A REVIEW OF MOOSE FOOD HABITS STUDIES IN NORTH AMERICA

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A REVIEW OF MOOSE FOOD HABITS STUDIES IN NORTH AMERICA[1]

J. M. PEEK[2]

Department of Entomology, Fisheries and Wildlife,
University of Minnesota, St. Paul, Minnesota, United States

Résumé

Cet article passe en revue 41 études portant sur les habitudes alimentaires de l'orignal, dont 13 ont été effectuées dans la cordillière intérieure, 6 en Alaska et 22 au Canada, au Minnesota, à l'Isle Royale et dans le Maine. Seulement neuf de ces études traitent des habitudes alimentaires estivales, alors que seulement quatre de celles-ci traitent de la phénologie annuelle des habitudes alimentaires de l'orignal et seulement deux études s'étendent sur plus d'un an. Les variations locales des habitudes alimentaires sont très importantes et des généralisations concernant les espèces préférées, sans que soit corroborée l'information pour une région donnée, apparaissent risquées. Une combinaison des méthodes utilisées semble pertinente, car chaque méthode a ses restrictions propres. Bien qu'une vue d'ensemble pour l'Amérique du Nord puisse être tracée à partir de l'information disponible, l'auteur conclut néanmoins que les données manquent pour comparer, entre différentes régions, les patrons d'utilisation annuels, saisonniers de même qu'en fonction des différents types d'habitats. L'auteur estime qu'il est essentiel d'évaluer les habitudes alimentaires avant d'apprécier les conditions du milieu et leurs changements, ou, avant d'entreprendre des recherches portant sur la valeur nutritive et la digestibilité des différentes espèces végétales concernées.

Abstract

This review covers 41 studies of moose food habits, including 13 from the intermountain west, 6 from Alaska, and 22 from Canada, Minnesota, Isle Royale, and Maine. Only nine of these studies include information on summer food habits, only four on year-long food habits and only two studies were longer than one year. Local variations in forage preferences were very important, and generalizations about preferred food items without confirming data for any given area appeared risky. A combination of methods for obtaining food habits data appears the most useful, since any given method in use has limitations. It was concluded that, although a generalized picture of moose forage preferences for the North American ranges can be obtained from the data on hand, there was not enough information to compare the annual, seasonal, or habitat-type forage use patterns between areas. Evaluation of forage preferences is a prerequisite to evaluating habitat conditions and trends, and investigations of nutritive values and forage digestibility.

Introduction

Food habits express a fundamental relationship between animals and their environment. The feeding habits and plants used by moose for food should be ascertained in order to fully understand the interspecific, intraspecific and environmental relationships of the species. A variety of moose food habit studies have become available since Peterson (1955) compiled the availa-

[1] Paper No. 8170, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, Minnesota 55101.

[2] Present address: College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho 83843.

ble data in the 1950's for North America. The purpose of this review is to bring all known studies together for the continent and summarize the major findings.

It has been well established that moose are primarily a browsing species, especially during winter. Moose occupying western ranges seem to use willows (*Salix* spp.)[3] as a primary food source (Hosley, 1949), while trees such as paper birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*) assume importance on the eastern ranges (Pimlott, 1961). Forbs and aquatic plants may be important during the growing season, while grass and grass-like plants assume relatively little importance, with some exceptions. Food habits studies have been summarized according to general region as follows: (1) Alaska; (2) the mountain states of Idaho, Montana, Utah, Washington and Wyoming; (3) western Canada (British Columbia-Manitoba); (4) eastern Canada, Isle Royale, Maine and Minnesota.

Alaska food habits studies

Spencer and Chatelain (1953) provide data on moose food habits in south-central Alaska based on spring browse surveys (Aldous, 1944). Willows and Kenai birch (*Betula kenaica*) head the winter preference list, and quaking aspen was considered important because of the quantity of forage it produced. Cottonwoods (*Populus balsamifera*), high bush cranberry (*Viburnum edule*), red elder (*Sambucus racemosa*), rose (*Rosa* spp.) and raspberry (*Rubus idaeus*) were less important browses in the diet. Willow, birch, aspen and cottonwood supplied 95 percent of the winter forage in their studies. Conifers were apparently not important in the diet of Alaskan moose, primarily because the two major species present, white spruce (*Picea glauca*) and black spruce (*Picea mariana*), were not palatable (Murie, 1944).

Spencer and Hakala (1964) recorded *Salix depressa, S. scouleriana, S. arbusculoides*, and *S. barclayi* as particularly important willow species on the Kenai peninsula. These species attain small tree size in that area. Bog birch (*Betula glandulosa*), dwarf birch (*B. nana*), serviceberry (*Amelanchier alnifolia*), mountain ash (*Sorbus scopulina*), and high-bush cranberry were considered of minor importance. Hosley (1949) reported work done by L. J. Palmer on the Kenai in the 1930's which indicates that tree and ground birches, willows, mountain ash, red and black currant (*Ribes* spp.) and serviceberry were highly palatable. The winter diet according to Palmer was mainly willows, ground birches, cottonwood and the green bases of bunch and marsh grasses.

LeResche and Davis (1973) provide information on moose food habits from Kenai peninsula. Summer foods of three semi-tame moose were two thirds birch leaves, one fourth forbs, including cloudberry, (*Rubus chamaemorus*), sundew (*Drosera rotundifolia*), fireweeds (*Epilobium angustifolium* and *E. latifolium*) and lupine (*Lupinus nootkatensis*). Mushrooms were eaten whenever encountered and grasses, sedges and aquatics constituted about ten percent of the observed diet.

Winter forages varied according to conditions of winter range. When snow depths were less than 30 cm sedges were used. After snow depths increased beyond that figure, birch stems

[3] Scientific plant names follow Fernald (1950) for eastern North America, Davis (1952) for the mountain states and Hultén (1968) for Alaska.

comprised 72 percent of the use from February to May, low-bush cranberry (*Vaccinium vitis-Idaea*) 26 percent, willows and alder (*Alnus* spp.) 6% each, and occasionally a fruticose lichen (*Peltigera sp.*) was taken on range considered to be representative of the wintering area.

