SUMMER BROWSING BY MOOSE IN RELATION TO PREFERENCE, AND ANIMAL DENSITY: A NEW QUANTITATIVE APPROACH

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Abstract: We measured the summer diet of moose in two study areas at Isle Royale, Michigan, by counting recently browsed stems, inventorying the numbers of plants fed upon, and estimating intake rate from direct observation of feeding animals. Applying these techniques in two study-area forest types, we found that among species important as summer browse, *Sorbus americana* and *Acer spicatum* were preferred over *Betula alleghaniensis* and *B. papyrifera*; this was based on relative frequency in the diet compared to relative availability. An average adult moose consumed about 4.2 kg/day of browse, dry-wt; total consumption was 4.8 kg/day because moose were also eating aquatic vegetation. Based on intake per animal and removal of browse per unit area, summer density averaged 3.8 adult equivalents/km^2, a relatively high level. Current browsing pressure upon the plants appears responsible for a trend of decline in the abundance of preferred species.

As part of a program to measure the flux of energy and minerals in the soil-vegetation-moose-wolf system at Isle Royale National Park, Michigan, we have been analyzing the quantity and species composition of food taken by moose. The island, maintained primarily as a wilderness park and lying in the northern Lake Superior, is one of the few sites in the world today where one can observe interactions, undisturbed by man, among original, major components of a northern-forest community. We began this study by focusing on summer, the season of greatest nutritional demands in moose and the period of growth and reproduction in plants; soon we will be measuring foraging during other seasons. This is a partial report on work carried out during summer 1972; a more complete one is in preparation and will include results of aquatic-feeding studies (Belovsky et al.).

Isle Royale, a 550-km^2 archipelago (referred to here as "the island"), is forested with boreal and northern-hardwood elements. Interspersed over the island are many poorly drained areas, beaver ponds, and inland lakes. Moose were not known at Isle Royale until the early 1900's when they appeared and, in the absence of wolves, displayed an irruptive population growth culminating in die-offs during the 1930's. Wolves arrived in the late 1940's, after which the moose population appeared to be more stable than before. In recent years, however, the population has increased without a concomitant increase in wolves (see discussion in Jordan et al. 1973, this volume). These points and other natural history aspects are covered in reports on ecological studies at Isle Royale dating back nearly 70 years: Adams 1909, Cooper 1913, Murie 1934, Aldous and Krefting 1945, Krefting 1951, Mech 1966, Shelton 1966, Jordan, Shelton and Allen 1967, Jordan, Botkin and Wolfe 1971, and Allen et al. 1959-1973.

All studies reported here were conducted during 1972 in two areas at the west end of the island. The study areas were delineated by forest type during 1971 when production and mineral content of available moose browse was measured (Jordan et al. in prep.). In 1972 the soils of these areas were surveyed (Dominiski in prep.). Production, mineral composition, and utilization by moose of aquatic vegetation in ponds adjacent to or contained within these study areas is also under investigation.

The study areas are known as "Yellow Birch" and "Coastal". The former is dominated by a partial canopy of mature *Betula alleghaniensis* with *B. papyrifera*, *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* also in the canopy. Understory includes reproduction of all the canopy species plus *Sorbus americana*, *Corylus cornuta*, *Lonicera canadensis*, *Diervilla lonicera*, *Acer spicatum*, and *A. saccharum*. The site lies several kilometers from the shore of Lake Superior. The Coastal area lies close to the lake shore and tends to have poorer growing conditions than the Yellow Birch. With its cool, often foggy weather, the Coastal supports a more boreal forest dominated by *Abies* and *Picea*; intensity of lake storms causes extensive wind-throw openings in the canopy. *Betula papyrifera* is the dominant deciduous tree in the Coastal study area, occurring commonly in the understory along with *Sorbus*, *Acer spicatum*, and *Prunus pennsylvanica*. In both areas, moose browsing greatly suppresses tree reproduction, leading to canopy openings which in turn promote a productivity of shrubs not commonly observed in similar-aged stands of the region.

