

## The Time-Energy Budget of a Moose

GARY E. BELOVSKY

*Society of Fellows 16 Holyoke Street, Cambridge, Massachusetts 02138*

AND

PETER A. JORDAN

*Department of Entomology, Fisheries and Wildlife,  
University of Minnesota, St. Paul, Minnesota 55455*

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As the first step in developing an optimal foraging model for moose (Belovsky 1978), a time-energy budget for a moose was developed. For the summer period (late May through early September) at Isle Royale National Park, Michigan, we made various behavioral observations on feeding moose and inventoried their food resources. Employing these various sets of data, we were able to determine the quantity of each food consumed by moose, the time required to acquire the foods, preferences for different food plants, and differences demonstrated by the sexes. In addition to this information, we collected data on the moose's ability to utilize each of the forage plants and the population densities of moose in different years (1972-1974) in two forest types. This enabled us to examine energy flow within each of the populations and determine in what manner energy limits the moose population.

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 measured the time-energy budget of a moose. The construction of a time-energy budget is essential for an analysis of an animal's foraging strategy, and the data presented in this study are used for this purpose in the following paper (Belovsky, 1978).

Isle Royale National Park is an island in Lake Superior which is maintained as a wilderness park and 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. Our study focuses on summer, the season which we believe poses the greatest nutritional demand for moose (the raising of young and the storage of fat for winter), and the period of growth and reproduction in plants. During several summers (1972-1974), we developed

an integrated technique involving transects, plots, and direct observation of feeding moose. Current browse removals were counted along transects; plant production and biomass removed were measured in plots; and feeding rates were determined from the close observation of moose. These measurements were then combined to estimate the composition of diets, daily food intake, total amount of herbivory, and the density of moose.

#### STUDY AREA

Isle Royale, a 550-km<sup>2</sup> 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 observed at Isle Royale until the early 1900s when they presumably swam some 30 km from the Canadian north shore of Lake Superior to the island. In the absence of wolves, the newly arrived moose displayed an irruptive population growth culminating in die-offs during the 1930s. Wolves arrived in the late 1940s, after which the moose population appeared to stabilize. In recent years, however, the moose population has increased without a concomitant increase in the wolf population (see Jordan *et al.*, 1973). 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, 1946; Krefting, 1951; Mech, 1966; Shelton, 1966; Jordan *et al.*, 1967, 1971; Hansen *et al.*, 1973; Allen *et al.*, 1959–1973).

All studies reported here were conducted between 1972 and 1974 in two areas at the west end of the island. The study areas are known as "Yellow Birch" and "Coastal." The former is dominated by a partial canopy of mature *Betula alleghaniensis* with *Betula papyrifera*, *Abies balsamea*, *Picea glauca*, and *Thuja occidentalis* also in the canopy. The understory includes the reproduction of all the canopy species plus *Sorbus americana*, *Corylus cornuta*, *Lonicera canadensis*, *Diervilla lonicera*, *Acer spicatum*, and *Acer saccharum*. This site lies several kilometers from the shore of Lake Superior.

The Coastal area lies close to the lakeshore and tends to have poorer growing conditions than the Yellow Birch. With its cool, often foggy weather, the Coastal area supports a more boreal forest dominated by *Abies balsamea* and *Picea glauca*. Also, intense lake storms create 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 americana*, *Acer spicatum*, and *Prunus pennsylvanica*. In both study 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. The lowland areas in both study regions are dominated by *Thuja occidentalis*, *Picea mariana*, and *Alnus rugosa* and are interspersed with beaver ponds and stream drainages.

## METHODS AND RESULTS

Browse utilization methods described elsewhere were not appropriate for our investigation. McMillan (1953) relied on direct observations of moose for all of his data. We attempted this, but the lack of open vegetation at Isle Royale made direct observation difficult. Krefting (vide Hosley, 1949) used visual estimates of browsed vegetation, similar to the Aldous (1944) technique, but his method is not sufficiently quantitative to permit statistical analysis. In 1971 our research group initiated measurements of production and utilization by protecting sets of plants within randomly placed small exclosures (ca. 4-m diam) (Jordan and Botkin, unpublished data); exclosure sites were chosen randomly on a map-grid system, with the exclosures constructed to exclude only moose (6-in. mesh). Plants were selected outside of the exclosure to match each one inside, and utilization was measured as the difference in current growth, clipped and weighed, at the end of the summer. Current growth represents the leaves, twigs, or needles produced during the annual growing season (late May-early September). The current production was determined by examining twigs for the most recent bud scar (leaves, being deciduous, are necessarily current growth), and for some conifer needles color differences between current and older growth were employed. Exclosures were found to be expensive, time consuming and requiring a large number of plots. Finally, Cole's (1960) feeding site technique was not used since it does not attempt to quantify use on a biomass basis. Simply recording the incidence of use is important, but leaves vary in size and different species provide different amounts of food.