On depleted ranges, browse consumption declined to 23 percent of the diet between February and May, with birch predominant, while lichen consumption increased to 24 percent. In late April and May, when snow depths declined, lichens and low bush cranberry comprised most of the diet. The northern Kenai Peninsula wintering area exhibits moderate snow conditions, which provide access to low-growing shrubs and forbs and lichens. The more persistent snows of interior Alaska require that taller browse species be available for moose in winter. The Kenai work also reflects changes in food habits relative to availability, where lower-growing forms were used more on heavily used range. Murie (1944) considered willows the major summer and winter food of moose in Mt. McKinley Park. Dwarf birch was regularly browsed. Quaking aspen (*Populus tremuloides*) and cottonwood were used, but were less important because of their limited occurrence. Murie (1944) started that grasses, sedges, various herbs and submerged vegetation was eaten in summer.

The following willows, listed in order of decreasing preference, were important forage species in interior Alaska near Fairbanks (Milke, 1969): *Salix interior, S. alaxensis, S. arbusculoides*, and *S. pulchra*. The relative abundance of a species did not seem to affect the utilization, perhaps due to inherent palatability differences detectable to the moose. However, less palatable species were more heavily utilized when in proximity to species of higher palatability. Milke's analysis showed that the tallest plants (over 151 cm) were preferred. A positive correlation between plant density and intensity of browsing was also noted, suggesting that the stands were not acting as barriers to moose. A combination of high moisture, protein, and caloric contents were possibly related to the high preference for *Salix alaxensis*, and the low values of *S. niphoclada* could explain its low palatability, although such conclusions were considered tentative.

Montana, Utah, Washington and Wyoming food habit studies

Since Peterson (1955) mentioned the lack of detailed moose food habit studies on western ranges, several studies have become available. These studies generally support the contention that moose primarily depend upon willows for forage on western ranges. The feeding site examination method (Cole, 1956) and rumen analysis (Martin *et al.*, 1946) have been the main means of obtaining data in the following studies.

Comprehensive food habits studies have been done in Jackson Hole, Wyoming and southwestern Montana areas. These areas represent two generally different types of moose winter range in the intermountain west. The Jackson Hole winter range (Harry, 1957; Houston, 1968) was mostly an extensive valley wherein floodplain vegetation was the major area used by moose. Some use of adjacent forest communities was also recorded (Houston, 1968). Knowlton (1960) reported that willow bottoms, the most extensively used winter range, were limited to moist areas along streams and springs in the Ruby River area of Montana.

This study area of 148 km² contained 58.3 hectares of willow bottom communities along 33.5 km of streams (Peek, 1961). While willow communities generally typify moose winter range in the mountain west, some areas are much more extensive than others. This causes considerable variation in length of time used, and degree of concentration of moose on the willow. Densities on the extensive willow community in Jackson Hole, ranged up to 19.3 moose per km² in winter (Houston, 1968). Harry (1957) and Houston (1968) reported winter moose food habit studies in Jackson Hole. Harry (1957) rated serviceberry (*Amelanchier alnifolia*), red osier dogwood (*Cornus stolonifera*), mountain ash (*Sorbus scopulina*), bog birch (*Betula glandululosa*), snowbrush (*Ceanothus velutinus*) and bitterbrush (*Purshia tridentata*) as "very highly palatable" to moose in winter. Since willows (*Salix* spp.) made up over three quarters of the winter diet and were extensively distributed on winter ranges, he considered these the most important forage species. Houston (1968) regarded blueberry willow (*Salix pseudocordata*) as the "key" forage plant. Forage preferences were related to vegetative type and blueberry willow, interior willow (*S. interior*) subalpine fir (*Abies lasiocarpa*) and bitterbrush were species receiving 50 percent or more of the use observed on the specific types in which they occurred. While Harry felt that red-osier dogwood, service-berry, mountain ash, and bog birch were in danger of being eliminated from the winter range in 1954, an indication of the degree of use these species received, Houston reported that condition of red osier dogwood and interior willow plants improved from 1964 to 1966 suggesting that the winter range was less intensively browsed during his study. While individual subalpine fir trees were often browsed heavily, the average percent of browsed trees was light during Houston's studies, which may indicate differences in palatability among individual fir trees. In this area, willow conditions have varied over the 1950-1966 period, suggesting differential browsing pressure. In 1966, 3 to 5 year old blueberry willow stems were producing most of the forage and receiving most of the use for this species, older live stems being severely hedged and younger stems being unbrowsed.

Bitterbrush and chokecherry (*Prunus virginiana*) were the only two species which Chadwick (1960) observed eaten by moose on the Juniper Buttes, Idaho winter range.

Knowlton (1960) reported moose winter food habits in the Ruby River area of Montana. Early winter foods of importance were willow, subalpine fir and currant (*Ribes* spp.). Later, willows, silverberry (*Eleagnus commutata)* and thinleaf alder (*Alnus tenuifolia*) were important. Willow constitued 67 and 59 percent of the early and late winter diets, respectively. This range was being heavily browsed at that time, with willow and silverberry plants deteriorating in condition (Peek, 1963).

Browse constituted 99.8 percent of the observed diet in winter on the Red Rock Lake Refuge, Montana, with *Salix myrtillifolia*, *S. planifolia*, *S. bebbiana*, and *S. geyeriana* each constituting over 10 percent of the use (Dorn, 1970). Red osier dogwood was not important because of its scarcity. Use of low-growing species like *S. wolfii* and bog birch was limited to early winter when they were available to moose browsing close to the snow level. Use of *S. wolfii* in summer by cattle was also heavy, probably because the low growth form renders it available. In the Douglas fir type, subalpine fir received mo-

re use than Douglas fir (*Pseudotsuga menziessi*), but use was restricted to certain trees which seemed to be consistently browsed.

Smith (1962) and Stone (1971) reported moose food habits in the Rock Creek area of western Montana. Willows comprised the major share of the winter diet; *Salix discolor* and *S. lemmoni* were preferred to *S. commutata*. Plants less than 15 years old received the heaviest use. Red osier dogwood was important in March. On this range, red osier dogwood was either very heavily used or, else, was in poor condition affording only limited forage.

Stevens (1970) reported food habits studies on a mountain winter range in the Gallatin region of Montana. Timber types received 82 percent of the observed use during the study period. Willow constituted 25 percent of the diet, sub-alpine fir 16 percent, mountain maple (*Acer spicatum*) 16 percent and red osier dogwood 11 percent. This winter range was being heavily used.

Wilson (1971) reported that *Salix drummondiana* made up 92 percent and *S. geyeriana* made up 4.7 percent of the total observed winter browse use in the Uinta Mountains of Utah. River birch (*Betula occidentalis*) comprised 2 percent of the use and 7 other species were observed to be browsed.