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METHODS

Browse-utilization methods described elsewhere were not appropriate for our investigation. McMillan (1953) relied on direct observations of moose for all his data. We attempted this, but the lack of open vegetation at Isle Royale and the need for replication among a number of individual animals showed this to be inadequate. Krefting (vide Hosley 1949) used visual estimates of browsed vegetation, but his method is not sufficiently quantitative to permit statistical analysis.

In 1971 our group initiated measurements of production and utilization by protecting sets of plants within randomly placed small exclosures (ca 4-m diam.); plants were selected outside to match each one inside, and utilization was measured by the difference in current growth, clipped and weighed, at the end of summer as well as at the end of winter. This technique has proven unsatisfactory, both economically and statistically.

In summer 1972, we developed an integrated technique involving transects, plots, and direct observation upon feeding animals. Current browse removals were counted along transects; plant densities and biomass removed were tabulated in plots; and feeding rates by plant species were determined from close observations of moose. These measures were then combined to estimate composition of diets, daily food intake, total herbivory, impact upon vegetation, and the density of moose.

Several transects of up to 1500 m were established in both study areas and were run every 2 to 3 weeks. Transects comprised straight lines along a given bearing; essentially the same ground was covered on each run because the observer was guided by flagging put out during his first run. The summer's total, combining 12 separate runs of individual transects, covered some 16.5 km of sampling. The observer walked the transect, counting within 2 m on either side of him all individual instances of leaf removal by moose during the past 10 days or so. We restricted this counting to recent removals because of our interest in comparing dietary composition in different periods of summer. Criteria of recent removal, a critical aspect of the technique, were developed through study of the cut surfaces of petioles or new leaders. A scab-like structure soon forms on newly cut surfaces, and, after 10 days or so, it becomes recognizably different in colour and thickness. From observation of control specimens, we conclude our criteria of freshness, under the existing environmental conditions, provide a reliable means for distinguishing recent removals.

For inventorying browse plants and the total forage removed during summer, we established 52 known-area plots, spacing them regularly along the transects. Plants of all species used by moose and having current growth within reach of moose ($<$ 2.8 m high) were counted -- those 0.5 m high within a 1-m radius and taller ones within a 2-m radius of the plot center. Each evidence of a leaf being removed since the beginning of summer was counted; from this a total was extrapolated based on a summer browsing period of 124 days and the assumption that post-browsing regrowth is negligible. These data provide estimates of biomass removed per plant and per unit area as well as the density of browse plants.

To determine individual intake by feeding moose, we observed animals through 7 x 35 binoculars at distances no greater than 30 m. Two sets of data were collected, not necessarily simultaneously: bites per unit time and leaves per bite. To determine activity cycles in moose we made a series of 24-hr activity observations from fixed vantage points in the forest and at ponds. A pair of observers recorded all feeding, moving and resting of moose within their sight or hearing. Because moose are noisy when moving and feeding, one can monitor activity during hours of darkness. Density of moose is high in these forests, and the animals make frequent trips to ponds: several 24-hr records from a point allowing radial coverage of 100-150 m provided a large number of data on individual animals, and we believe the sample was adequate for us to reconstruct the daily activity cycle from it.

From the direct observations we calculated the average number of leaves ingested during periods of feeding. Combined with our measurements of biomass/day and feeding hrs/day, we calculated an estimate of biomass-intake/day accounting for each browse species. We also measured aquatic feeding, using similar techniques, and thus were able to estimate total food consumption by the moose of the study area during summer. Total time required for the summer browse survey was 20 man-days of data collecting in the field plus several days for establishing study sites and a number more for analyzing data.

RESULTS AND DISCUSSION

Moose Diets in Relation to Available Browse

Composition of browse species available differed between the Coastal and Yellow Birch study areas (Table 1), with the relative abundance of 10 of the 16 species encountered being significantly different (chi-square $p < 0.05$). These vegetation differences no doubt reflect the sharp climatic differences between coastal and inland zones. The summer diets of moose are, we believe, well represented by the relative proportions of leaf removals accounted for on the transects: Table 2 shows the averages of all transect runs in the two study-area forest types. Percentages are based on the proportion (dry-wt basis) of each species removed; this was determined by weighting the percent removals counted in each time period by the respective species' mean leaf-weight for that period.

