advantages of the cool water may have enabled moose to feed longer and thereby minimize weight loss (Chapter V, Renecker and Hudson 1986b).

Moose used grassland snowberry and forest edge habitats more than expected during autumn. Most activities in these areas were carried out during the night when animals were less subject to high levels of solar radiation and black globe temperatures ≤20°C. Nevertheless, the use of these communities in relation to forested areas probably reflects the selection of specific foods preferred by moose.

Although selection of habitats was primarily a response to both food resources and security needs, the modified meterological conditions under closed canopy forests would reduce thermal stress. Shade provided by poplar and aspen cover types during late spring is probably attractive during periods of higher ambient temperatures when insect activity is low and accounts for large portions of the diurnal period spent bedded in these habitats in late spring. Similarly, the advantage of canopy cover to moose in winter probably translates into energy conservation as indicated by higher black globe temperatures recorded under forest cover. However, benefits of these habitat options would only become prominent factors during severe winters, since moose have been shown to be extremely cold tolerant (Renecker et al. 1978). Although moose do not have any natural predators in this area of the aspen-dominated boreal forest, these animals were alert to noises and tactically selected bed sites at the base of a tree or clumps of shrubs, as a defense strategy.

E. Conclusions

The moose is a selective browser. Although the staple winter foods consist of woody twigs, moose will consume large amounts of leaf litter and bark under some environmental conditions. During spring, moose depended heavily on bark from trees which was highly digestible. Choice of habitats during spring and summer was to maximize the intake of food and to mitigate thermal imbalances through altered behavioral patterns and habitat use. Moose foraged most selectively during autumn when variation in forage quality was greatest.

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XI. SEASONAL ACTIVITY PATTERNS OF FREE-RANGING MOOSE

A. Introduction

Wild ruminants spend a large part of each day either feeding or resting/ruminating while other behavioral categories (grooming, travel, security and social disturbance) occupy surprisingly little time. Time spent in these activities (particularly feeding and ruminating) shows marked diel and seasonal variations (Dulphy et al. 1980). The challenge is to determine the adaptiveness of these patterns.

Activity budgets have now been documented for a number of northern ruminants including red deer (Georgii 1981), roe deer (Turner 1979, Cederlund 1981), muskox (Jingfors 1982), reindeer (Eriksson et al. 1981, Skogland 1984), wapiti (Gates and Hudson 1983) and white-tailed deer (Jacobsen 1973, Moen 1978). Activity budgets previously reported for moose are limited to specific seasons (Belovsky and Jordan 1978, Best et al. 1978, Risenhoover 1986).

Among ruminants, moose are particularly interesting since, being large browsers, they should have relatively long foraging times (Lewis 1977) but, since the rumen is small and rate of passage high, bouts should be more frequent but shorter than in other ruminants. The objective of this study was to evaluate these predictions of daily and seasonal activity patterns. Preliminary results of the December trial were presented by Renecker and Hudson (1983). This chapter presents data collected during 7 diel activity scan periods over a 13 month period.

B. Methods

Two hand-reared moose cows (No. 727; No. 211) were maintained within a 2 ha pasture on a pelleted aspen-concentrate ration (Schwartz et al. 1985) supplemented with hand-cut browse. Body weights of the moose ranged from 262 to 387 kg during the period of observation. Animals were 2.5 years old at the beginning of the study and were habituated to human presence.

The animals were released into a 65 ha enclosure for 7 periods between December, 1982 and January, 1984 to monitor daily activity. They were allowed an average of 4 weeks for digestive and spatial adjustment to natural forage before each trial.

Activity of each animal was monitored once by continuous time-sampling during 24-hr periods every 6-8 weeks. This method was selected because of difficulties with time-sampling techniques (Jacobsen and Wiggins 1982). Activities of individual moose were categorized as feeding, bedded-ruminating, bedded-other and miscellaneous. Feeding activity was further classified as grazing (forbs or graminoids), feeding on leaf litter (cratering), browsing low (below the brisket level), browsing middle (between brisket and topline of the moose), browsing high (above topline) and feeding on bark (stripping) as described in Chapter VII (Renecker and Hudson 1985). Subclasses of the bedded-other category included dozing, ruminating, alert, grooming, eating or insect harassment. Miscellaneous activities included standing, standing alert, standing ruminating, grooming, walking, running and insect harassment.

During each 24-hr observation period, ambient temperature, blackglobe temperature as described in Chapter V (Renecker and Hudson 1986a), wind velocity, precipitation and cloud cover were recorded.

C. Results

Seasonal Activity Budgets

Patterns of major activities were similar between the two moose, but varied significantly ($P<0.05$) among seasons (Fig. XI.1). In winter and early spring, both animals spent more than half (53.9±0.5%) of their time bedded. Most of this time was spent ruminating with a smaller percentage allocated to dozing (Tables XI.1 and XI.2). Feeding times averaged 40% on an annual basis.

Fig. XI.1. Seasonal change in the proportion of time spent in major activities by two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

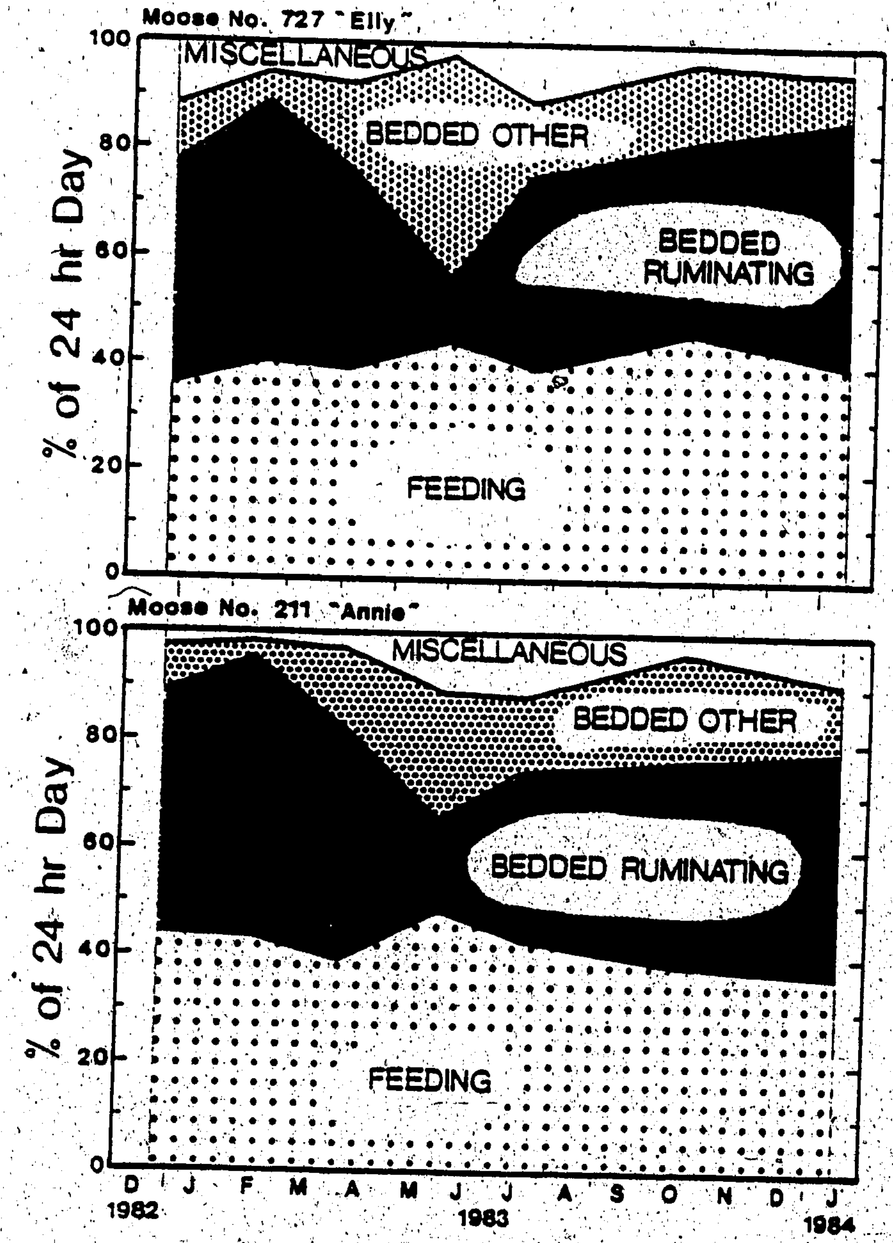

Moose No. 727 "Elly"
100
80
60
40
20
0
% of 24 hr Day
MISCELLANEOUS
BEDDED OTHER
BEDDED RUMINATING
FEEDING
Moose No. 211 "Annie"
100
80
60
40
20
0
% of 24 hr Day
MISCELLANEOUS
BEDDED OTHER
BEDDED RUMINATING
FEEDING
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1982
1983
1984

Table XI.1. Percentage of 24-hour day allocated to different activities by moose no. 727 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Percentage of Day						
	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	6.83	4.02	8.48	38.33	11.14	9.84	6.18
Ruminating	41.42	48.64	37.60	11.67	35.86	35.49	46.62
Alert	0.92	1.73	4.61	1.67	2.15	3.55	1.29
Grooming				0.83		1.0	
Other	3.08		2.12	0.04	0.38	0.05	1.32
Feeding							
Stripping Bark			17.24		0.13		8.77
Cratering	19.83	23.25	9.91			0.44	1.21
Grazing				0.03	17.78	2.35	
Low	9.04	9.88	2.96	8.75	6.73	39.99	16.77
Middle	7.17	6.60	5.49	35.0	11.97	3.90	12.79
High	1.54	0.85	3.73	0.83	3.06	0.05	0.79
Miscellaneous							
Stand-Standing Alert	5.09	2.95	3.27	0.67	1.55	1.77	1.63
Stand-Ruminating		0.20			1.32		0.07
Stand-Grooming							0.20
Drinking-Eating Snow			0.49	0.42	0.24	0.26	0.17
Walking	4.33	1.99	4.03	1.25	7.34	1.32	2.05
Running				0.01	0.27		0.13
Other				0.21			1.04

Table XI.2. Percentage of 24-hour day allocated to different activities by moose no. 211 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

	Percentage of Day						
Activity	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	6.04	2.66	10.99	18.37	12.21	15.61	8.07
Ruminating	44.54	52.14	43.94	17.71	31.63	38.07	41.54
Alert	2.0	0.11	2.27	5.17	1.17	3.02	3.82
Grooming						0.19	0.003
Other		0.11	0.64	0.04	0.28	1.63	1.45
Feeding							
Stripping Bark			13.76				
Cratering	1.08	4.43	9.90			14.37	2.15
Grazing					1.78		
Low	17.75	13.85	1.83	17.71	18.42	13.36	26.36
Middle	25.25	25.16	11.71	28.67	17.77	9.52	4.45
High	0.79	0.20	2.18	1.71	4.99	1.25	3.96
Miscellaneous							
Stand-Standing Alert	1.96	0.49	1.43	3.09	2.80	2.06	3.66
Stand-Ruminating		0.28		0.04	0.14		0.02
Stand-Grooming				0.17	0.11	0.15	0.03
Drinking-Eating Snow			0.27	0.50	0.21	0.25	0.14
Walking	0.29	0.56	0.96	6.50	8.16	0.55	3.77
Running				0.31	0.26		0.16
Other							1.21

Feeding Times and Movements

Moose increased time spent foraging in late spring from an average high of 10.1±0.4 hr/d in February to 11.1±0.4 hr/d in late May. Daily feeding times decreased during July to an average of 9.9±0.4 hr. With autumn senescence of plant material, moose were more selective and searched for succulent green foliage which resulted in a 1.7 hr increase in feeding time for animal no. 727 over values observed during summer, whereas a 1.1 hr decrease was observed for moose no. 211. Time spent feeding decreased to 9.3±0.4 hr in January as snow conditions made foraging more difficult.

Use of forage categories changed over the seasonal cycle. Winter feeding times were divided between browsing on woody stems and cratering for fallen leaves under the snowpack. In early spring, moose spent more time "stripping" bark from trembling aspen and balsam poplar. When food was abundant and of high quality in late spring and summer, moose foraged in the low and middle height categories stripping leaves from shrubs. However, more time during summer was spent grazing aquatic plants. Both moose (particularly no. 211) selected fallen leaves in October as the main food item. Feeding activities in January differed from the subsequent winter because the dense snow crust prevented access to leaf litter resulting in moose spending more time browsing low. Also, moose no. 727 spent 2.1 hr stripping bark from trembling aspen trees.

Total daily distances travelled were highest during summer (Table XI.3) when harassment from mosquitoes was high and animals moved greater distances between feeding sites. Average distance travelled was reduced to 1,494±252 m during winter from 6,452±942 m during summer. However, distances increased during January, 1984 when the moose abandoned cratering for leaves to search for browse.