Poelker (1972) found browsing on false box (*Pachistima myrsinities*) in early fall in the Kalispell Basin of northeastern Washington. As snow covered this species, snowbrush, Douglas maple (*Acer glabrum*) and willows were taken. In mid-winter, instances of browsing on lodgepole pine (*Pinus contorta*) and alders were noted.

Table I provides a resume of important moose winter forage species as derived from six studies reported for five areas of the intermountain west. While willows were the primary forage plant in three of the four areas, all of the studies indicated that red-osier dogwood was a more palatable forage species, although it was less abundant and therefore less important than willows. Subalpine fir was an important forage species in the spruce-fir communities. Douglas fir received only limited use in the Jackson Hole and Gallatin studies, but Smith considered it to be a palatable species. Lodgepole pine (*Pinus contorta*) received sparing utilization.

Bog birch, silverberry, snowbrush, serviceberry, chokecherry, currant, mountain ash, mountain maple, and bitterbrush are palatable browses to moose and may be important locally. *Salix discolor, S. lemmoni, S. myrtillifolia, S. pseudocordata, S. drummondiana, S. geyeriana*, and *S. interior*, all taller growing, seem to be preferred willow species.

Forbs, grasses and grasslike plants receive only sparing use by moose in winter. Harry (1957) did not record use of these forage classes, but Houston (1968) recorded use on bluegrass and bromegrass on agricultural (hayfield) situations in Jackson Hole. Green algae received use in aquatic situations. These forage classes received less than one percent of the total winter forage in Houston's studies.

Elk thistle (*Cirsium foliosum*) and niggerhead (*Rudbeckia occidentalis*) received less than one percent of the winter use in Knowlton's study. Stevens (1967) however, reported that grass and grass-like plants constituted 26 percent of the contents of 10 moose rumens taken in December and January on a winter range associated with hay fields in the Big Hole valley of Montana. Since snow depths were high enough

TABLE I

Winter food habits of shiras moose on western ranges

Reference	*Location*	*Years*	*Most important species*	*Remarks*
Houston, 1968	Jackson Hole, Wyo.	1967	*Salix pseudocordata*[1], *S. wolfi*, *S. interior*, *S. lucida*, *Abies lasiocarpa*.	Feeding site examination
Knowlton, 1959	Gravelly Range, Montana	1959	*Salix* spp., *Ribes* spp., *Abies lasiocarpa*, *Populus tremuloides*, *Eleagnus commutata*, *Alnus tenuifolia*.	Early winter ; 95% of forage late winter ; 96% forage feeding site examination
Smith, 1962	Rock Creek Montana	1959	*Salix* spp., *Cornus stolonifera*, *Populus tremuloides*, *Shepherdia canadensis*, *Physocarpus malvaceus*, *Rosa* spp., *Pinus contorta*.	Rumen analysis Feeding sites ; *Salix* 90% (*S. discolor*, *S. lemmonsi*)
Harry, 1957	Jackson Hole, Wyo.	1954-54	*Salix* spp., *Abies lasiocarpa*.	See text for additional details
Stevens, 1970	Gallatin, Montana	1966	*Prunus virginiana*, *Cornus stolonifera*, *Salix scouleriana*, *S. myrtillifolia*, *S. drummondiana*, *Ribes* spp., *Amelanchier alnifolia*.	Dec.-March feeding site examination
Dorn, 1970	Red Rock Refuge, Montana	1968-69	*Salix myrtillifolia*, *S. geyeriana*, *S. planifolia*, *S. bebbiana*, *Betula glandulosa*	Feeding site examination, Dec. 20, 1968 – March 17, 1969,

[1] Houston (1968:16) indicates that the following willow species may be synonymous in his data : *Salix myrtillifolia* and *S. pseudocordata*.

to make this forage class generally unavailable, haystacks were considered the main source of grass forage in the area. Smith (1962) reported that grasses, grass-like plants, and forbs received less than one percent of the observed winter diet on his study area, while Stone (1971) reported some use of bull thistle (*Cirsium vulgare*) and lupines.

Browse species apparently constitute increasingly greater percentages of the Shiras moose diet from early to late fall. Knowlton (1960), Houston (1968) and Smith (1962) reported that browse plants constituted from 70 to 90 percent of the fall diets. Willow, subalpine fir, currant, aspen, huckleberry (*Vaccinium scoparium*) mountain ash, serviceberry, *Ceanothus*, bitterbrush, buckthorn (*Rhamnus* sp.), honeysuckle (*Lonicera canadensis*), paper birch (*Betula papyrifera*) and red osier dogwood were important fall forage plants. Forbs and grasses comprised relatively larger percentages of the fall diets than winter diets. There was more variation in the fall diets between areas than in the winter diets, perhaps because the use of a greater number of vegetative types occurred in the fall, and there was greater chance of variation in communities between areas.

Summer food habits studies reveal even greater variation between areas. In Yellowstone National Park, McMillan (1953) recorded willow as 88.5 percent, aquatics as 9.3 percent, and grasses and forbs as 2.2 percent of the diet, based on amount of time spent feeding on each forage class. *Salix geyeriana* was used three times more frequently than *S. wolfii*. Bluegrasses and wheat grasses (*Agropyron* spp.) were the grass species utilized.

Knowlton (1960) reported that browse constituted 28.6 percent, forbs 70.6 percent, and grasses and grass-like plants 0.6 percent of the summer diet in the Gravelly Range area. Willows comprised 19.3 percent and sticky geranium (*Geranium viscosissimum*) 64.2 percent of the diet. This area is one example of a western moose range wherein aquatic vegetation is extremely limited because of the high gradient nature of streams.

Houston (1968) reported that browse constituted the greatest share of the summer moose diet in the Jackson Hole area, with willow again receiving extensive utilization. Quaking aspen (*Populus tremuloides*) menziesia, (*Menziesia ferruginea*), thimbleberry (*Rubus parviflorus*), Utah honeysuckle (*Lonicera utahensis*), and fireweed (*Epilobium* spp.) were other important items. Water crowfoot (*Ranunculus aquatilis*) and leafy pondweed (*Potomageton foliosus*) were used extensively in aquatic situations.

Dorn (1970) found that *Salix myrtillifolia, Salix geyeriana,* and *Salix planifolia* and bog birch leaves constituted 86% of the summer moose diet at Red Rock Lakes Refuge, Montana. Most leaf-stripping occurred on plants over one m tall. Use of aquatics was considered minimal.