Table 1. Percentage of Individuals of Browse Species in Two Study Areas.
Browse plants are of species eaten by moose in summer and having current growth below 2.8 m.

SPECIES	STUDY AREA	
	Yellow Birch	Coastal
Sorbus americana	19	46
Acer spicatum	20	11
Acer saccharum	0.6	0
Betula alleghaniensis	14	1
Betula papyrifera	8	18
Other species	38.4	24
	100.0	100.0

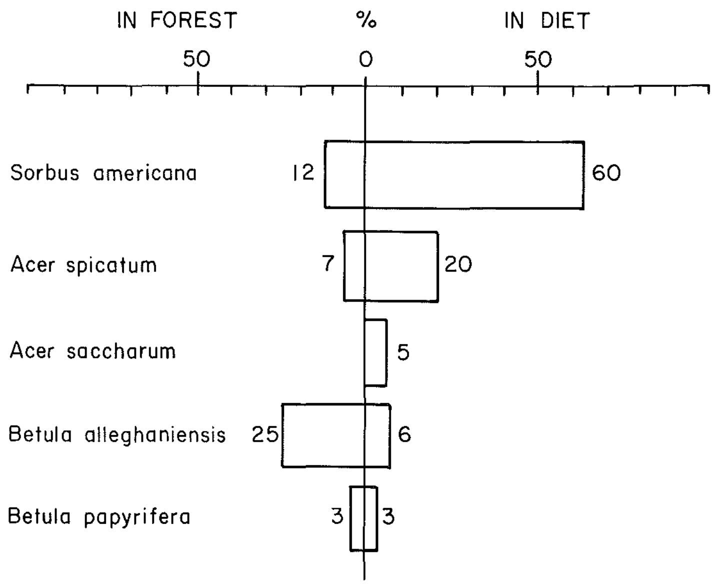

Figure 1. Browse production and utilization in the Yellow Birch study area.

Species percentages for production are based on total available browse production (1971 study); those for usage are from dietary data (Table 2). Absence of a production figure for Acer saccharum reflects its not being encountered in any of the 93-0.25 m^2 clipping cells of the 1971 sample, while it was encountered along the transects in 1972.

Table 2. Percentage by Weight of Species Removed by Moose in Two Forest-Type Study Areas. These are interpreted by us as representing the over-all summer diet. Weight of leaves removed was established by using average leaf weights for the respective species and time period in conjunction with leaf-removal counts.

SPECIES	STUDY AREA	
	Yellow Birch	Coastal
Sorbus americana	60.2	77.7
Acer Spicatum	20.3	15.3
Acer saccharum	5.3	0.0
Betula alleghaniensis	6.5	3.6
Betula papyrifera	2.9	2.4
Other species	4.8	1.1
	100.0	100.0

Comparing Tables 1 and 2, one notes that diets are more alike between the two study areas than are the sets of browse available in those areas. This suggests that, in seeking browse, moose make selections which are not merely related to what is available. This fits our impression that moose distinguish and select among species according to a hierarchy of preferences; the diet from a given area or year then represents the degree to which these preferences can be satisfied. We suspect that moose, in addition to specific preferences, seek to combine intake of two or more species during a given period. However, while pointing out below that variations in diversity do occur, we cannot yet say whether diversity *per se* is sought by preference. The percentages of species in the diet are significantly different from those available in the forest except for Betula papyrifera, according to a chi-square contingency-table test ($p<0.05$).