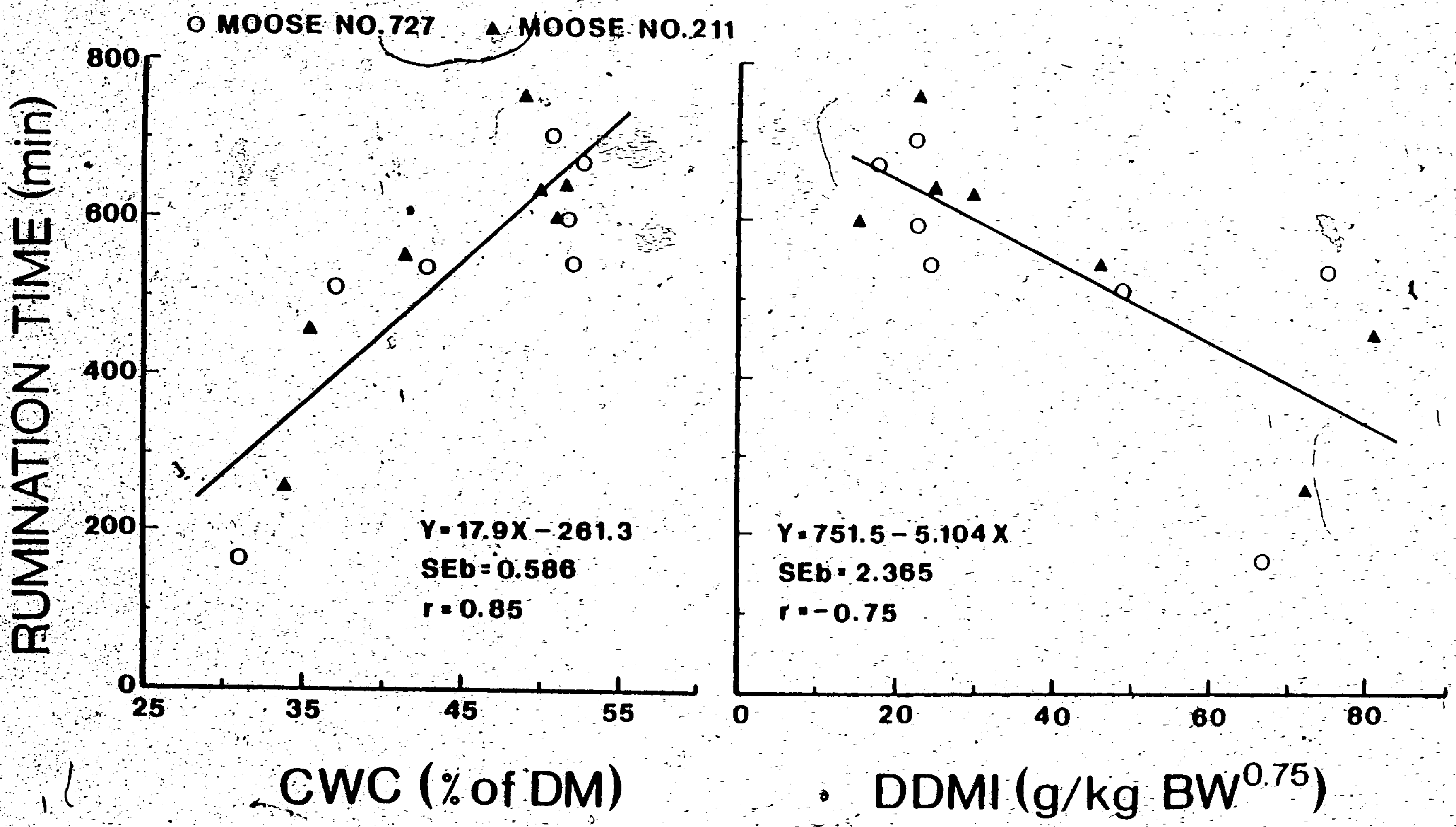
Rumination Time

Time spent ruminating was positively correlated ($P<0.001$) with dietary cell wall constituents (neutral detergent fiber) in the diet and inversely related ($P<0.01$) with digestible dry matter intake (Fig. XI.2) (data on cell wall constituents and digestible dry

Table XI.3. Distance travelled by two free-ranging moose cows during 24-hour periods from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

	Distance (m)						
Animal No.	Dec	Feb	Apr	May	July	Oct	Jan
727	2065	1682	2239	1283	7391	1760	3391
211	1378	728	870	5283	5513	2052	3891

Fig. XI.2. Regression of seasonal change in time spent ruminating on cell wall constituents (CWC) in the diet dry matter and digestible dry matter intake (DDMI) (Renecker and Hudson 1985) of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.


○ MOOSE NO.727
▲ MOOSE NO.211
RUMINATION TIME (min)
800
600
400
200
0
25
35
45
55
CWC (% of DM)
Y = 17.9X − 261.3
SEb = 0.586
r = 0.85
0
20
40
60
80
DDMI (g/kg BW^0.75)
Y = 751.5 − 5.104 X
SEb = 2.365
r = −0.75

matter intake were obtained from Chapter VIII). Ratios of rumination time/unit of cell wall constituents were highest during mid-winter reaching a mean (±SE) of 0.25±0.01 when lignin content of woody stems was highest (Chapter IX, Renecker and Hudson 1986b). With the occurrence of nutrient flush in early spring, values (rumination time/unit of cell wall constituents) decreased steadily to seasonal minima of 0.09 and 0.13 during late May when succulent forage was abundant. Ratios increased simultaneously with increased dietary cell wall proportions and higher voluntary intakes by mid-summer (0.21±0.01). As fibrosity of the diet increased in winter, rumination times increased with a corresponding decrease in daily intake.

Moose altered their rate of chewing, which ranged from 24 to 107 chews/min, with changes in diet quality and intake. The highest mean rate of chewing was observed during winter (72±4 chews/min) and mid-summer (81±4 chews/min) concomitantly with a high level of dietary fiber and intake, respectively. Similarly, the number of chews/regurgitated bolus and the time spent chewing each bolus was greater during winter (133±0.6 chews/bolus; 129±17 sec/bolus) than summer (78±4 chews/bolus; 56±6 sec/bolus). The lowest rates of chewing during rumination were recorded during late May (62±0.2 chews/min; 66±0.3 chews/bolus) when forage was succulent. Moose were highly selective when foraging during autumn and maintained a low chewing rate (58±0.9 chews/min), however the effort/bolus (83±11 chews/bolus) and time/bolus (81±10 sec/bolus) increased from summer with maturation of browse species.

Chewing intensity varied markedly within a period of rumination. Generally, chewing rates were highest at the commencement of a bout decreasing as the animal entered a dozing period. Range of chewing rates during bouts were greatest during autumn and winter (77 to 65 chews/min) and least during late spring (59 to 57 chews/min) and summer (82 to 76 chews/min).

Diel (24-hr) Activity Patterns

Daily cycles of feeding and bedding followed a polyphasic pattern with 4-7 cycles during a 24-hr period (Fig. XI.3). During winter, spring and autumn, feeding was generally crepuscular, being concentrated around sunrise and sunset. However, the precise timing shifted with season and daylength. Nocturnal feeding was more prevalent during late spring and summer. However, this probably reflects the short period of darkness and cooler ambient temperatures.

When feeding on fibrous forage, moose increased the duration of rumination bouts ($P<0.001$) and decreased the length of feeding bouts ($P<0.05$) (Fig. XI.4). The duration of feeding bouts ranged from 87 to 161 min with a mean (±SE) of 107±5 min. Generally, the longest bouts were recorded during late May when insect harassment was minimal and forage quality high (Table XI.4). During July, moose shortened feeding bouts to 92±3 min. Other factors such as heat and insects appeared to influence behavior during July, as suggested by the high mean value of 27±1 min/bout recorded for other activities (such as walking, running and standing in water).

D. Discussion

Seasonal Adaptation

What Regulates Feeding Times?

Feeding times (hrs/d) are expected to increase when requirements for energy and nutrients are high or when forage supplies are sparse. However, rumination time appears to increase at the expense of feeding time when forages are of low quality. Compared with other herbivores, forage intakes of ruminants (especially selective feeders) are strongly dictated by digestibility and passage rate of the diet (Foose 1983). Therefore, there is a complex seasonal interaction between forage availability and quality, photoperiod and animal requirements. To a large degree, seasonal changes in time spent feeding, resting and

Fig. XI.3. Seasonal change in the proportion of time spent in major activities by two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta. The solid line (closed circle = % of hr active) represents percent of time spent active during a hr interval while the dotted line (open circle = % of time feeding) the percent of active time spent feeding. Arrows indicate sunrise (upwards) and sunset (downwards).

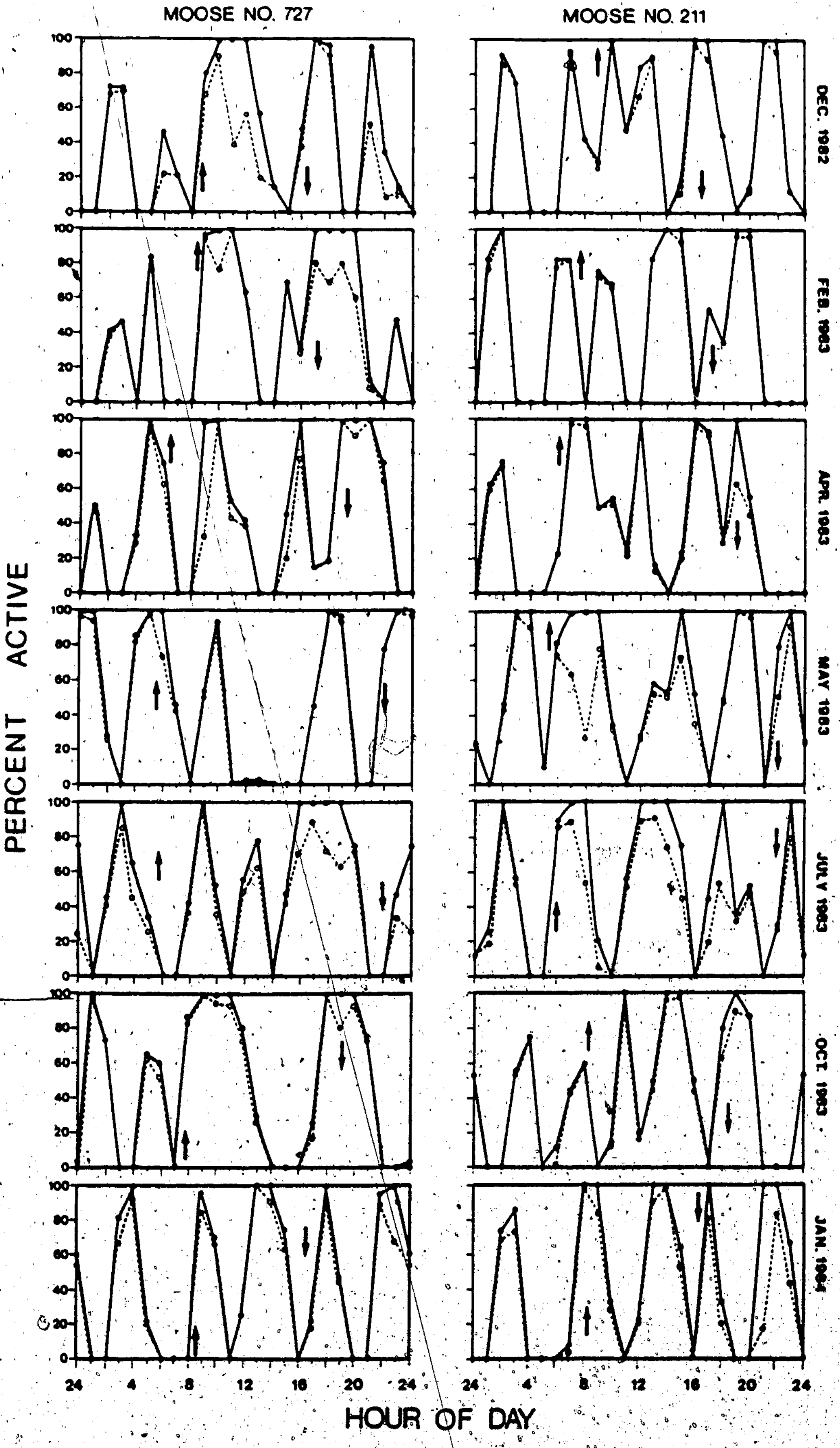

MOOSE NO. 727
MOOSE NO. 211
PERCENT ACTIVE
100
80
60
40
20
0
DEC. 1962
FEB. 1963
APR. 1963
MAY 1963
JULY 1963
OCT. 1963
JAN. 1964
24
4
8
12
16
20
24
HOUR OF DAY

Fig. XI.4. Relationship between cell wall constituents (CWC) in the diet (Renecker and Hudson 1985) and either mean length of rumination or feeding periods in two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