Knowlton (1960), comparing the various summer food habit studies of moose available, felt that variations were attributable to differences in vegetation on the study areas. Subsequently, Peek (1961) reported that on the Gravelly-Snowcrest study area, browse increased in importance during summers which were drier than the 1958 summer from which Knowlton obtained data. Consequently, it appears that annual variations in food habits of moose may occur within the same area.

Western Canadian food habit studies

In British Columbia, Hatter (*fide* Hosley, 1949) considered red-osier dogwood, paper birch, willows, serviceberry, quaking aspen, mountain ash (*Sorbus scopulina*) and bog birch to be palatable winter moose forage plants. Cowan, Hoar, and Hatter (1950) added hazel (*Corylus californica*), highbush cranberry (*Viburnum pauciflorum*), and alpine fir (*Abies lasiocarpa*). Scouler and Bebb willows (*S. scouleriana, S. bebbiana*), were the important willow species. Douglas Fir (*Pseudotsuga menziesii*) was seldom eaten on their study areas. These data suggest that moose food habits in British Columbia more closely approach those of moose on more eastern ranges, as will be reported.

Ritcey (1965) recorded instances of use of forage by moose on the Wells Gray Park, British Columbia, winter range. Willow and false box (*Pachistima* sp.) comprised over 75 percent of the observed use, with paper birch, hazel and red osier dogwood also receiving use. Extensive overlap in the diets (but not the areas of use) of moose and mule deer (*Odocoileus hemionus*) was found. An experimental clear-cutting increased browse production and utilization by moose for at least four years following the cutting.

Aquatic species used by moose in summer at Bowron Lake Park, B. C., included swamp horsetail (*Equisetum fluviatile*), burreed (*Sparganium* spp.), and pondweeds (*Potomageton richardsonii, P. robinsii, P. gramineus, P. natans*, and *P. amplifolius*, in order of importance) according to Ritcey and Verbeek (1969). Aquatic plants appeared to form the bulk of the summer diet. Burreeds were considered to be the chief aquatic food in Wells Gray Park by these investigators.

Analysis of 23 moose rumen contents collected in February 1970 in Cypress Hills Provincial Park in southeastern Alberta was reported by Barrett (1972). Serviceberry comprised 56 percent of the identified material on a dry weight basis, quaking aspen 21 percent and *Prunus* spp. 12 percent. Red osier dogwood, willows, honeysuckle, *Clematis* spp. Rosa spp. and lodgepole pine contributed less than 10 percent of the identifiable material. Cypress Hills form a low plateau surrounded by treeless grass plains, an island of moose habitat. The moose population increased from a transplant of four animals in 1956 to 130-180 animals in 1970, and severe browsing was common at the time of collections. This study represents the highest proportion of serviceberry reported in the diet of moose, and Barrett considered this species to be preferred over willow.

Howard (pers. comm.) reported that browse surveys along the Saskatchewan River delta in northern Manitoba taken by J. E. Bryant in 1955, showed that red osier dogwood and willows were the main species eaten. Balsam fir, quaking aspen, *Viburnum* spp. box elder (*Acer negundo)* balsam fir, balsam-poplar (*Populus balsamifera*) and raspberry (*Rubus idaeus*) were also commonly taken. In more southerly portions of moose range in Manitoba, mountain maple, quaking aspen and hazel appeared to be important.

Eastern Canadian, Isle Royale, Maine and Minnesota food habit studies

Moose food habits have been investigated primarily in winter in eastern North America. Newfoundland studies include those of Dodds (1960), Pimlott (1953), and Bergerud and Manuel (1968).

Dodds (1960) recorded 35 species of woody plants browsed by moose based on examination of browsing intensities on woody plants within sampling plots. In an area of high moose density dominated by balsam fir, winter browse use was chiefly on balsam fir (47 percent), white birch (20 percent), and raspberry (13 percent). In a lighter moose density area dominated by uncut white spruce (*Picea glauca*) and balsam fir, balsam fir constituted 44 percent, willows 22 percent and alder 11 percent of the winter browse use. On a cutover area of high moose density, fire cherry (*Prunus pennsylvanica*) was 29 percent, white birch 25 percent, balsam fir 15 percent and quaking aspen 10 percent of the diet.

Pimlott (1953) considered balsam fir and white birch the two species of universal importance to moose in Newfoundland. White birch was the most important browse species in habitats which had been burned or logged, containing low or moderate moose densities (Pimlott, 1963). Balsam fir exceeded white birch in the diet where high density populations existed. Yew (*Taxus canadensis*) was most seriously affected by moose browsing, being highly palatable and relatively intolerant to browsing (Pimlott, 1963). Pimlott thought it possible to classify browse conditions on the basis of use of these three species. If yew was highly or moderately used, the range was below carrying capacity and many palatable browse species would be available. If white birch was available, balsam would provide a small percentage of the winter food. If fir was heavily browsed, yew would be killed out and the palatable deciduous species would be severely overbrowsed and a portion eliminated from the habitat. It should be noted that the absence or scarcity of yew may not be attributable to moose in some areas, including eastern Minnesota where this species occurs infrequently on the major moose range as well as on areas where moose and deer are scarce.

Evaluation of the ability of 12 year-old balsam fir to withstand varying amounts of browsing was determined by Bergerud and Manuel (1968). Over half of the trees from which 75% of growth was removed died two years after clipping, while only one of ninety clipped at 10-50% levels died. It was not stated whether current or total growth was removed. Balsam fir trees four-foot tall were found to withstand up to 12 years of heavy browsing without dying. A preference for balsam fir with dark green needles over chlorotic, light green colored fir was noted. Crude protein content was lower in chlorotic fir, indicating that moose were selecting the most nutritious plants. Clipping experiments resulted in some darkening of the foliage of chlorotic fir. Light browsing may improve protein content by stimulating adventitious nutrient-rich shoots.

It is significant that these investigators doubted that an equilibrium between moderate moose densities and a quantity of highly palatable diversified winter moose foods could be maintained in Newfoundland, because of inaccessibility of many moose to hunters, because foods such as yew and quaking aspen could not withstand moderate use, and also because moose tended to congregate on sites wherein sought-after species were intensively utilised. However, the diet of balsam fir and white birch was considered adequate to maintain a healthy moose population.

Summer moose food habit data from eastern ranges are scarce. Dodds (1960) stated that in Newfoundland moose fed on herbaceous materials during summer. Grasses and sedges,

leaves of shrubs were commonly taken. There were few aquatic areas in Newfoundland : however, small ponds, lakes and rivers were frequented. On an aquatic area used heavily within Dodd's study area, grazing was light until late June, heavy during July and decreased in August.