Sorbus americana, having the highest frequency of summer use, undoubtedly has a major influence in the nutrition of moose; this is especially germane to population processes since summer is the critical season of survival and growth in young animals. We assume, based on evolutionary logic, that herbivores can and do select plants according to nutritional value: the fact that Sorbus appears the most preferred among species available in the study areas indicates to us it has high nutritional value, at least relative to other species available. Therefore, since this plant of presumably high nutritional value occurs as the majority item in the diets, we strongly suspect that food resources here are favourable. This interpretation is corroborated by there being an unusually high summer density of moose, particularly in the Yellow Birch study area (see below). A common characteristic of ranges where ungulates do not obtain adequate nutrition is low availability, hence low intake, of preferred species. Considering that Sorbus apparently plays a pivotal role in the ecology of moose, the capacity of upland sites to support moose in summer may be more closely tied to the availability of Sorbus than to any other type of terrestrial forage. We limit this to terrestrial forage because a critical role is seen for aquatic vegetation (Botkin et al. 1973, Jordan et al. 1973), and to the summer season because in winter, welfare of moose may be relatable more to some other species such as Abies balsamea. However, even in winter, Sorbus is a highly preferred forage.

Diversity in Dietary Composition

In the Yellow Birch study area, compared to the Coastal, there were more species of browse encountered, and there was a greater uniformity in abundance among them. Moose in the Yellow Birch selected a more diverse diet. If we start with the assumption that the diversity of species available in the Coastal study area is adequate to support moose, then it might be suggested that, with subsequent increases in diversity of available browse, animals tend to increase the diversity of their intake. Klein (1962), comparing two insular deer herds, found dietary diversity related to forage diversity, and he showed that the habitat with greater forage diversity was nutritionally more favorable.

Diets of moose changed as summer progressed; we found significant differences in the relative frequency with which species were taken between consecutive 2-wk periods (chi-square, contingency-table test, $p < 0.05$) and in the number of species being browsed. Diversity in diets, as interpreted from the transect data, was examined by computing for each bi-weekly average of species removed along transects a Shannon-Weaver information theoretic value of diversity (Pielou 1969):

$H' = -\sum_{i=1}^{s} p_i \log_e p_i$, where p_i is the relative occurence of the ith member in a set of 's' species.

This single index reflects both the number of species being taken and the frequency of their consumption.

Figure 2 traces dietary diversity through the summer. We believe the higher values in early summer, when total production of new plant growth is still low, reflect the general low availability of any one species -- preferred or otherwise. To meet quantitative requirements, moose probably select from a wider variety at that season than later when each species by itself offers more biomass. Also, during the period of early leaf growth, moose may find more species of browse attractive than later when leaves are maturing. The mid-summer minimum in diversity of terrestrial woody plants may also reflect increased use of aquatics -- comprising up to 25% of the diet according to our measurements. In late summer, coincident with a dropping off of aquatic feeding, diversity in the diet begins to rise again.