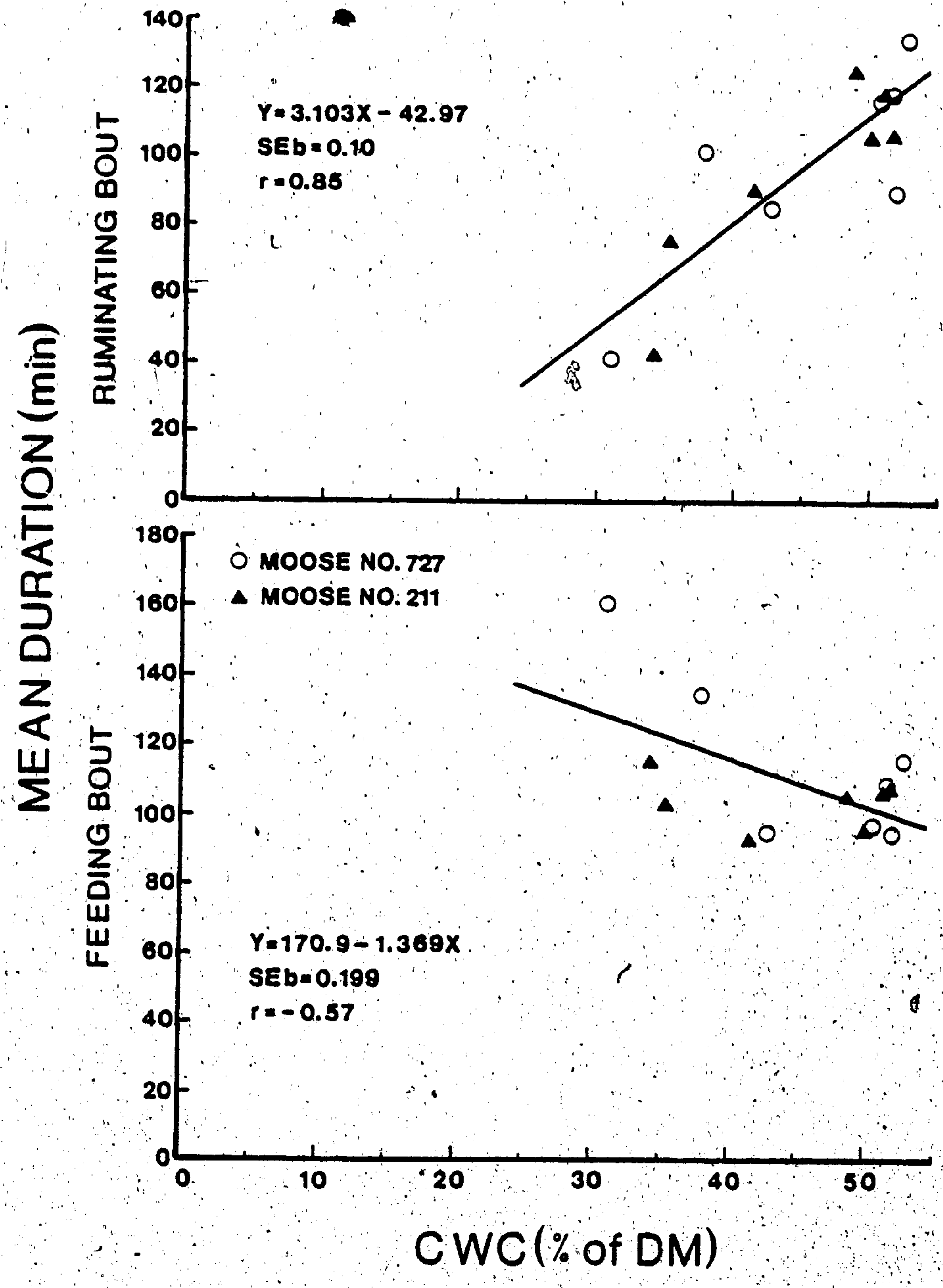

MEAN DURATION (min)
RUMINATING BOUT
Y=3.103X − 42.97
SEb=0.10
r=0.85
FEEDING BOUT
○ MOOSE NO. 727
▲ MOOSE NO. 211
Y=170.9 − 1.369X
SEb=0.199
r=−0.57
0
20
40
60
80
100
120
140
160
180
0
10
20
30
40
50
CWC (% of DM)

Table XI.4. Seasonal changes in daily duration of foraging and resting bouts of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Mean Time±SE (min/bout)						
	Dec	Feb	Apr.	May	July	Oct	Jan
Moose No. 727							
Foraging	97±31	97±32	94±30	161±33	95±33	135±47	105±7
Bedded	162±19	130±23	127±17	190±67	119±24	144±44	157±19
Moose No. 211							
Foraging	108±10	105±18	94±18	114±17	87±26	92±21	104±17
Bedded	126±25	130±30	147±42	99±16	109±16	141±17	157±26

ruminating by moose can be explained on this basis.

The ultimate constraint on feeding time is its preemption by the need to ruminate. Rumination times are determined largely by total cell wall intake since food particles must be reduced in size before they can pass from the rumen. Studies of moose suggest that, during winter, moose submit to the constraints of long ruminal retention times of woody stems and the highest rumination to feeding ratio. However, as dietary quality increased they selected highly digestible plant parts and propelled larger fragments through the gastrointestinal tract (Chapter VI) which resulted in a reduced requirement for particle size breakdown. Short rumination periods in late spring reflect the high dietary quality, digestibility and cell solubles of forage (Chapter VIII, Renecker and Hudson 1985).

Moose foraged longer in late spring as the relative rumination requirement decreased. Similar seasonal trends have been reported for muskox (Jingfors 1982) and impala (*Aepyceros melampus*) (Jarman and Jarman 1973). Shorter feeding times during July may have resulted from the increasing stage of growth of browse in addition to the greater proportion of cattails in summer diets which contained a higher fiber content (Chapter VIII, Renecker and Hudson 1985). Under favorable conditions during this period, moose can attain feeding rates as high as 23 g/min which reduces time required to achieve gut fill (Chapter IX, Renecker and Hudson 1986b). With autumn senescence, one moose travelled further in search of succulent green foliage (Chapter IX, Renecker and Hudson 1986b) and this increased total foraging times, but resulted in a lower rumination to feeding ratio than during summer. The other animal allocated considerable time towards cratering which may have spared additional time for bedded-dozing activity.

Perhaps the most interesting question is why moose did not show greater seasonal differences in feeding times in spite of wide variations in forage quality and availability. One reason may be that moose use additional free-time to forage more selectively.

Duration and Periodicity of Feeding and Resting Bouts

Feeding bouts of undisturbed animals in thermoneutral environments should be longer when forage availability is low or opportunities for selective feeding are high. The duration of rumination bouts are related to the fibrosity of forage (Balch 1971, Murphy et al. 1983). The relative lengths of these bouts should, in turn, dictate the frequency of diel activity cycles. However, this is complicated by thermal stress which influences timing within the 24-hr cycle.

Results of this study conformed to these expectations. Foraging bouts were shortest when foraging efficiency was high (summer) and when forage quality was low (winter). The longest bouts occurred in spring and autumn when forage was moderately digestible but widely distributed. Rumination generally occurred during bedded periods as active time was either spent searching or eating food. However, these changes in duration of foraging and resting bouts did not change the frequency of activity cycles which remained at about 5 feeding/resting cycles per day.

Perhaps as a direct consequence of daylight or associated thermal conditions, not all feeding bouts were of equal length. The occurrence of major (longest) foraging bouts appeared to shift with season. Nocturnal feeding was more prevalent during late spring and summer, as have been reported for Dall's sheep (*Ovis dalli*) (Hoefs and McTaggart Cowan 1979) and wapiti (Gates 1980).

Comparison With Other Species

Like other ruminants studied, moose divided their time approximately equally between feeding and resting/ruminating. Because large herbivores have high absolute forage requirements and browsers generally must forage longer than grazers (lag time spent searching for food), moose might be expected to spend more time foraging than other wild ruminants. However, results of this study showed little departure from data available for other temperate species.

However, closer comparisons with wapiti in the same study area (Gates 1980) indicate some differences. Wapiti varied more; they spent more time feeding in winter (55%) and less in summer (35%). Moose spent about 40% of the time feeding throughout the annual cycle. Part of the reason may be the high asymptotic foraging rate of moose relative to other species and the fact that availability of their main winter forage (browse) is less affected by snow cover than forages used by wapiti. If extreme winter snow conditions limit food supply, then depressions in feeding time may occur (Craighead et al. 1973). In summer, biomass and nutritional quality of forage increased concurrently with foraging efficiency which were higher than maxima reported for wapiti (Wickstrom et al. 1984, Hudson and Nietfeld 1985) and mule deer (Wickstrom et al. 1984) (Chapter IX, Renecker and Hudson 1986b). During the snow free period, moose appear to use additional free time (made possible by their high foraging rate) to forage more selectively.

Average durations of activity and bedded cycles of moose appear to be intermediate among values reported for other wild ruminants. Short (ie. 56 min) but frequent cycles (11 per day) during the winter period have been reported for small ungulates such as roe deer (Cederlund 1981), white-tailed deer (Moulton 1967) and mule deer (Carpenter 1976) which have a smaller body size and digestive capacity than moose while upper extremes have been reported for muskox (Jingfors 1982). However, when forage quality is high during mid summer, the duration of active and resting periods of moose is similar to that of other large ruminants (Jingfors 1982). It is likely that this seasonal change could be an adjustment to forage quality (Chapter VIII, Renecker and Hudson 1985), rapid particle size breakdown and rate of passage of digesta, environmental heat stress (Chapter V, Renecker and Hudson 1986a) and insect activity (Gates 1980).

Among moose and wapiti (Gates 1980) using the same area, moose tended to bed for shorter periods than wapiti during winter and summer however, only the length of winter feeding bouts was different. Insect activity during the nocturnal portion of summer days undoubtedly influenced resting times. However, moose found it difficult to compensate for higher energetic costs of thermoregulation and movement (Chapter V, Renecker and Hudson 1986a) from insects as illustrated by reduced weight gains in mid-summer (Chapter V, Renecker and Hudson 1986a). Differences between moose and wapiti (Gates 1980) in length of winter feeding and resting bouts can probably be explained as a result of diet selection. A menu of browse and leaf litter consumed by moose may require a different rumination time than foods selected by wapiti (Nietfeld 1983). It is therefore likely that differences in feeding and digestive strategies explain winter differences.

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XII. TIME-ENERGY BUDGETS OF FREE-RANGING MOOSE

A. Introduction

Ecological metabolism, defined as total energy expenditures of free ranging animals (Moen 1973), may represent a specific adaptation of ungulates to seasonally fluctuating environments. Energy budgets may provide a meaningful interpretation of how large ruminants optimize behavioral patterns to ameliorate seasonal hardships and capitalize on environmental opportunities.

In spite of the importance of this parameter, few studies have overcome the technical difficulties of making such measurements. Overall energy expenditures can be measured with labelled bicarbonate (Young and McEwan 1975) or doubly-labelled water (Nagy and Costa 1980), but these methods do not partition expenditures by specific activities. A potentially more useful approach is to sum the products of time engaged in various activities and simultaneous rates of energy expenditure (Lund 1979). Heart rate has shown promise for estimating energy expenditures of undisturbed animals and Renecker and Hudson (1983, 1985) have found satisfactory relationships between heart rate and metabolic rate of moose. In this paper, this technique was applied to estimate seasonal energy expenditures of tame free-ranging moose cows. A preliminary report was published by Renecker and Hudson (1983) on partial data. Here, analysis of energy allocations is presented over a complete annual cycle.

B. Methods and Materials

Two hand-reared moose cows (Nos. 211 and 727) were maintained in a 2 ha enclosure on a pelleted aspen-concentrate ration (Schwartz et al. 1985). The animals weighed an average of 320 ±5 kg, were 2.5 years old at the beginning of the study and were conditioned to human presence.

They were released into a 65 ha enclosure every 6-8 weeks to monitor heart rate and behavior. Animals were given an average period of 4 weeks for digestive adjustment to the natural forage and behavioral adjustment to the habitats prior to each scan. Activity budgets for these animals have been reported in Chapter XI.

Heart Rate Telemetry

Heart rate was transmitted from a transmitter implanted in each moose (Model HR13, Wyoming Biotelemetry, Inc.) following the methods in Chapter IV, to a transceiver neck collar (Model RRF-3, Wyoming Biotelemetry, Inc.) which relayed the signal to a central laboratory. The transmitters were tuned to frequencies between 150.800 and 151.880 MHz. A modified identification neck collar (Freddy 1977) maintained the external repeater collar in close proximity to the implant (Chapter IV, Renecker and Hudson 1985).

The telemetered signals were monitored with a receiver (TRX-48A, Wildlife Materials, Inc.), a digital data processor (TDP-2, Telonics) and a pulse-period to pulse rate converter (J. Cupal Consulting Engineer) installed in a dual channel recorder (TDR-1, Telonics) which generated a moving average of heart rate over 2, 4 or 8 heart rate pulses. The performance of this telemetry system has been discussed in detail in Chapter IV.

The two moose cows, equipped with repeater-type heart rate transmitters, were released into the 65 ha enclosure. Each animal was monitored for a 24-hr period every 6-8 weeks. While on pasture, heart rate was sampled for at least 10 minutes during each behavioral category, when possible, using a strip-chart recording and from visual sampling of interpulse periods from the digital data processor. Heart rates for specific activities were averaged over each 24-hour period and then normalized to body weight-$^{0.25}$ (Brody 1945).