Telfer (1967) reported winter range surveys in Nova Scotia. Speckled alder (*Alnus rugosa*), Canada honeysuckle (*Lonicera canadensis*), allegheny blackberry (*Rubus allegheniensis*) sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) were the five most highly preferred browse species of nine species which were used in a moose yard. Beaked hazel (*Corylus cornuta*) was ranked over balsam fir, mountain maple, Allegheny blackberry and meadow-sweet (*Spiraea latifolia*). For the entire winter range, yellow birch, red maple (*Acer rubrum*), sugar maple and mountain maple (*A. spicatum*) were important forage species.

Dyer (1948) reported browse surveys in Baxter State Park, Maine. Balsam fir, mountain maple, mountain ash, white birch and fire cherry were the five most important browse species for moose. Two types of moose yards were described in this region. On high altitude yards, near summits of mountain tops, snow depths of 2.5 to 3.2 m limited browsing to reproduction above that height. Balsam fir was stripped of lateral branches up to 1.25 cm in diameter. Low altitude yards were the most common type of yarding situation in the region. Seven species made up 99 percent of the food eaten : balsam fir, mountain maple, mountain ash, white birch, striped maple (*Acer pensylvanicum*), fire cherry and quaking aspen in that order of importance. Fir constituted 54 percent of the diet,. mountain maple 23 percent. Apparently these studies were made at a time when heavy browsing by moose was occurring in the area.

DesMeules (1965) determined winter moose food habits from browse surveys in Laurentide Park, Québec. In four yards examined, balsam fir comprised most of the winter diet, while in four other yards, deciduous species dominated the diet and balsam fir was moderately used. Mountain maple, white birch and willows were the most commonly browsed deciduous species. Red-osier dogwood, willows, and mountain ash the highest palatability ratings where available. Balsam fir became more heavily utilised as snow depths increased to highs in late winter. Fire cherry bark was used more commonly than quaking aspen, mountain ash or red maple bark, but all were fed upon where palatable twigs were available and hence were considered preferred foods. No evidence of browsing on arboreal lichens was noted although they were abundant in some areas studied.

DesMeules (1965) postulated that heavy utilization of balsam fir in late winter may save energy, since fir twigs weigh eight to 13 times more than deciduous twigs of similar length and therefore require less time and efforts to consume equivalent amounts. In one late winter yard, balsam fir comprised 86 and white birch 14% of the diet. This yard was about ten acres in size and was believed capable of supporting one moose for 200 days of winter (DesMeules, 1962).

Stomach analyses of 24 Ontario moose, one Manitoba and one Québec moose, taken from October 19 to May 5 (Peterson, 1953) indicated that balsam fir occurred in 21 of 23 stomachs where the tree occurs, and white cedar (*Thuja occidentalis*) occurred in small amounts in 4 stomachs, willow in 16,

white birch in 11, beaked hazel in 10, quaking aspen in nine, fire cherry in four, bog birch and red-osier dogwood in two and serviceberry and maple in one each.

Browsing investigations in Ontario on St. Ignace Island (Peterson, 1953) suggested that balsam fir constituted 27 percent of the available diet, white birch 12 percent, mountain maple and red osier nine percent each and highbush cranberry five percent. Considerable seasonal variation was found in foods eaten. Conifers were practically untouched from early spring to late fall. Quaking aspen was commonly barked on St. Ignace. Mountain maple was most consistently barked, though mature trees were very scarce.

The Isle Royale browse studies (Aldous and Krefting, 1946 ; Krefting, 1951) illustrate annual variations in winter utilization patterns of moose on the same range (Table II). The diet included 33 woody species but seven species (quaking aspen, white birch, balsam fir, mountain ash, willows, red osier dogwood, yew) contributed 80 percent of the total diet and three (quaking aspen, white birch, balsam fir) contributed 48 percent, based on three years of spring browse survey data. Changes in importance of individual species were primarily related to the heavy browsing which occured during the period (Krefting, 1951). Quaking aspen became less important in the diet after 1945 because the amount eaten up to then was in excess of production. Quaking aspen accounted for 54 percent of all trees and shrubs destroyed by moose in very heavy browsing situation. Conversely, whit birch, because of its higher ability to withstand browsing, increased in importance. Krefting (1951) concluded that balsam fir could not withstand continued heavy browsing and was being replaced by black spruce on Isle Royale. Yew was considered a highly preferred moose food, and was once widely distributed across Isle Royale (Murie, 1934). By 1950, it was not considered to be a source of food on the island. Mountain maple ranked higher on the palatability lists than beaked hazel, but light utilization for both species was encountered.

Krefting (1951) reported that stomachs of moose collected in the fall of 1949 contained mountain maple, balsam fir and quaking aspen. Murie (1934) reported stomach contents analysis of six moose taken between May 20 and August 10 of the summers of 1929, 1930 and 1931. Mostly browse species were found, including quaking aspen, alder, fire cherry, yew, bush honeysuckle (*Lonicera* sp), mountain maple, raspberries, beaked hazel, and willow. Small amounts of sedge, grass, mushrooms, horsetail (*Equisetum* spp.) pondweeds and large-leaved aster (*Aster macrophyllus*) were also found. Murie (1934) reported that wood fern (*Dryopteris* sp.), and swamp horsetail (*Equisetum* sp.) sedges, marsh marigold (*Galtha palustris*), jewelweed (*Impatiens* sp.) and large-leaved aster were extensively grazed. Large yellow pond lily (*Nymphaea advena*), sweetscented white pond lily (*Castalia odorata*) and *Potamageton* sp. were reported as extensively fed upon when available but were rare due to heavy use by moose on Isle Royale (Murie, 1934).

Manweiler (1941) stated that the main winter foods of moose in Minnesota were maples, ash, dogwood, hemlock (*Tsuga* sp.) quaking aspen, balsam poplar, birches, willows, juneberry (*Amelanchier* sp.), fire cherry, chokecherry and basswood (*Tilia* sp.). The basis for this was not reported, and hemlock and basswood are rare on Minnesota moose ranges. The Red

Lake area of northwestern Minnesota consists of willow, quaking aspen and bog birch communities interspersed with small stands of spruce and jack pine (*Pinus banksiana*) (Ledin and Karns, 1963). A browse survey in that area in 1949 indicated that willow formed 58 percent of the winter food, while balsam fir, white cedar, bog birch, balsam poplar, red osier dogwood, raspberry, mountain ash, aspen and tamarack (*Larix laricina*) comprised 39 percent, while black spruce, black ash (*Fraxinus nigra*), beaked hazel, white birch, highbush cranberry and alder comprised two percent of the diet. The range was considered to be in good condition. Although there was no mention of moose-deer competition for any dominant species, one suspects that white cedar was probably used more by deer than by moose.