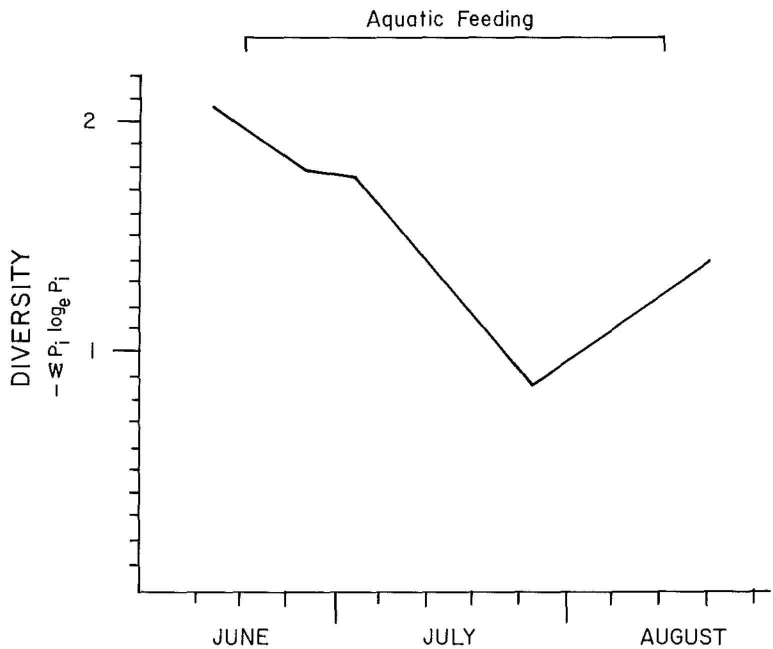

Figure 2. Diversity of woody-plant species being taken by moose during summer, with special reference to the period of aquatic feeding. Diversity is quantified by computing a Shannon-Weaver information theoretic value for the distribution of species (dry-wt basis) in the diet for each 2-wk period.

Forage Consumption

We found that moose spent some 4.85 hr/day feeding, according to data from our series of 24-hr observations at forest and pond sites. During a 60-day, mid-summer period, some 20% of the feeding time of adult moose was at aquatic habitats. Our estimate of total daily feeding corresponds closely with an extrapolation of 5 hrs from Geist's (1963) work. The daily dry-wt intake of browse was computed for an average adult moose as

$$Br = L\ R\ T,$$

where L is the weight of individual leaves by species in the proportion they occur in the diet, R is the rate of intake, leaves/hr, and T is time spend feeding, 4.85 hr/day.

This shows a daily intake of 4.2 kg for the summer period. Water content of summer leaves is around 80% (Robbins et al. 1950), making the wet weight consumption 21 kg. According to our studies of aquatic feeding, moose ate an estimated 6 kg/day of aquatics for a total of 27 kg wet or 4.8 kg dry-wt/day, assuming aquatic foliage contains 90% water. Kellum (1941) found that captive, adult moose from Isle Royale, when fed fresh-cut browse _ad libidum_, consumed 23 to 27 kg/day. That our figure lies at Kellum's upper limit may result from free-living animals requiring a greater intake of energy and from the water content of aquatic vegetation being higher.

Density of Moose

Extrapolating from measurements of total leaf-removal in known-area plots, we estimated that 1980 kg browse/km^2 was removed during a 124-day summer period. This figure, F, combined with daily browse intake, Br, and with number of days, D, is used to calculate moose density:

$$F/Br\ D = 3.8 \text{ adult equivalents/km}^2 \ (9.8/\text{mi}^2).$$

An adult equivalent is defined as a 358-kg animal without sex, age, or reproductive condition specified. We estimate that some 29% of the island's 550 km^2 land area is covered by forests similar to those occurring in our two study areas. While our study areas are not representative in a statistical sense, we take the liberty of extrapolating these density estimates for comparative purposes. The 29% area would have, by extrapolation, hosted 600 adult equivalents. If the total biomass of these 600 is apportioned according to age-specific weights and according to the age and sex composition of the population for mid-summer, using previous population estimates for Isle Royale (Jordan et al. 1971), this represents 726 animals.

Our density calculation agrees generally with the densities estimated for winter in the yellow birch and coastal forests of western Isle Royale by Jordan and Wolfe (in prep.) from 7 years' aerial survey and pellet counts. If the approximate mid-summer moose population at Isle Royale is 1280 (Jordan et al. 1971), then the 726 animals which occupied 29% of the land area comprise 57% of the population. Our general impression is that these habitats are among the best summer environments for moose on the island, and that densities are well above average.

Impact of Moose on Browse Productivity

Our measurements indicate moose were cropping 25.2 kg (dry-wt)/ha of current browse in the Yellow Birch study area. Based on production measurements in the same area the previous summer, this is 7% of total production below 2.8 m in all browse species. Certain species, however, are being cropped far more heavily. Figure 3 summarizes the degree of impact of summer usage on current growth in the five most commonly eaten species. The one which provides the greatest quantity of forage, *Sorbus americana* (Table 2), is also the one most severely cropped. Essentially all *Sorbus* plants being browsed are wholly within the reach of moose, i.e., shorter than 2.8 m. The 35% removal thus applies to reduction of photosynthetic surface for the whole plant. Much of the *Acer spicatum* population is similarly restricted to plants wholly available to moose; however, on Isle Royale there are some places where this species has commonly outgrown the reach of moose. In contrast, rarely does one find a *Sorbus* plant having outgrown the reach of moose during the past several decades.