Energy Expenditures

Energy expenditures during specific activities were computed using regression equations developed in other sections of this study (Chapter IV, Renecker and Hudson 1985). Daily energy budgets for each trial were derived from an estimate of the rate of energy expenditure (EE) and activity data using the equation:

$$EE = \sum E1A1 + E2A2 + \ldots\ldots EnAn$$

where E is the rate of energy expenditure for each activity and A represents the time spent in individual activities of each moose during each 24-hour scan sample period.

C. Results

Heart rates of adult moose cows varied seasonally, ranging from 27 to 144 bpm over a 13 month period. The highest heart rates were recorded in late spring and summer (Fig. XII.1) when forage supplies were best and the animals were growing (Chapter V, Renecker and Hudson 1986). Heart rates declined from summer until January with the decline in food supply and quality. A marginal decline was observed through the winter period until early April when seasonal minima were recorded prior to the pulse of vegetation growth. This strong cyclic pattern in bedded-dozing heart rate represented an amplitude of about 142%.

Energy Expenditures of Specific Activities

Energy expenditures during various activities changed seasonally (Tables XII.1 and XII.2). While bedded-dozing with the head tucked into the abdomen, moose had an expenditure of 10.8 ±0.4 kJ/hr/kg$^{0.75}$ during winter and early spring increasing to a high of 32.9 ±1.4 kJ/hr/kg$^{0.75}$ in mid-July. Since this represented the least costly activity for free-ranging animals, it was considered an appropriate base (resting metabolic rate) for determining the increment cost of other activities.

Resting/Ruminating

Energy expenditures while lying-resting with the head up incurred an increment of 1.1±0.3 kJ/hr/kg$^{0.75}$ or 6.9% (Table XII.3). The apparent cost of lying-ruminating was 14±1% or 2.2±0.5 kJ/hr/kg$^{0.75}$. In December, a range of 31 to 84 chews/min represented an energy change of 13% or 1.5 kJ/hr/kg$^{0.75}$, whereas, during summer, fluctuations from

Fig. XII.1. Seaonal change in heart rate of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

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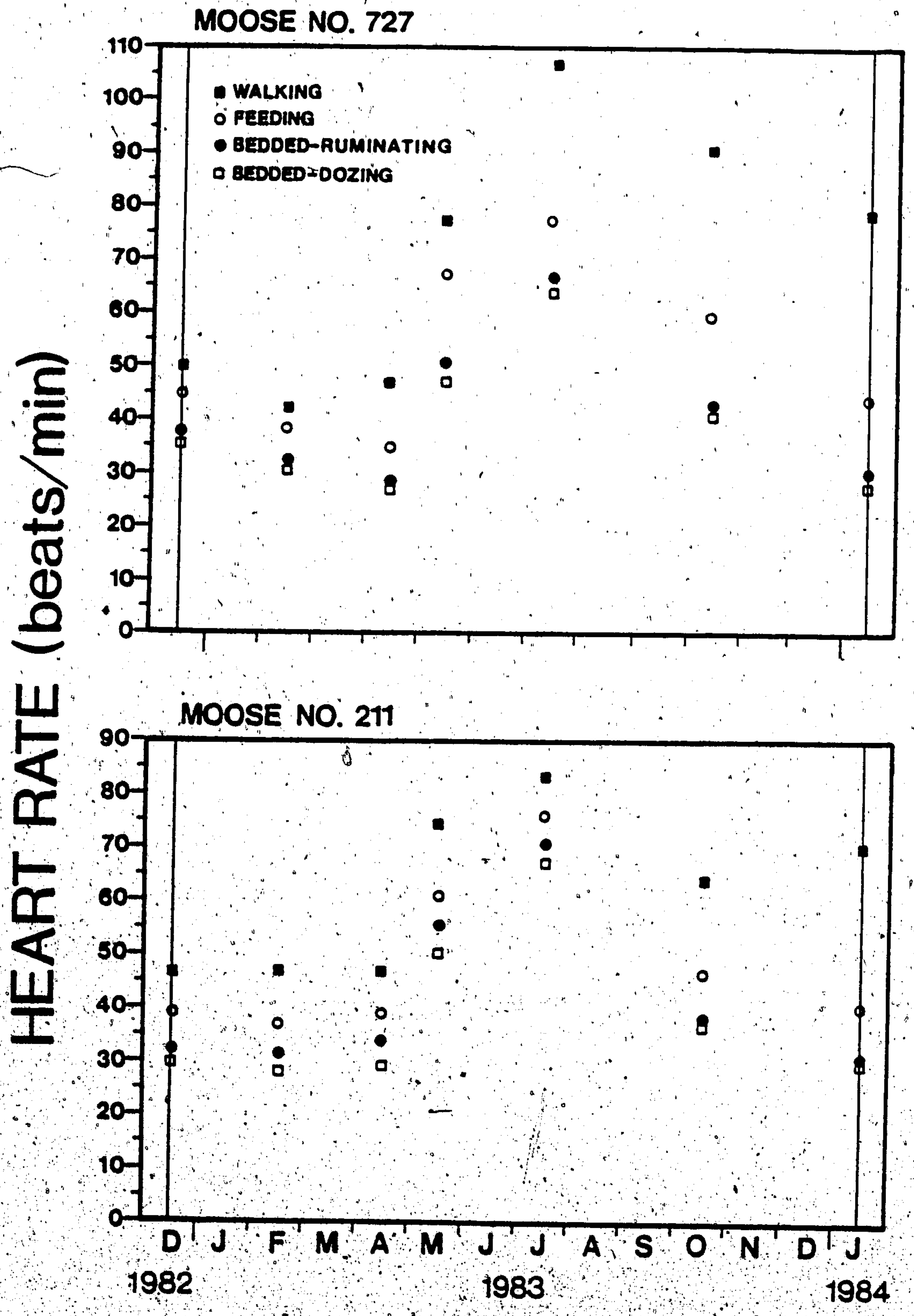

MOOSE NO. 727
■ WALKING
○ FEEDING
● BEDDED-RUMINATING
□ BEDDED-DOZING
110
100
90
80
70
60
50
40
30
20
10
0
HEART RATE (beats/min)
MOOSE NO. 211
90
80
70
60
50
40
30
20
10
0
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1982
1983
1984

Table XII.1. Energy expenditures for various activities of free-ranging moose no. 211 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Metabolic Rate (KJ/hr/kg $BW^{0.75}$)						
	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	11.5	11.0	11.0	20.3	36.9	14.8	11.8
Ruminating	12.4	12.1	12.5	23.3	41.4	15.0	12.2
Alert	12.8	12.1	11.1	22.1	38.1	15.8	12.5
Grooming						17.6	13.1
Other		11.9	11.9	33.6	39.8	16.8	12.9
Feeding							
Stripping Bark			15.1				
Cratering	14.7	15.0	14.0			21.4	15.0
Grazing					39.7		
Low	14.9	14.4	14.4	28.3	53.4	21.7	16.7
Middle	15.3	14.3	15.0	26.2	52.4	17,9	16.2
High	15.3	13.6	15.0	26.7	49.0	19.0	18.3
Miscellaneous							
Stand-Standing Alert	15.3	16.6	15.1	34.7	58.2	21.1	18.8
Stand-Ruminating		14.1		33.8	41.1		15.2
Stand-Grooming				71.0	43.8	32.8	18.7
Drinking-Eating Snow.			15.9	39.2	59.7	20.9	19.0
Walking	18.9	19.3	18.2	40.2	85.0	33.4	41.0
Running				91.3	131.3		46.6
Other							16.4

Table XII.2. Energy expenditures for various activities of free-ranging moose no. 727 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Metabolic Rate (KJ/hr/kg $BW^{0.75}$)						
	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	13.5	11.7	10.3	18.8	31.5	16.5	10.9
Ruminating	14.5	12.3	10.5	20.5	34.8	17.1	11.9
Alert	14.4	11.6	10.5	19.1	35.0	17.3	12.4
Grooming				19.3		18.5	
Other	14.3		10.8	17.7	39.1	17.6	13.7
Feeding							
Stripping Bark			12.3		44.3		17.9
Cratering	17.7	14.4	14.6			32.6	15.6
Grazing				37.2	48.7	22.4	
Low	17.6	15.1	11.4	31.0	47.7	24.1	17.2
Middle	17.8	14.9	13.8	30.2	50.0	35.5	17.4
High	18.8	15.0	12.0	34.8	48.8	33.8	20.5
Miscellaneous							
Stand-Standing Alert	16.7	14.3	12.4	40.2	72.2	31.1	18.2
Stand-Ruminating		15.3			41.1		16.7
Stand-Grooming							18.6
Drinking-Eating Snow			14.8	36.8	59.7	45.6	21.6
Walking	20.7	16.5	18.4	44.4	114.9	73.5	51.6
Running				86.9	351.6		64.9
Other					85.7		16.9

Table XII.3. Energy expenditures of activities of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Energy Increment of Activity[1]						
	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing-Head Down	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Dozing-Head Up	1.05	10.7	1.08	1.05	1.10	1.07	1.06
Ruminating	1.12	1.15	1.17	1.18	1.16	1.12	1.12
Alert	1.13	1.11	1.10	1.10	1.11	1.16	1.16
Grooming				1.05[2]		1.26	1.20[3]
Feeding							
Stripping Bark			1.39		1.41[2]		1.69
Cratering	1.34	1.39	1.46			1.86	1.43
Grazing				2.03[3]	1.36	1.45[2]	
Low	1.35	1.39	1.26	1.59	1.54	1.59	1.58
Middle	1.38	1.37	1.47	1.52	1.56	1.82	1.57
High	1.42	1.34	1.37	1.66	1.49	1.81	1.82
Miscellaneous							
Stand-Standing Alert	1.33	1.46	1.40	2.02	2.00	1.80	1.72
Drinking-Eating Snow			1.57	2.04	1.82	2.26	1.89
Walking	1.65	1.68	1.86	2.28	2.57	3.63	4.32
Running				4.84	7.50		4.70

[1] (Predicted energy expenditures of activity-predicted energy expenditure of resting animal with head down)/predicted energy expenditure of resting animal with head down.

[2] Activity only observed in animal no. 727.

[3] Activity only observed in animal no. 211.

71 to 86 chews/min incurred an expenditure of 26% or 8.2 kJ/hr/kg$^{0.75}$.

Posture and Locomotion

Higher rates of energy expenditure were associated with postural change. The energy expenditure of standing above bedded-dozing behavior represented a 36% increase during winter and early spring. As expected, the incremental expenditure of this change in posture was considerably higher (75%) during May and July when thermoregulatory demands were undoubtedly high.

A higher rate of energy expenditure, associated with travel, is noteworthy and expected as animals walked between food patches. The most costly activity was running, and was measured infrequently.