Peek (1971) investigated forage preferences in northeastern Minnesota on a year long basis (Fig. 1), using the feeding site examination. Willows were the most important browse, yearlong, but received greatest use in September through December. Bebb and pussy willows (*Salix bebbiana, S. discolor*) were the most preferred willows. Quaking aspen was the most important browse in June, declined in value through late summer, fall, and early winter, then received increased use in mid-winter. White birch ranked third in importance year-long, and remained relatively constant throughout the year. Beaked hazel, fourth in overall importance, was most intensively used in mid-winter. Fire cherry was important primarily in summer and early fall. Red osier dogwood was used primarily in fall and though remaining important, decreased in value as the winter progressed. Virtually no use occurred until twigs reddened. June berry and mountain ash remained in the diet at low but constant levels yearlong. Balsam fir, almost entirely a wir ter forage, received progressively mor use through the winter and was a important late winter forage supply Mountain maple was used most com monly in late summer and again du ring the winter, but was never a ma jor item in the diet.

Winter severity, especially snow depth and its rapidity of accumulation (Van Ballenberghe and Peek, 1971), appears to have some influence on food habits Balsam fir and beaked hazel became important items in the diet at relatively later dates during two milder winters than during the severest winter of the study. Red osier dogwood remained important in the diet for a longer period during the mildest winter than during the others. Since movement to dense cover occurred most rapidly during the severest winter, use of forage species characteristic of communities dominated by balsam fir and the spruces also occurred earlier. Snow depths appeared to be critical in use of red osier dogwood, since many plants disappeared under one m of snow.

Except in summer, browse constituted all of the observed diet. The relative importance of forbs in summer was low, but aquatics were probably the major forage source during early summer. Yellow pond lily (*Nuphar variegatum*), wild rice (*Zizania aquatica*), pondweeds, burreed (*Sparganium* spp.) and wild calla (*Calla palustris*), were commonly used.

Table II lists the five most important browse species for ten separate surveys in six areas of eastern North America. White birch, mountain ash, mountain maple and balsam fir occurred in four of the five areas. The Nova Scotia study area (Telfer, 1967) was lightly browsed, and balsam was used only sparingly. No mountain ash or quaking aspen was reported in that study area

and Rowe (1957) does not mention mountain ash as being a common species in his description of Nova Scotia area. Balsam fir served mainly as a late winter forage in northeastern Minnesota, where forage supplies were not severely browsed by moose (Peek, 1971).

Mountain maple, balsam fir, and willows were important in four areas. Quaking aspen may be important only locally in Newfoundland. With the ex-

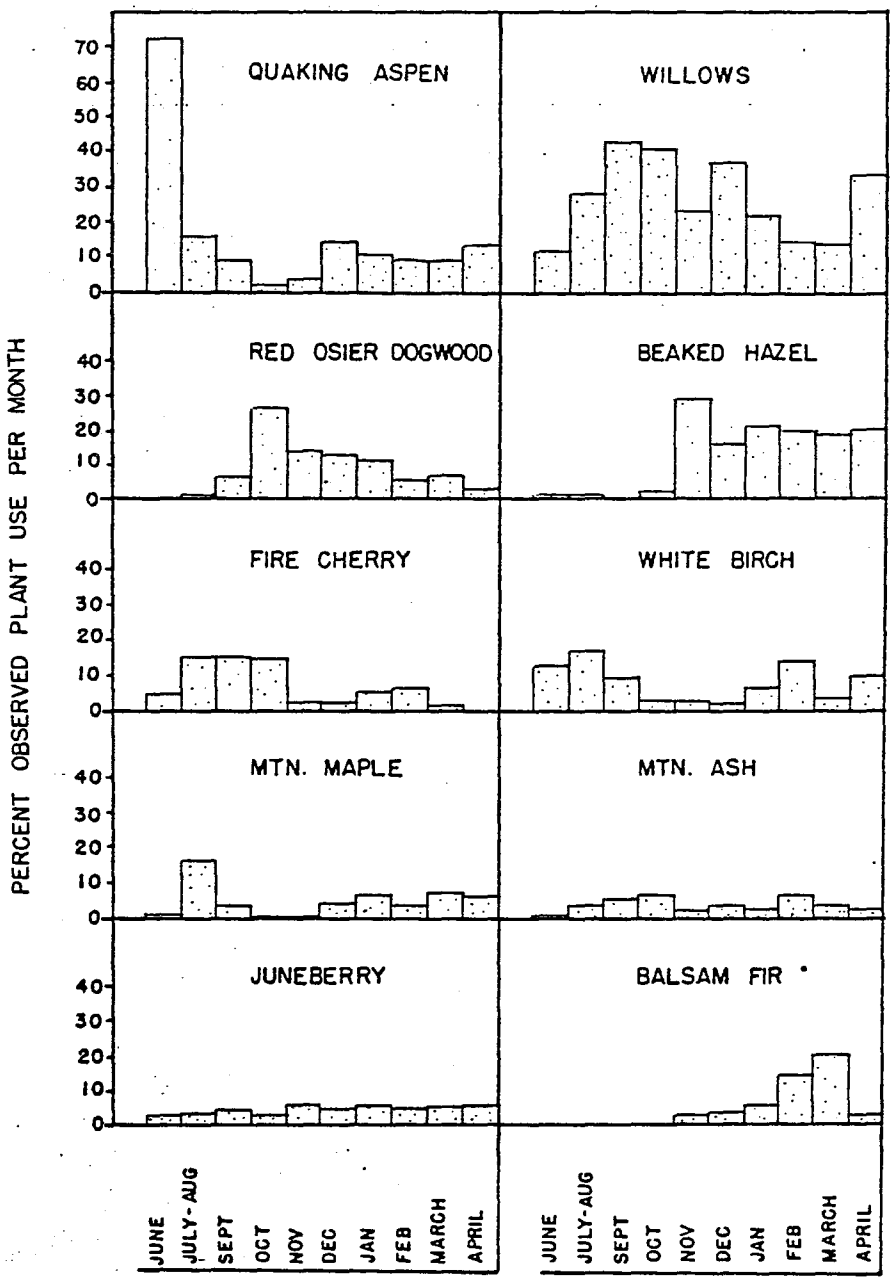

Figure 1. Percentage use of ten important browse species by moose in Northeastern Minnesota as determined by feeding site examination, after Peek (1971).