Based on studies by Baker (1964) of insect defoliation in oaks and pines, consistent removal of 35% foliage during the growing season can lead to 10% to 30% mortality within 10 years. If mortality in *Sorbus* is 1% to 3% per annum, such loss could theoretically be replaced by the extension

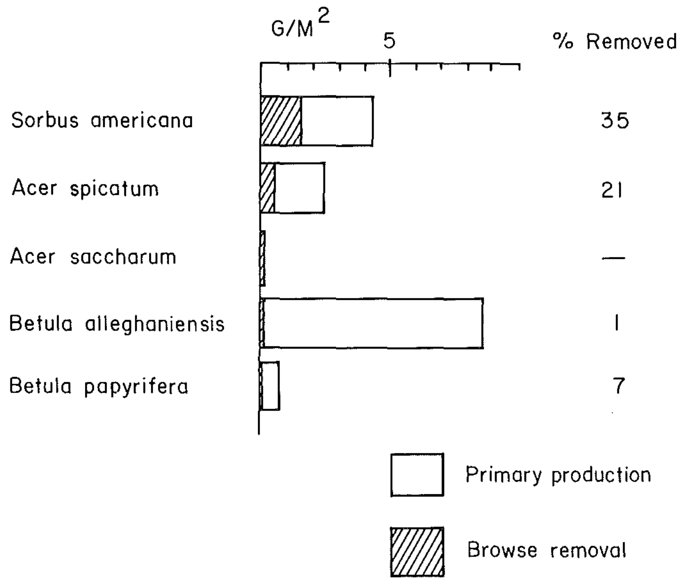

Figure 3. A comparison between current production within reach of moose and the amount of this removed by the animals during summer for five important browse species in the Yellow Birch Study Area. No estimate was obtained for production in Acer saccharum, as explained under Fig. 1.

of smaller individuals (< 0.5m), the density of which we found to be about the same as of the larger plants. However, even were the smaller ones able to grow, there would not be an equal replacement of browse productivity. Furthermore, these estimates only recognize defoliation by moose in summer:

there are two other major impacts upon Sorbus. In some summers Sorbus is widely defoliated by insects: it appears more subject to insect impact than any other browse species. In winter, most all current twigs of Sorbus are removed by moose; it is winter impact that prevents larger individuals from outreaching the moose and smaller ones from growing up to replace the larger ones that have died. Overall, Sorbus appears highly adapted to withstand animal impact; however the current extent of impact is apparently too great, and a decline in productivity of Sorbus at Isle Royale appears underway.

There also appears to be declining productivity in Acer spicatum, Cornus stolinifera, Betula papyrifera, and, due to winter browsing alone, Abies balsamea. Many years earlier, Taxus canadensis was reduced by over-browsing from an abundant to an insignificant position in the shrub layer (Murie 1934). Finally, while moose ordinarily have little impact on shrubs less than 0.5 m in height, during winter the showshoe hare (Lepus americana) is also browsing Sorbus, Acer sp., Cornus sp., Betula sp., and other plants important to moose. When browsing pressure is severe, competition between these two herbivores could well reduce the range capacity for one or both (Dodds 1960).

CONCLUSION

We believe our integrated approach to the study of moose browsing has produced promising results, including valuable data for the monitoring of mineral and energy flow within an ecosystem. The method appears quite efficient for estimating diet and total browse removal. It has the added advantage of providing a population estimate and a means for evaluating range trends. We conclude from our survey of summer browsing in two study areas that the current browse resource, characterized by an ample supply of *Sorbus americana*, is favorable for maintaining a high density of moose. At the same time, trends in productivity of key browse species indicate that capacity for moose at Isle Royale is declining.

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