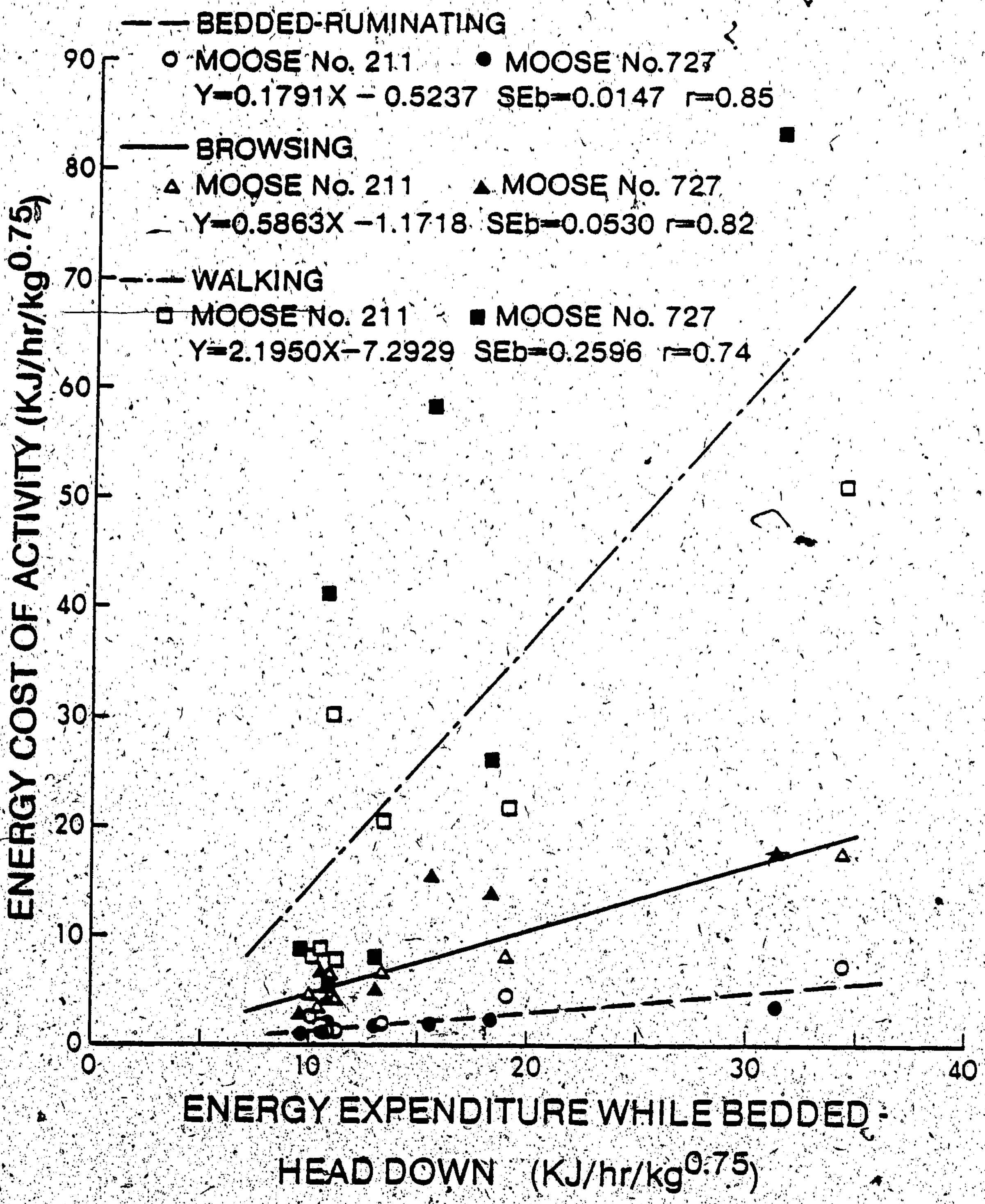
Foraging

Minor variation in energy expenditures was associated with consumption of certain food items as well as season. Noteworthy was the energy cost of grazing on cattails, during July, in sloughs where water depth was at the height of the brisket. This foraging activity was only undertaken during daylight hours when ambient temperatures and insect activity were extreme and offered a maximum reduction in heart rate and energy expenditure of 9.1 bpm or 12.7 kJ/hr/kg$^{0.75}$, respectively, over similar feeding activity in open pastures. Surprisingly, activities (grazing, stripping bark from trees and cratering), which might seem to require more effort, were not much more expensive.

Energetic Relationships

Incremental expenditures of bedded-ruminating ($P<0.001$), browsing ($P<0.001$) and walking ($P<0.01$) were highly correlated with resting metabolism (Fig. XII.2). Energy expenditures of various activities increased concurrently with higher ambient temperatures and thermoregulatory requirements, however, energetic efficiency tended to remain constant among seasons with increments ranging from 13% to 16% and 47% to 55% above bedded-dozing headdown activity when animals were bedded-ruminating and

Fig. XII.2. –Relationship between the energy costs of activity and energy expenditure while lying with head down in two free-ranging moose cows at the Ministik Wildlife Research Station, Alberta. The x-axis represents the resting metabolism of the animal whilethe y-axis represents the incremental expenditures of the three major activities.


BEDDED-RUMINATING
MOOSE No. 211
MOOSE No.727
Y=0.1791X − 0.5237 SEb=0.0147 r=0.85
BROWSING
MOOSE No. 211
MOOSE No. 727
Y=0.5863X −1.1718 SEb=0.0530 r=0.82
WALKING
MOOSE No. 211
MOOSE No. 727
Y=2.1950X−7.2929 SEb=0.2596 r=0.74
ENERGY COST OF ACTIVITY (KJ/hr/kg^0.75)
0
10
20
30
40
50
60
70
80
90
0
10
20
30
40
ENERGY EXPENDITURE WHILE BEDDED - HEAD DOWN (KJ/hr/kg^0.75)

browsing, respectively. Only incremental expenditures for walking varied markedly from 59% and 195% between winter and summer, respectively.

Thermoregulation and Insect Harassment

Ambient thermal conditions influenced rate of energy expenditure and activity of moose especially during late spring and summer when ambient and black globe temperatures were high. For example, moose no. 727 bedded in an open sedge meadow habitat during late afternoon in July where the water was 15-20 cm deep. Energy expenditures were reduced 2.9 kJ/hr/kg$^{0.75}$ below the daily average for a bedded-resting animal. Similarly, respiratory rate declined from 26 breaths/min recorded for a lying-resting animal near midday to 7.5 breaths~~/min~~ when the moose was bedded in wet sedge meadow. The use of water in cattail stands decreased standing heart rates of moose by 11 bpm from values recorded in willow-dominated habitats.

Open-mouthed panting (90 breaths/min) was observed in lying-resting postures during late May when ambient and black-globe temperatures approached 26°C and 31°C, respectively. Compared with mid-day, respiratory rates during bedding fell to 7 breaths/min in early morning (0600 h) when cooler ambient temperatures (10°C) prevailed. A change of 0.7 KJ/hr/kg$^{0.75}$ was detected in energy expenditure between these two times of day. Respiratory rates while bedded, decreased to 3-5 breaths/min when winter ambient and black globe temperatures dropped below -16°C.

During late spring, warm and dry weather exacerbated the activity of horn flies (*Haemotobia irritans*), horse flies (*Tabanus* spp.) and deer flies (*Chrysops* spp.) during the daylight period. The energy expenditures incurred from responding to insect harassment represented a 4.2 KJ/hr/kg$^{0.75}$ or 22% increase over bedded-resting activity. Although activity was generally suppressed when it was hot, extreme harassment from mosquitoes was seen to prevent bedding on two occasions in July. This harassment was of considerable importance during the brief bedded period, representing a 52% increase in energy expenditure above bedded-dozing behavior. During the peak of mosquito activity, animal movement increased during browsing in the aspen forest. Animals walked continuously while stripping leaves from beaked hazel.

Disturbance

The occurrence of a human intruder elicited a 38% increase in heart rate of bedded moose. If the noise was recognized and presumably judged harmless, then pulse rate decreased within about 15 sec to the level of the previous activity. However, other stimuli elicited a cascade of degenerating peaks over a period of 2.5 min until the intruder was apparent and identified visually.

Time-Energy Budgets

Time-energy budgets of free-ranging moose fluctuate in a circannual pattern with forage quality and thermal conditions. Total energy expenditures, throughout the year, were highest in July and lowest in April (Fig. XII.3).

Over trial periods, bedded-ruminating activity was the largest contributor to the daily energy expenditure of moose cows (Tables XII.4 and XII.5). The exception to this pattern was late May when foraging became the most important component of the energy budget. The daily energy expenditure of foraging increased from 44% in April to 52% in late May. Daily energy expenditures of active moose doubled between May and July probably in response to greater heat loads and extreme harassment by insects. This is reflected in a 15% daily allocation of energy for movement and travel.

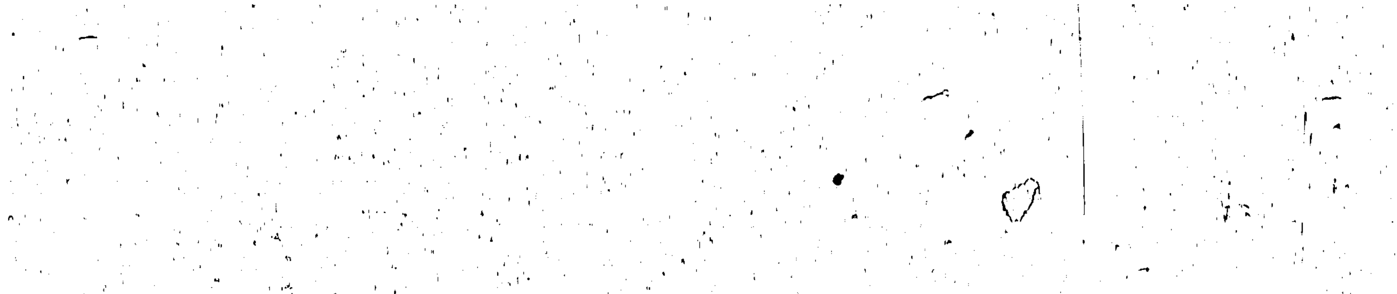


Fig. XII.3. Seasonal time-energy budgets of two free-ranging moose cows from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

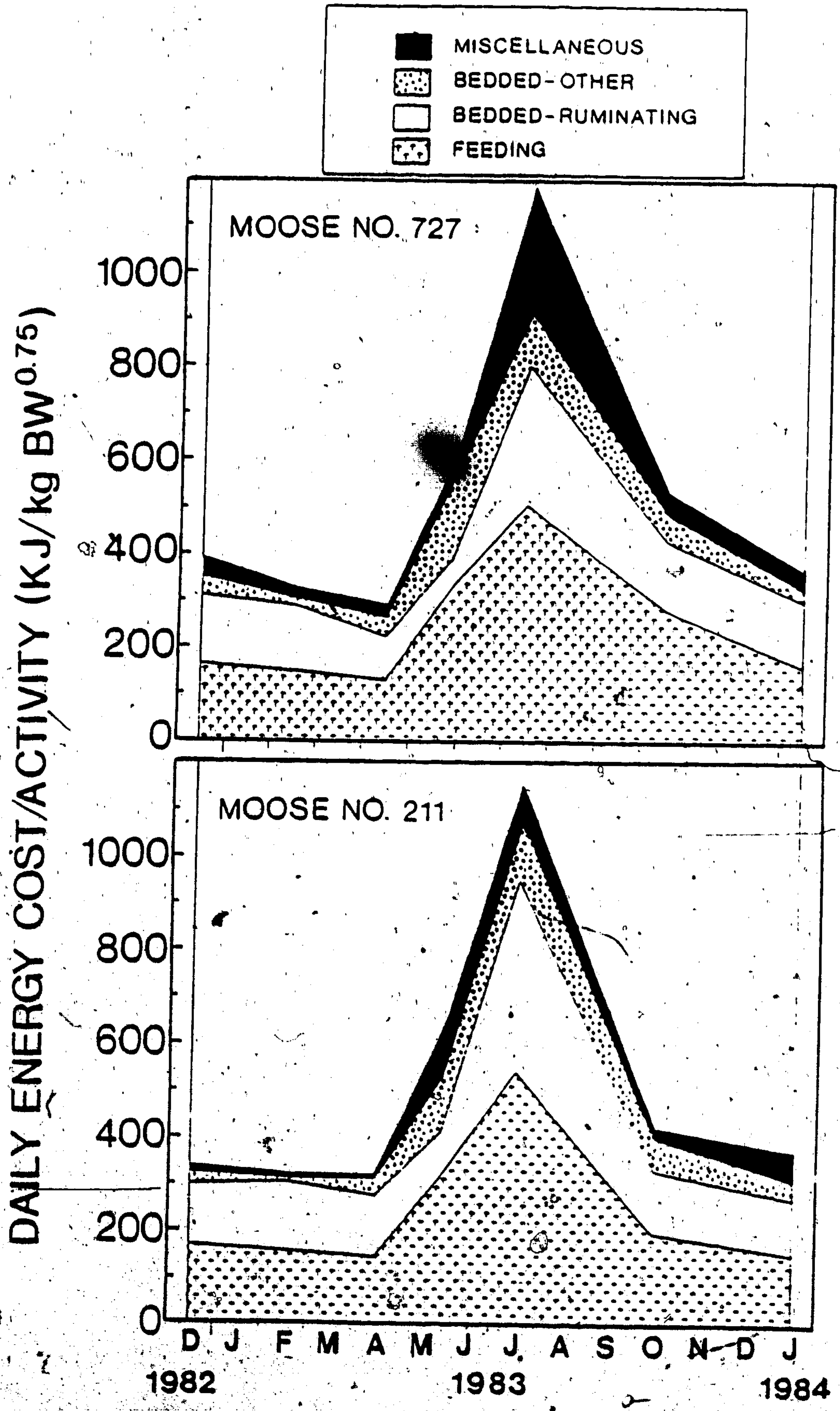

MISCELLANEOUS
BEDDED-OTHER
BEDDED-RUMINATING
FEEDING
MOOSE NO. 727
MOOSE NO. 211
DAILY ENERGY COST/ACTIVITY (KJ/kg BW$^{0.75}$)
0
200
400
600
800
1000
D
J
F
M
A
M
J
J
A
S
O
N
D
J
1982
1983
1984

Table XII.4. Daily time-energy budgets for free-ranging moose no. 211 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

	Energy Expenditure/Activity (KJ/kg $BW^{0.75}$/d)[1]						
Activity	Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	16.7	7.0	29.0	89.5	10.1	55.4	22.9
Ruminating	132.6	151.4	131.8	99.0	314.3	137.1	121.6
Alert	6.1	0.3	6.0	27.4	10.7	11.5	11.5
Grooming						0.8	0.1
Other		0.3	1.8	0.3	2.7	6.6	4.5
Feeding							
Stripping Bark			49.9				
Cratering	3.8	15.9	33.3			73.8	7.7
Grazing					17.0		
Low	63.5	47.9	6.3	120.3	236.1	69.6	105.7
Middle	92.7	86.3	42.2	180.3	223.5	40.9	17.3
High	2.9	0.7	7.8	1.0	58.7	5.7	17.4
Miscellaneous							
Stand-Standing Alert	7.2	2.0	5.2	25.7	39.1	10.4	16.5
Stand-Ruminating		0.9		0.3	1.4		0.13
Stand-Grooming				2.9	1.2	1.2	0.1
Drinking-Eating Snow			1.0	4.7	3.0	1.3	0.6
Walking	1.3	2.6	4.28	62.7	130.6	4.4	37.1
Running				8.3	8.2		1.8
Other							4.8
Total	326.8	315.3	318.5	632.4	1154.6	418.7	369.7

[1] Calculated from time-action budgets for free-ranging moose reported in Chapter XI and predicted energy expenditures in Table XII-3 (Renecker and Hudson 1985).