TABLE II

Important browse species to moose in eastern North America

Reference	*Area*	*Five most important browse species in order or importance*	*Remarks*
Peek, 1971	NE Minnesota	Willows, quaking aspen, white birch, beaked hazel, fire cherry	Moderately high moose population Feeding site examination technique
Aldous & Krefting, 1946	Isle Royale Michigan	Quaking aspen, white birch, balsam fir, mountain ash, willows	High moose population (1945) Browsé survey technique
Krefting, 1951	Isle Royale Michigan	Balsam fir, white birch, mountain ash, quaking aspen, willows	1948 higher moose population than 1945
Krefting, 1951	Isle Royale Michigan	White birch, quaking aspen, red-osier dogwood, willows, mountain ash	1950 lower moose population than 1945.
Peterson, 1953	St. Ignace Island, Ontario	Balsam fir, white birch, mountain ash, red-osier dogwood, mountain maple	1947-48. Most important species rather than most palatable
Dyer, 1948	Maine	Balsam fir, mountain maple, mountain ash, white birch, fire cherry	1940's, browse survey technique
Telfer, 1967	Nova Scotia	Mountain maple, yellow birch, sugar maple, red maple, Canada honeysuckle	1968 light browsing pressure, stem counts in spring (his Fig. 3)
Pimlott, 1953	Newfoundland	White birch, balsam fir, mountain maple, mountain ash, fire cherry	Stem count method, heavy browsing pressure
Dodds, 1960	Newfoundland	Balsam fir, white birch, raspberry, elderberry, june berries	High moose density, cutover area 1953, '56, '57. Area different from below.
Dodds, 1960	Newfoundland	Balsam fir, willows, alders, mountain maple, rhododendron	Low moose density, stem count method. Area different from above.

ception of areas in which balsam fir and white birch occur only sparingly or are absent, these two species appear to be major forages of moose on eastern North American ranges. Aldous (1952) concluded that white birch produces well under moderate to heavy use and should be used at least moderately if plant growth is to be kept within reach of deer. Bergerud and Manuel (1968) indicate that balsam fir has a strong survival tenacity.

The role of aquatics in the diet of moose

Moose are so frequently observed or photographed in water that it is easily assumed that the aquatic environment is a necessity for the species. However, major populations exist in areas across the continent, such as the Matanuska Valley of Alaska, the Gallatin Mountains of Montana, and the Cobequid Hills of Nova Scotia, where the aquatic habitats are of little significance. By contrasts, aquatics on Isle Royale have been reduced, following heavy use by moose (Murie, 1934; Krefting, 1951).

Use of aquatic areas has been attributed to escape from insect attack (Flook, 1959; Ritcey and Verbeek, 1969) and to the presence of palatable plants (Peterson, 1955; Murie, 1934; deVos, 1956). Use of aquatic vegetation has been correlated with the phenological state of the important forage species, yellow pond lily and wild rice, in northeastern Minnesota (Peek, 1971). Pond lily was used primarily before seed-set, and wild rice was used most before plants floated on the water surface. Use of aquatics was variable between years in that area, apparently dependent upon water levels which may control phenological development, but occurred primarily in early summer. Based on observations by DeVos (1956) and Peterson (1955) in Ontario and Peek (1971) in northeastern Minnesota, moose appeared to begin and end use of aquatics earlier further south.

Table III shows major aquatics used in ten different areas of North America. While considerable variation occurs and is to be expected, yellow pond lily, pondweeds, and horsetail appear to be preferred wherever they occur.

Discussion and conclusions

This survey has covered 41 different reports, 13 from the intermountain west, six from Alaska, and 22 from Canada, Minnesota and Maine. Since Peterson's (1955) review, at least 29 food habit studies have become available. Only nine of these studies include information on summer food habits; only four studies contain information on year-long food habits; only two were longer than one year's duration.

Although the general conclusions are that willows are important to Shiras and Alaskan moose, and that balsam fir, quaking aspen, and paper birch are important to Canadian moose, local variations in forage preferences are important. This is especially relevant because habitat management should favor the locally preferred species. However, species such as red osier dogwood may be highly preferred items in the diet across the entire Canadian moose range, but may vary in abundance enough between areas to affect management considerations. Some species such as juneberry, mountain maple and beaked hazel appear to be preferred in some areas and unimportant in others. Although woody species are generally preferred, several studies suggest that forbs and aquatics may be of high local significance to moose when available and palatable.

It therefore does not appear to be very illuminating from the mana-

gement standpoint to generalize about moose forage requirements, except that many preferred species appear characteristic of successional stages. Even this may be misleading because willows characteristic of riparian communities, or, of alpine tundra may be extremely long-lived, and mature balsam fir plants may be important winter forage sources.

The various forage species may respond to management practices in different ways. For instance, quaking aspen may sprout more readily and in denser stands from winter cutting than from summer cutting (Stoeckler and Macon, 1956), which in turn will affect the density of associated species, some of which may be more palatable than aspen. Response of various moose forage species to various cutting treatments and to prescribed burning should be further investigated.

Many of these studies do not give a measure of the intensity of utilization of the various species, which causes problems in comparing food habits between areas. Heavy browsing, to the point where forage preference and availability has been affected, may preclude determination of true forage preferences for an area. Food habits stu-

TABLE III

Summarization of aquatic plants preferred by moose in ten areas of North America

Location	*Major plants used*	*Reference*
Bowron Lake, B.C.	Swamp horsetail, burreed, pondweeds	Ritcey & Verbeek, 1969
Wells Gray Park, B.C.	Burreed	Ritcey & Verbeek, 1969
Little Missinaibi Lake, Ontario	Horsetail, eelgrass, pondweed, yellow pond lily, bullrush	deVos, 1958
St. Ignace, Ont.	Pondweeds	Peterson, 1955
Isle Royale	Swamp horsetail, pondweeds, sedges, yellow pond lily, sweet-scented pond lily	Murie, 1934
Algonquin Park Ontario	Yellow pond lily, watershield, sweet-scented pond lily	Peterson, 1955
Yellowstone National Park	Mud plaintain, water milfoil, bladderwort, pondweeds	McMillan, 1953
Alaska	Horsetail, rush, pondweed, burreed	Palmer (in Hosley, 1949)
Jackson Hole, Wyoming	Water crowfoot, leafy pondweed, hornwort, green algae	Houston, 1968
NE Minnesota	Yellow pond lily, wild rice, burreed	Peek, 1971

dies should include information on utilization and availability of forage species.