Table XII.5. Daily time-energy budgets for free-ranging moose no. 211 from December 1982 to January 1984 at the Ministik Wildlife Research Station, Alberta.

Activity	Energy Expenditure/Activity (KJ/kg $BW^{0.75}$/d)[1] Dec	Feb	Apr	May	July	Oct	Jan
Bedded							
Dozing	22.1	11.3	21.0	172.9	84.2	39.0	16.2
Ruminating	144.1	143.6	94.8	57.4	299.5	145.7	133.2
Alert	3.2	4.8	11.6	7.7	18.1	14.7	3.8
Grooming				3.8		4.4	
Other	10.6		5.5	0.2	3.6	0.2	4.3
Feeding							
Stripping Bark			50.9		1.4		37.7
Cratering	84.2	80.4	34.7			3.4	4.5
Grazing				0.3	245.8	12.6	
Low	38.2	35.8	8.1	65.1	77.1	231.6	69.2
Middle	30.6	23.6	18.2	253.7	143.6	33.2	53.4
High	6.9	3.1	10.7	6.9	35.8	0.4	3.9
Miscellaneous							
Stand-Standing Alert	20.4	10.1	9.7	6.5	26.9	13.2	7.1
Stand-Ruminating		0.7			13.0		0.3
Stand-Grooming							0.9
Drinking-Eating Snow			1.7	3.7	3.4	2.9	0.9
Walking	21.5	7.9	17.8	13.3	202.4	23.3	25.4
Running				0.2	22.8		2.0
Other					4.3		4.2
Total	381.8	321.3	284.7	591.7	1181.9	524.6	367.0

[1] Calculated from time-action budgets for free-ranging moose reported in Chapter XI and predicted expenditures in Table XII-3 (Renecker and Hudson 1985).

D. Discussion

Heart Rate as an Index of Ecological Metabolism

Although seasonal energy expenditures of penned moose have been reported (Regelin et al. 1985, Renecker and Hudson 1986), difficulties encountered with measurements under field conditions have limited knowledge of daily energy allocations of free-ranging animals. We have derived our estimates with the heart rate index.

An important assumption is that heart rate is a reliable index of energy expenditures in these circumstances. Regressions were based on tethered moose whose metabolic rates varied with energy uptake and thermal stress. Thus, relationships have been extrapolated to activities other than those used in calibration. Other workers have suggested that heart rate and energy expenditure may become uncoupled during alert behavior (Johnson and Gessaman 1973) precluding these increases as direct increments of energy expenditure (Jacobsen 1979). However, these periods are infrequent during the circadian cycle and probably result in a small partition of time and energy for adult moose.

Energy Expenditures of Activity

Resting metabolic rates were somewhat lower than those reported for domestic (Blaxter 1962) and other wild (Pauls et al. 1981, Regelin et al. 1985) ruminants. Seasonal minimum metabolic rates of bedded animals were as low as 264 kJ/kg$^{0.75}$ which is lower than the usually-accepted interspecies mean. This compares with minimum basal metabolic rates of 394 kJ/kg$^{0.75}$ in penned Alaskan moose (Regelin et al. 1985). Although this may show a bias in the heart rate index, basal metabolism is influenced by previous nutrition and therefore may be higher in pen-fed animals.

Expenditures, while lying-ruminating, corresponds to those determined by Pauls et al. (1981) for wapiti. If rumination is considered to be the expenditure above lying with head up, then a 7±1% increase detected in moose cows is consistent with reports for domestic sheep

(Graham 1964). Adult moose spend a relatively large portion of each day ruminating (Chapter XI, Risenhoover 1986). During the 4-6 daily periods allocated for rumination, moose must adequately reduce the cell wall component of ingested food to permit passage of undigested residues and subsequent intake of additional forage. The range of energy expenditures which correspond with rates of chewing reflects the variable cost of regurgitation, mastication and swallowing.

Standing invoked an increment of 40-100% with highest values in summer. Similar increases have been reported for Alaskan moose (Regelin et al. 1985) and moose in Alberta (Chapter V, Renecker and Hudson 1986) using indirect calorimetry.

Contrasts among foraging tactics were small. Although cratering and bark stripping may seem to be more strenuous activities, cost per unit time was not inordinately high. Moose seemed to simply forage more slowly. Minor differences in energy expenditure of foraging on different food items may reflect variable expenditures of prehension and handling. However, another factor may relate to thermoregulation (Chapter V, Renecker and Hudson 1986) since the lower energy expenditure of feeding on cattail during mid-day seemed associated with standing in water. It is possible that the water surrounding the appendages served as a mechanism of heat dissipation and relief of insect harassment. Ultimately, this permitted the moose to forage extensively during daytime hours while minimizing energy costs.

During summer, standing moose have been shown to have upper thermal limits of between 14 and 20°C (Chapter V, Renecker and Hudson 1986). Use of water by moose ameliorates thermal stress (Flook 1955, Knorre 1959, Kelsall and Telfer 1974) and provides a refuge from insects. Energy expenditures associated with heat and insects correspond with those of wapiti during summer (Gates 1980). Similarily, mountain goats (*Oreamnos americanus*) use snow banks as a behavioral strategy to minimize heat stress during high ambient temperatures (Fox 1978). The dense underfur and long guard hairs of moose provide adequate insulation during winter (Chapter V, Renecker and Hudson 1986) at lower ambient temperatures.

Energy costs of activity are expressed either as absolute expenditures or multiples of basal (or resting) metabolic rate. The choice is usually based on convenience. Results of this study suggest the choice may be more critical since incremental costs were correlated with seasonal changes in resting metabolism but remained a constant multiple of basal expenditures. Watkins and Hudson (1985) observed a similar relationship in wapiti except that incremental costs were an increasing proportion of basal at higher levels of basal metabolism. But these measurements were based on rates of expenditure rather than costs per unit work accomplished. In good nutritional condition, wild herbivores are more alert and move more quickly. However, in this study, relationships were based on pooled seasonal measurements, so thermal conditions and insect annoyance may complicate interpretation.

Differences among slopes of these relationships may also have adaptive significance. Moose spend a large part of each day consuming and masticating forage (Chapter XI). Consequently, it would be beneficial to minimize energy expenditures of dominant activities. Similar relationships have been reported for wapiti (Hudson et al 1985).

Ecological Metabolism

Ecological metabolism (energy costs of free-ranging animals), as defined by Moen (1973), is usually considered to be 2-3 times basal metabolic rate. Even in the absence of pregnancy and lactation, moose cows in this study increased metabolic rate, seasonally, more than 300%. This resulted from both increased levels of activity and higher incremental expenditures. Although cold temperatures and deep snow influence energy expenditures of smaller herbivores, heat and insects during summer imposed a much greater energetic penalty for moose.

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XIII. SYNTHESIS

A large body size is a common characteristic of ruminants which exploit open environments with more abundant but lower quality food resources (i.e grasslands). Evolution of this trait was probably shaped by a need to reduce risk of predation, enhance mating opportunities and increase mobility of these species in the absence of abundant cover (Hudson 1985). Accordingly, a relationship also exists between body size, habitat characteristics and food habits. Ruminants with a large body size require large absolute amounts of food and are normally constrained by the time required to search for large quantities of rare food items which limit their ability to consume sufficient quantities. Thus, a trade-off occurs between forage abundance, distribution and quality in environments utilized by large or small ruminants which in turn forms the basis of the "Bell-Jarman Principle" (Bell 1969, 1971; Jarman 1974). However, moose appear to be an exception to the "Bell-Jarman Principle" in that they are large in body size and utilize resources which are widely spaced (but clumped) in a strongly seasonal environment.

Numerous forces may have shaped evolution of the moose. Moose (browsers) are cervids inhabiting boreal regions which are often associated with periods of extreme cold and deep snow. In these environments, a large body size is a prerequisite for efficient conservation of energy and mobility. In addition to climate, adaptations for acquisition and processing of a wide range of food items, which show seasonal extremes in abundance and in quality (highly lignified), would be important morphological specializations influencing energy intake and balance in the animal. Other aspects, which shape morphological characteristics of ungulates, are security and defense. The advantages of large group size decline in the openness of habitats as animals are often heard before they are seen in forested environments. Thus, throughout the evolution of moose, there have been many bioenergetic, digestive and morphological adaptations. However, to fully understand why moose developed their trophic strategy requires an immediate need to first examine the environment in which they live.

Predation

Moose have been in constant association with their primary natural predator, the wolf (*Canis lupus*), throughout much of their boreal range. Wolves exert the greatest pressure on calves during winter when movements are restricted or on mature animals if conditions become stressful (Coady 1983). More recent investigations by Franzmann et al. (1980) have documented that bears (*Ursus* spp.) can be important local predators which prey primarily on young calves. However, human hunting practices have become more important and Telfer (1984) considered that it must not be dismissed as a limiting criteria, especially when in combination with severe winters and heavy wolf predation. With an increase in the risk of predation, there are important trade-offs between time spent foraging and security that may limit energy intake of the animal.

Snow

A variety of climatic factors influence boreal environments, but snow is paramount during winter. Generally, accumulations of 40-80 cm of snow occur in the continental portion of the boreal forest and persist for about 6 months. Characteristics of snow (depth and hardness) also vary markedly throughout the region. Dense coniferous cover intercepts snow reducing snow depths on the ground, whereas deep soft snow occurs in deciduous feeding sites. Freeze-thaw cycles, insolation and wind are variables which can alter snow cover in open sites and result in crust formation. Snow under coniferous cover is less modified by environmental changes and is characteristically less dense.

Snow cover also contributes to the patchiness of winter food resources. Where snow accumulates, forage is often covered or made inaccessible. This barrier to feeding and locomotion has marked effects on ungulate distributions and often results in extensive migrations to ameliorate the impediments presented by snow.

Thermal Environment

Winters are typically harsh and cold in northern environments. In montane habitats of western Canada, temperatures frequently fluctuate to above 0°C as a result of short-lived chinook conditions. Similarly, adverse climatic conditions in other boreal habitats are often preempted by moderating weather in late winter.

Although summers are generally brief, daily temperatures are often very warm. However, shaded areas under mature stands in the boreal forest afford less severe microclimates as cooling water in streams or aquatic communities are often available. The effects of warm summer weather are also exerted indirectly through extreme insect activity of biting flies and mosquitoes.

A. Environmental Resource

Forage Distribution and Availability

Throughout the geographical distribution of moose, boreal habitats are largely dominated by mature coniferous or mixed forest stands. However, fire, logging practices, flood plains and riparian environments have altered succession favorably and created a mosaic of habitat types. The interspersed patches of shrubs and early successional stages of regenerated growth within mature stands are favorable to moose, as they supply both food and cover. Growth and productivity of moose populations within these vegetative patches depends on seasonal succession including disappearance of snow cover which results in structural and density changes within plant clumps.

During winter, moose occupy an area of approximately one-quarter the size of their summer ranges. Forage patches tend to be scarce consisting mainly of woody stems and accumulations of leaf litter where it can be obtained. Although food areas are patchy, food is generally clustered within these areas allowing the animal to reach several clumps without much movement. Because feeding sites of shrubs or forest regeneration are dispersed among mature stands, movement is required between food patches.

Numerous factors have a profound influence on forage quality. Nutritional quality of available woody forage declines as food becomes temporarily scarce and more fibrous during winter. In addition, certain food items may have high concentrations of secondary metabolites making them unsuitable for consumption. Similarly, plant defenses can be stimulated by heavy browsing resulting in unpalatable food items (Bryant 1981). Thus, quality of winter food resources offered to a browser will be considerably less than that of grazing ungulates which utilize extensive grasslands and sedge meadows. In response to this habitat structure, moose must spend more time for search, pursuit and travel between food producing areas.

In the boreal forest, plants respond to the disappearance of snow with a green flush of vegetation of high nutritive quality. During the brief period of active leaf growth in late spring and summer, the distribution of forage resources becomes more continuous in addition to the increased biomass of shrubs during the main production season. The emergence of forbs offers options for the dietary menu of moose. This concomitant increase in forage biomass with diet quality allows greater intake of food and allows for compensatory body growth after depletion of energy stores during the winter.