A related problem that involves considerations beyond moose management is demonstrated by the Newfoundland studies. Apparently a productive and relatively dense moose population can be maintained on a winter diet of paper birch and balsam fir, while other preferred, but less browsing-tolerant species are being eliminated. Since balsam fir was reproducing itself satisfactorily from the timber management standpoint, and the moose population was being maintained, by traditional criteria of wildlife management and forestry, the situation appeared to be satisfactory. However, when elimination or an important reduction occurs of other nonmerchantable species, the situation may be considered to be unduly altered from the standpoint of species diversity. If moose habitat management is to be fully integrated into other land uses, perhaps forage deterioration which does not affect moose densities or timber resources should not be considered the proper management goal. Of course, the problems of achieving adequate moose harvest to actually regulate densities, distributions and forage resources are among the practical limitations which must probably be given more immediate priority. Nevertheless, the wildlife biologist should be aware that resources other than moose or merchantable timber may be adversely affected under such conditions.

There is also a need to distinguish between the effects of natural succession and of previous over-utilization on forage preferences. For instance, balsam fir was important in the diet in an area of virgin timber supporting a low density moose population, as well as in a logged area supporting a much larger population which was intensively browsing the available forage in Newfoundland (Dodds, 1960). The high use of balsam fir in both situations appeared to be primarily related to availability, and may not be a good measure of the actual palatability of this species. Balsam fir appears to be less important when a variety of other species are present.

During the 1940's the use of balsam fir on Isle Royale was considered to be causing deterioration and elimination of the species, while the Newfoundland studies suggested that balsam fir could withstand very heavy use for as long as 12 years and survive. On Isle Royale, heavy browsing had caused quaking aspen to become less available and apparently white birch was replacing it as the most used item because of this.

Besides being influenced by species composition and intensity of grazing, forage preferences may be influenced by weather conditions, and general activity and whims of the animal (Stoddart and Smith, 1955). For instance, Peek (1971) found that increased use of alder during the rutting period in lowland types in northeastern Minnesota could be related to intensive rutting activity, wherein this highly abundant species may serve as displacement feeding source during moments of high interaction between individuals. Many of these food habit studies were made by examinations of browse in spring. The major disadvantage of this type of survey is that changes in forage preference which may occur during the winter cannot readily be determined, as these studies depict woody stem use for the whole period when woody stems are eaten. Moose may browse woody stems during the growing season, as well as during dormancy. When relating moose food ha-

bits to range condition-trend, it is important to know when a species is most intensively browsed: the physiological response of a shrub to browsing may be expected to differ according to its phenological state. Young and Payne (1948) found that summer use of four browse species by domestic sheep in northern Idaho had a more detrimental influence upon the plant than fall use.

Dodds (1960) listed several other problems with relying on this method to obtain food habits data: 1) rebrowsing of already browsed stems, 2) overlap in food habits between two or more species present on the same area, 3) early fall frosts may kill terminal shoots of same plants, including elders, which may resemble browsing. Also, this approach does not usually consider use of leaves. Yet, the major advantage of the browse examination, is that one does not have to locate individual animals, a tedious procedure in some habitat types; moreover, adequate sample sizes may be relatively easy to obtain and only one examination of an area during the year is necessary to obtain information.

Rumen analysis is also fraught with certain problems. Several biases of this technique include: larger plant fragments, being most easily identifiable, may not be representative of the entire rumen contents because of differential digestion between plants (Bergerud and Russell, 1964). Although this may be a minor bias when only woody stems are eaten, certain shrubs such as elder and the honeysuckles may be more quickly digested than balsam fir and willows and the smaller, more delicate stems may also be digested more quickly than the coarser stems, making identification more difficult. For animals which may frequent different habitat types during a feeding period, the method does not readily de termine forage preferences for eacl habitat type. Forage availability an(feeding habits of the animals unde various conditions are not considered Ordinarily, only a small number o rumens can be obtained, and one o two samples which may reflect aty pical circumstances may misrepresent the usual diet. Analysis is time consuming and often only a small portion of the rumen is identifiable.

Feeding site examinations require extensive field effort, but yield information which can be specific to a given habitat type. Problems using this technique include 1) determining what constitutes "fresh use" or use by the individual which one is following, 2) the fact that use on certain species such as willows and balsam fir may be more readily observable than on species in the herbaceous stratum, such as mushrooms, 3) the subjective determination of what constitutes a "bite" for each plant species, and 4) the problem of securing feeding sites on areas where tracks and sign are more readily observable but where the animal may only be cursorily browsing on its way to a more preferred feeding area which is less readily observable.

The use of "feeding minutes" as by McMillan (1953) in Yellowstone Park is applicable only to areas where the animals and forage species can be readily observed at close range, and when plant composition is simple enough that items in the diet can be readily identified. Also, whether semi-domesticated animals reflect forage preferences of wild conspecifics or not remains to be evaluated. In view of the problems associated with each method of obtaining food habits data, several approaches should be used whenever possible.

It must also realized that a short-term study may not provide adequate information on the forage preferences of moose for any given area. Preferences have been found to vary between years in southwestern Montana and on Isle Royale. And on areas as close together as Yellowstone Lake, the Ruby River of southwestern Montana, and Jackson Hole, Wyoming, summer food preferences appear to be quite different.

Assessment of winter forage sources alone may not provide enough information to determine whether forage supplies are a limiting factor or not; spring, summer and fall diets may have an important influence on production and survival, as indicated for deer (Klein, 1970). Most certainly a knowledge of year-long forage requirements will be important in effecting proper management involving habitat manipulation. Peek (1971) recommended logging practices that would favour creation of areas which could provide spring and fall habitats for moose as an important management procedure in northeastern Minnesota.

Food habits data are probably best interpreted when supporting information on habitat condition and trend, and population performance are also available. Until a measure of actual forage preferences of a population in a given area can be obtained through experimental procedures, habitat and population performance are meaningful ways of determining the adequacy of a diet based on field observation.

It is concluded that these studies do not depict food habits well enough to adequately compare annual, seasonal and habitat-type forage use patterns in all but a few instances. Trends in food habits according to successional sequence are inadequately reported. The influence of weather, precipitation, plant phenology and succession, as well as social behaviour, on forage use should be further investigated. A knowledge of forage requirements and preferences is prerequisite to investigations of nutritive values and digestibility of forage sources.

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