B. Consequences of Trophic Specialization of Moose

The advantages of specialized adaptations in ungulates are readily apparent. However, in the case of moose, specialization also produces disadvantages to certain environmental constraints. One of the key features of adaptation for northern environments is a large body size to minimize heat loss. However, the larger-bodied animals have greater total nutrient requirements. This problem becomes complex because moose are also specialized for feeding on browse which is widely dispersed in the environment. Browsers have specialized mouth parts which enable them to harvest certain plant parts. This adaptation in a patchy environment requires considerable movement for search and capture of adequate energy. The rumen of a browser is also specialized. It is small and depends upon rapid digestion and passage to obtain adequate energy from cell solubles in lignified browse. Thus, moose, because of this specialization in rapid passage, cannot accomodate bulky grass or sedge diets which require slow passage.

C. Energetic Economy of a Large Body Size

Thermal Inertia

Another fundamental problem confronting ruminants is the acquisition of sufficient nutrients within the constraint of their changing thermal environment. Because of a large body size and effective insulation, standing moose are extremely cold tolerant. Furthermore, bedding with appendages tucked under the body as well as bedding in powdery snow can further reduce heat loss during cold periods. This larger size conserves heat and reduces energy requirements during winter when the quality and quantity of available forage are insufficient to meet maintenance requirements.

Hot weather appears to be oppressively uncomfortable to moose in both winter and summer. Heat stress leads to higher energy expenditures and a suppression of activity which is particularly evident during chinook conditions in winter, when animals have maximum thermal insulation and are physiologically adapted for cold environments. Warm temperatures influence thermoregulatory mechanisms and time-energy budgets of moose during summer also. Although the insulative factor is reduced, the low surface area to volume factor provides inertial homeothermy creating thermal imbalance at high ambient temperatures. When the ability to dissipate metabolic heat by convection, conduction and radiation is compromised, heat stress occurs taxing the regulatory mechanisms, and animals feed in open and aquatic environments to take advantage of long appendages and the cooling effects of wind and water to dissipate heat. However, the higher cost of ecological metabolism (the energy cost of the free-living animal; Moen 1973) finally results in static body weights.

Locomotion

Unfavorable snow characteristics tend to make locomotion difficult and restrict activity of many wild ungulates. However, the relative costs of movement are less for moose than for smaller ungulates such as deer (Taylor et al. 1970).

Generally, northern ungulates will not tolerate snow depths greater than chest height and are impeded when snow is at knee depth (Kelsall and Prescott 1971). Moose have an advantage, due to size and longer legs, over other boreal browsers, such as white-tailed deer which permits them to remain active and exploit widely dispersed food resources (Telfer and Kelsall 1984). Nevertheless, moose and deer have similar foot loadings and therefore similar sinking depths. Thus, the selective advantage of the large body size of moose is due to the long legs which permit use of deep soft snow to access clumps of browse.

D. Food Acquisition

Viewing boreal habitats in light of the "Bell-Jarman Principle", there should be a clear pattern between body size and the food that an ungulate would eat. Because food is often scarce and well-dispersed in a patchy setting, considerable travel is required to obtain highly digestible foods. One might then expect a browsing herbivore to be small-bodied since smaller absolute quantities of nutrient would be required. It is therefore surprising to find a forest-dwelling herbivore of a large body size aligned along the gradient of concentrate selectors. In terms of resource utilization, it is interesting to speculate as to how this ungulate successfully exploits its particular niche.

It has been argued that food acquisition of the browsing ruminant should maximize the net rate of nutrient extraction. This study revealed that moose allocated time to foraging in habitats in proportion to foraging returns (efficiency) (Fig. XIII.1) in terms of g crude protein (CP) and digestible dry matter intake (DDMI) consumed per min. Also, an increase in habitat breadth resulted in greater foraging opportunities and returns (in terms of g CP/min and DDMI/min) (Fig. XIII.2). However, other factors such as thermal stress, summer insect

Fig. XIII.1. Relative percent of total foraging time spent in major habitats in relation to relative foraging returns expressed as proportion of crude protein (g of CP) consumed/min and proportion of digestible dry matter intake (g DDMI/min) divided by the total for all habitats at the Ministik Wildlife Research Station, Alberta. Symbols enclosed with a large open circle represent habitat use during periods of high ambient temperatures, insect harassment, selective foraging or snow crusts. The solid line represents the isometric line.

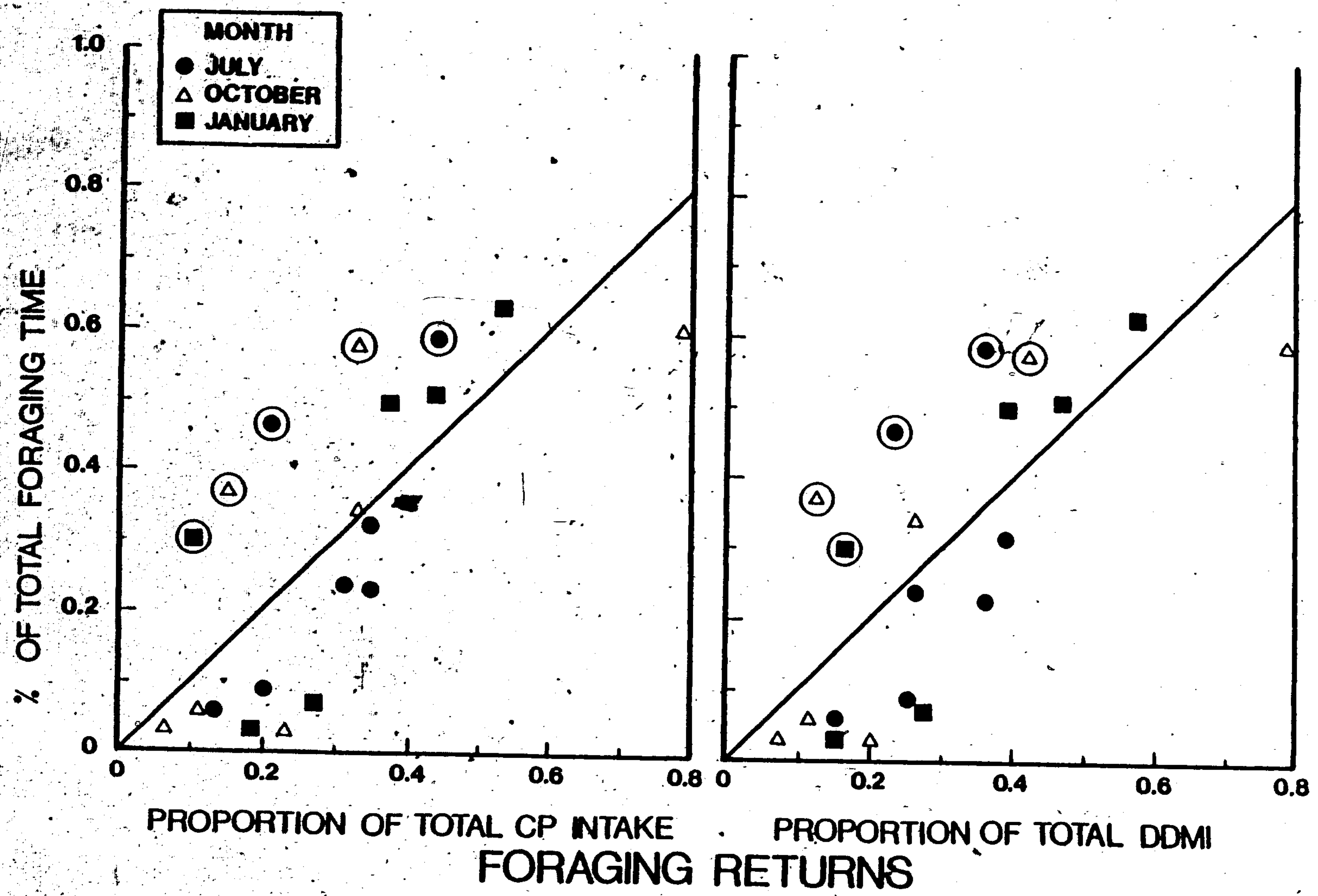
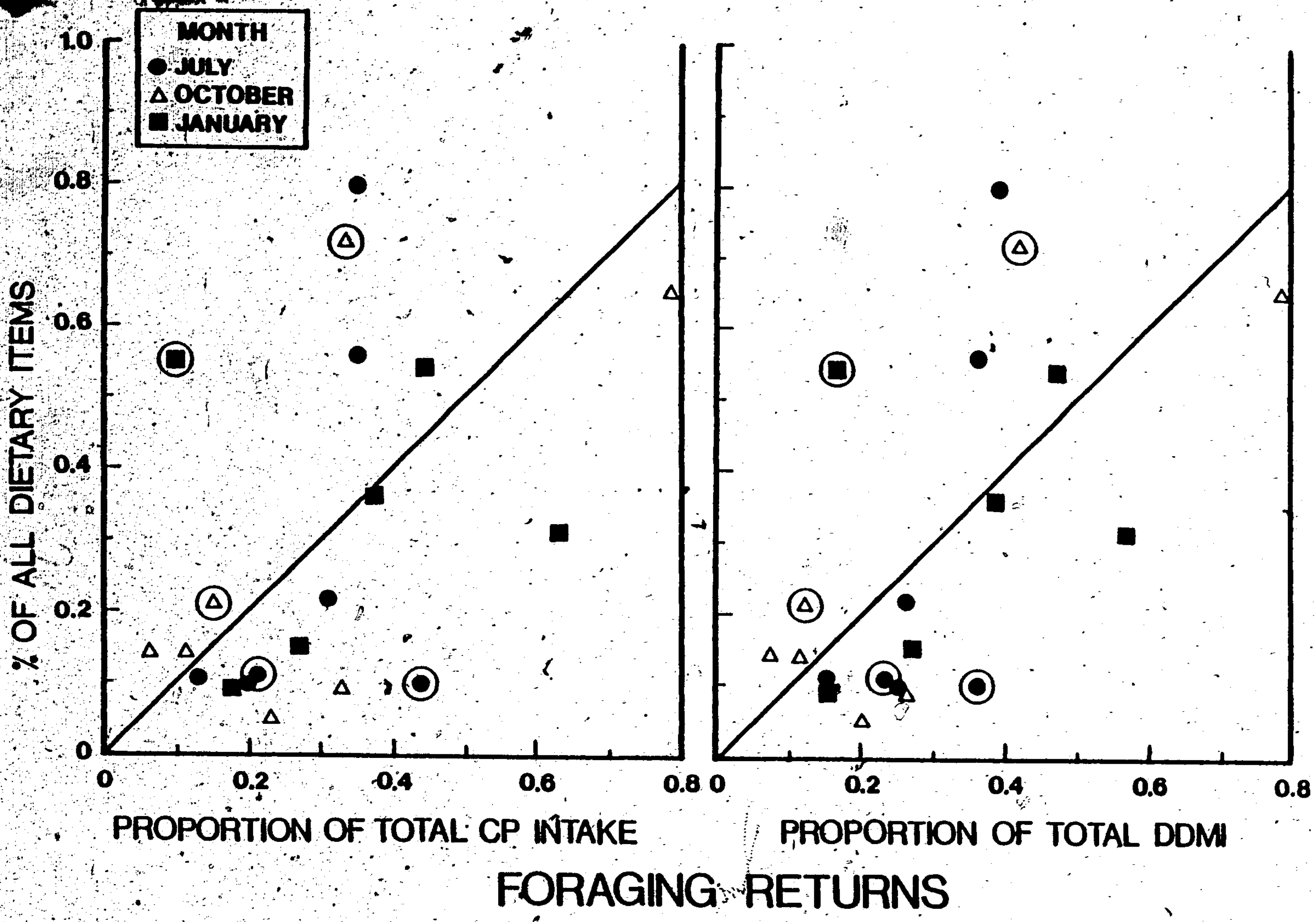

MONTH
● JULY
△ OCTOBER
■ JANUARY
% OF TOTAL FORAGING TIME
1.0
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
PROPORTION OF TOTAL CP INTAKE
0
0.2
0.4
0.6
0.8
PROPORTION OF TOTAL DDMI
FORAGING RETURNS

Fig. XIII.2. Relative percent of total number of useable dietary items found in major habitats in relation to returns relative foraging returns expressed as proportion of crude protein (g of CP) consumed/min and proportion of digestible dry matter intake (g DDMI/min) divided by the total for all habitats at the Ministik Wildlife Research Station, Alberta. Symbols enclosed with a large open circle represent habitat use during periods of high ambient temperatures, insect harassment, selective foraging or snow crusts. The solid line represents the isometric line.

MONTH
● JULY
△ OCTOBER
■ JANUARY
% OF ALL DIETARY ITEMS
1.0
0.8
0.6
0.4
0.2
0
0
0.2
0.4
0.6
0.8
PROPORTION OF TOTAL CP INTAKE
0
0.2
0.4
0.6
0.8
PROPORTION OF TOTAL DDMI
FORAGING RETURNS

harassment, winter melt-freeze cycles and seasonal change in the spatial distribution of forage appeared to influence the "decision rules" of moose which resulted in deviations from the isometric line in Figs. XIII.1 and XIII.2.

In summer, there are only small differences in quality between patches resulting in a decline in pursuit costs, all other factors being equal. Generally moose were nonselective during this period of green biomass since no penalty was incurred in terms of quality. As food quality declined, moose became highly selective choosing patches which reduced foraging efficiency but increased foraging returns in terms of nutrients. As a consequence, they compensated for the reduction in intake by maximizing nutrient capture. This behavior resulted in no penalty in diet quality or retention and clearly facilitated tissue anabolism. As resources became coarse-grained in winter, animals continued to proportion time according to quality and biomass. However, selectivity was no longer important and used as a compensatory mechanism for limited food resources.

Moose balanced energy cost of foraging during periods of high temperatures by choice of open, aquatic communities. Although foraging returns were lower in terms of quality relative to other habitats, moose tolerated greater extremes in ambient temperature and increased their energy economy. Similarly, feeding activity was suppressed when ambient temperatures were warm during winter. It appears, therefore, that apportioned time to habitat use was strongly influenced by thermal environments.

During winter, deviations in the use of habitats in proportion to foraging efficiency can be explained in terms of forage availability and snow conditions. Generally, moose minimized daily movements and utilized readily available food items, such as leaf litter. However, snow crusting resulted in a decline in the availability of forage biomass and a shift in habitat use and food selection. This resulted in an increase in search times as a trade-off for reduced foraging efficiency. Thus, moose were able to use a variety of different habitats which supported usable food items when biomass became limited.

Violation of the "Bell-Jarman Principle" (Bell 1969, 1971; Jarman 1974) in body size and foraging strategy should place moose in a precarious position. In answering this dilemma, I suggest that moose apparently get enough (large absolute quantities) highly digestible but low fiber food by choosing habitat types which offer maximum opportunities for efficient foraging of a variety of dietary items. It is therefore likely that moose perceive food patches, similar to deer (Hanley 1980), in terms of species breadth (crude protein content) and biomass (digestible dry matter intake). Spatial arrangement of food patches is diffuse in the boreal forest and large home ranges would also be required to meet metabolic demands of the moose (McNab 1963, Peters and Raelson 1984). Thus, we would expect that a wide dispersion of food results in a relatively low population density of animals which is generally observed for moose in the boreal forest.

E. Digestive Strategy

The ability of ruminants to utilize fibrous foods is determined by physiological requirements, anatomy and foraging strategy. Hofmann (1973) emphasized the browser/grazer separation. Concentrate selectors which have narrow jaws can separate different plant and plant parts in order to exploit diets, high in lignin and cell solubles, for rapid fermentation in small rumens. Large grazing ruminants must eat common fibrous foods which can be degraded in capacious rumens. These characteristics have been shown to be flexible and allow for seasonal changes in diet quality and selection. Understanding the factors which have promoted the development of each ruminant type is an intriguing problem.

My study has shown a marked distinction between the browser/grazer categories. Although moose (browsers) and cattle (grazers) extracted nutrients equally well from fibrous foods, browsers retained digesta longer. Because of a decrease in digestion and passage rates with increasing fibre content of the diet, each ruminant type consumed an amount of food equal to the maximum potential intake as defined by the limits of degradation of the forage and escape from the rumen (Table XIII.1). Conformity with the grazing strategy would suggest

Table XIII.1. Rumen contents of dry matter (DM), rate constants for digestion (kd) and passage (kp) of particulates, organic matter (OM) digested, OM passed and potential organic dry matter intake (OMI) for moose, wapiti and cattle fed four diets during winter and summer 1982.

Diet	Rumen Contents (g)	kd[1]	kp[2]	OM Digested (g/hr)	OM Passed (g/hr)	Potential OMI (kg/d)	Actual OMI (kg/d)
Winter							
Grass							
Moose	2,090	0.0446	0.0354	90.7	73.6	3.943	4.128
Wapiti	1,195	0.0386	0.0585	45.9	69.5	2.770	3.864
Cattle	5,527	0.0331	0.0483	182.0	265.6	10.742	13.824
Alfalfa							
Moose	3,000	0.0799	0.0306	232.7	91.4	7.778	4.296
Wapiti	1,917	0.0881	0.0570	168.2	108.8	6.649	4.368
Cattle	6,728	0.0476	0.0474	318.9	317.6	15.276	14.208
Aspen Twigs							
Moose	3,629	0.0590	0.0518	213.1	187.1	9.605	3.912
Wapiti	2,841	0.0803	0.0586	227.0	165.7	9.425	3.840
Cattle	6,758	0.0747	0.0421	502.4	283.2	18.854	5.280
Summer							
Grass							
Moose	3,584	0.0226	0.0554	80.6	197.5	6.674	6.744
Wapiti	3,059	0.0327	0.0600	99.5	182.6	6.770	7.128
Cattle	7,528	0.0213	0.0569	234.4	426.1	15.852	15.792
Alfalfa							
Moose	3,853	0.0408	0.0523	156.4	200.4	8.563	5.760
Wapiti	3,802	0.0433	0.0479	163.7	181.1	8.275	6.672
Cattle	11,302	0.0470	0.0470	528.3	528.3	25.360	14.880
Aspen Foliage							
Moose	3,224	0.0798	0.0809	256.2	259.7	12.382	5.770
Wapiti	3,378	0.0724	0.0713	243.5	239.8	11.599	6.144
Cattle	7,870	0.0463	0.0686	362.8	537.6	21.610	12.600

[1] Data from Chapter VI.
[2] Data from Chapter VII.

that rumens should be filled to maximum capacity at the end of each grazing bout as suggested by Sibly (1981). Intakes equal to the process of absorption of nutrients and passage of indigestible residues in browsers and mixed feeders suggested that these ungulates attempted to compensate for reduced fermentation rate by filling rumens to their maximum capacity thereby increasing actual organic matter intake. However, does this intake capacity provide an adequate adjustment in browsers with lower digestion rates?

On less fibrous diets, measured intakes were lower than calculated potentials. Large browsers appear to have adapted to utilizing highly lignified foods like browse. Perhaps the shorter retention of browse in moose may be interpreted as an adaptation to maximize returns through optimal retention of food. Generally, animals consumed grass rations in a series of bouts throughout the day which probably maintained rumen capacity. However, intake of alfalfa and aspen diets was more pulsed perhaps indicating that dry matter capacity of the rumen may have fluctuated more throughout the day. This conclusion was supported by the variation in marker concentration after time of administration. The fluctuating pattern of disppearance would tend to suggest that both intake and passage occurred in a pulsed pattern for rapidly digestible substrates.

Turnover time of food in the digestive tract is an important facet of nutrient extraction. As the quality of food deteriorates, rate of intake must increase to support requirements. However, ruminants encounter constraints at some level of diet quality where intake no longer compensates for fibrosity. Furthermore, if retention time increases as a result of a greater fiber content of the diet and rumination requirements, then intake would be expected to decrease. Therefore, it is suggested that large ruminants retain fibrous diets for an optimal time to maximize nutrient extraction and rumen capacity (Sibly 1981). If optimal residency retention times (ln 2/-kd) (Sibly 1981) for grass forages in the rumen are compared to rumen turnover times (RTT); we see an interesting pattern. Both the grazers and mixed feeders, known to tolerate levels of fibrosness, retained forage in their rumens at RTT which maximize absorption, but the browser (moose) retained grass diets longer than would be predicted by optimal digestion (Table XIII.2). Moreover, this probably reflects differences in trophic strategies of the browser/grazer groups.

As expected, RTT of moose were marginally higher than the predicted optimal residency times (Table XIII.2). I can imply that since cell wall components of browse are virtually indigestible because of the strong lignocellulose association, therefore effective extraction of nutrients from browse species would only consider rapidly digesting cell solubles while rapidly passing the indigestible fiber. Despite the grazing tendency of cattle and wapiti, both processed aspen foliage close to the optimal rate. However, cattle appeared less effective in extracting nutrients from aspen twigs. Because of the large total food requirements of grazers, it would seem that during periods of food shortage cattle could not obtain and process enough nutrients to sustain themselves. This is reflected by the low overall weight of the rumen contents.

It would appear that evolution of ruminant feeding patterns may be related to an optimal compromise between retention and nutrient extraction. We can see that during summer when foods are not limited in quality or quantity, browsers excel. This is largely because they maintain a strategy of rapid passage and digestion which does not restrict intake. When food would be scarce and of poor quality, grazers and mixed feeders have an advantage because they are able to extract more energy from fibrous foods. In contrast, browsers probably become restricted by fibrous grass diets.

Digestive Capacity

Feeding habits of ruminants are expected to vary with body size. Larger ruminants would be influenced by the ability to maintain intake on highly fibrous diets. However, the grazing strategy influences foraging time and allows them less time to be selective. Among the ruminants, I would expect large-bodied grazers to best exploit dense carpets of grass as would be predicted by the work of Foose (1982). These animals have low metabolic rate to gut capacity ratios and can afford to eat large quantities of fibrous food which are retained for

Table XIII.2. Rumen turnover times (RTT) of particulates and calculated optimal retention times (ln 2/-kd) of moose, wapiti and cattle fed four diets during winter and summer 1982.

Diet	RTT (hr)	Optimal Retention Times (hr)
Winter		
Grass		
Moose	28.2	15.5
Wapiti	17.2	18.0
Cattle	20.7	20.9
Alfalfa		
Moose	32.7	8.9
Wapiti	17.6	7.9
Cattle	21.1	14.6
Aspen Twigs		
Moose	19.3	11.8
Wapiti	17.2	8.6
Cattle	23.8	9.3
Summer		
Grass		
Moose	18.1	30.7
Wapiti	16.8	21.2
Cattle	17.6	22.1
Alfalfa		
Moose	19.1	17.0
Wapiti	20.9	16.0
Cattle	21.4	14.8
Aspen Foliage		
Moose	12.4	8.7
Wapiti	14.0	9.6
Cattle	14.6	15.0

maximum digestion (Demment and Van Soest 1982).

Because of greater energy requirements, I would expect small ruminants (browsers) to allocate more time searching for highly digestible food. Browsers must use energy dense and rapidly degrada[illegible]bstrates in order to meet the high metabolic demands of their small body. In adapting to its niche, the small browser has traded off the ability to digest fibrous forage in exchange for rapid passage of highly lignified food through the digestive tract. To counteract the high energy requirements, these herbivores consume forages high in readily fermentable cell solubles. Because absolute quantities of intake are much lower, these animals have more time to search for small patches of high quality food. This trophic strategy permits browsing ungulates to exploit forest habitats. Obviously, the large body size of the moose is a contradiction to this "Bell-Jarman Principle". For moose to follow the trophic lifestyle of a browser, they benefit from rapid passage of large particles through the digestive tract. This unrestricted nature of digesta passage and mobility of the larger body reduces limitations of intake.

F. Large vs Small Body Size

Forage Abundance

The oscillative nature of the availability of food biomass can influence foraging efficiency and eventually animal survival. Forage consumption rates of moose are reduced by more than one-half during winter from intakes during summer. This reduction in intake of nutrients undoubtedly taxes body tissue reserves as animals experience a negative energy balance. Although larger ruminants, such as the moose, have greater intake requirements, they can confront periods of food scarcity more favorably. The adaptation of relatively lower metabolic needs concomitant with the larger body size enables these animals to withstand food deprivation for longer periods (Case 1979) which occur in the boreal forest.

Thermal Stress

There can be little doubt that the larger body size of a moose is favored in cold boreal environments. As discussed in Chapter I, energy requirements scale approximately to the three-quarter power of body weight which implies that relative energy costs must decrease with a large body size. Large ruminants, such as moose, minimize heat loss by the low surface area to volume ratios. In contrast, ungulates with a small body size, such as deer, have a greater propensity to lose heat and must develop other energy-conserving mechanisms (behavioral and physiological) (Eisenberg 1983) to escape from the demands of high energy requirements.

Size favors a small-bodied animal in extreme heat. Due to a larger relative surface area, smaller ungulates, such as the deer, dissipate heat more rapidly than the larger moose. Effects of heat loading are substantial for moose as would be expected from their large body size. However, a morphological advantage for the moose is provided by the appendages which undoubtedly facilitate thermoregulation in a warm environment. Moose, throughout their boreal range, utilize aquatic habitats which may help dissipate heat. I can conclude that, while the large body size relaxes the constraints of cold environments, the stress imposed by heat actually limits the southern distribution of moose (Telfer and Kelsall 1974).

G. "Bell-Jarman Principle" - Generalization or Rule?

The theory known as the "Bell-Jarman Principle" has been proposed to explain how body size affects social behavior and diet selection in ruminant species (Bell 1969, 1971, Jarman 1974). While it generally explains distributions in ruminant body size relative to available forage resources, it fails to explain exceptions which violate the concept. For example; the reedbuck (*Redunca* spp.) and sheep (*Ovis aries*) are small in body size, yet are not especially selective for high quality forage (Hudson 1985). Conversely, two extremely large ruminants, the giraffe and moose, have each adapted to the niche of the concentrate selector. It is evident that for the giraffe and moose to exist food resources must be clumped. In such a case, long legs facilitate travel throughout the the niche in search of new patches of browse which may be widely dispersed. Although the theory of the "Bell-Jarman Principle" is justifiable in most instances and has been persuasively argued by Geist (1974), it is a generalization which oversimplifys and fails to explain many of the exceptions, such as the large browser, the moose.

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