*Quantity of Forage Consumed and Available*

For inventorying deciduous production and the total forage removed during the summer, we established 60 known area plots (Table I presents the number of plots examined in any year), spacing them regularly along transects. Plants of all species used by moose and having current growth within reach of moose (less than 2.8 m high) were counted—those less than 0.5 m high were counted within a 1-m radius, and taller ones within a 2-m radius of the plot center. Each indication that a leaf had been removed since the beginning of summer was counted; from this a total was extrapolated on the basis of a summer browsing period of 124 days, the period of leaf emergence to leaf fall. To make these computations it is assumed that postbrowsing growth is negligible, moose browsing is constant over the summer, and leaf production occurs entirely at the start of the summer. We do know from picking leaves from plants, a simulation of moose browsing, that regrowth did not generally occur.

The other two assumptions are approximately true. Since leaves reach a maximum size in midsummer and then decrease in weight as the plant withdraws various constituents, we can view both the size of leaves and the intensity of moose feeding as symmetric functions. Subsequently, we might expect

TABLE I

The Production of Deciduous Leaves, Herbaceous Plants, and Aquatic Vegetation (kg-dry wt/km<sup>2</sup>/summer) for Two Forest Types at Isle Royale National Park<sup>a</sup>

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
Deciduous leaves					
Area samples (m <sup>2</sup> )	477.5	502.9	125.7	150.8	125.7
No. sample points	38	40	10	12	10
Biomass present (g)	16,137.9	18,459.7	3,334.7	5,522.3	4,203.4
Production (kg/km <sup>2</sup> /summer)	33,800.0 (4,056.0)	36,710.0 (4,405.2)	26,530.0 (4,510.1)	36,620.0 (5,829.2)	33,440.0 (5,684.8)
Herbaceous plants					
Area sampled (m <sup>2</sup> )		5.0			
No. sample points		20			
Biomass present (g)		435.3			
Production (kg/km <sup>2</sup> /summer)		87,060.0 (12,623.7)			
Aquatic plants					
Area sampled (m <sup>2</sup> )		12.3			
No. sample points		49			
Biomass present (g)		1,587.1			
Production (kg/km <sup>2</sup> /summer)		129,030.0 (10,752.5)			
Production (kg/pond/summer) <sup>b</sup>		3,217.1 (268.1)			

<sup>a</sup> The values in parentheses are the standard errors.

<sup>b</sup> Our observations indicate that 32% of the pond is open water and the remainder is grassy hummock, which is twice as productive as the open water.

moose feeding intensity to be greatest in early and late summer, when leaves are small. To account for this differential distribution of feeding, sampling was restricted to midsummer, the presumed center of the moose's symmetric feeding distribution. Also, to compute moose consumption we employ the mean leaf weights averaged over the entire summer. In this way, we do not overestimate early or late summer consumption, or underestimate midsummer feeding. We are, therefore, confident that our measurements reflect an average summer consumption by moose.

From a sample of plants of each species (at least 30 plants), all leaves and leaf removals were counted to estimate the leaf production per plant. By multiplying this per plant leaf production by the number of plants of that

species encountered in the plots, one has an estimate of the number of leaves produced by each species. Both the leaf production and removal values are then multiplied by the appropriate mean dry weight of that species' leaves to estimate biomass production (Table I) and moose consumption (Table II). The appropriate leaf weights for the calculation of biomass production are the average weights at full leaf growth (midsummer), while for calculating consumption, it is the average leaf weight over the period from the initiation of leaf growth to leaf fall.

To inventory the amount of herbaceous vegetation available to moose, a  $\frac{1}{4}$ -m<sup>2</sup> plot was established in 20 of the 40 2-m-radius plots of the Yellow Birch forest during 1973 and all herbaceous plants were clipped. The clipped

TABLE II  
The Biomass Removed by Moose per Summer (kg/km<sup>2</sup>/summer) from  
Two Forest Types at Isle Royale National Park<sup>a</sup>

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
Deciduous leaves					
Area sampled (m <sup>2</sup> )	477.5	502.6	125.7	150.8	125.7
No. sample points	38	40	10	12	10
Biomass removed (g)	845.4	844.5	181.0	300.1	692.4
Consumption (kg/km <sup>2</sup> /summer)	1980	1680.3	1439.9	1990.0	5508.5
Herbaceous plants					
Area sampled (m <sup>2</sup> )		251.3			
No. sample points		20			
Biomass removed (g)		44.3			
Consumption (kg/km <sup>2</sup> /summer)		176.3			
Aquatic plants					
Area sampled (m <sup>2</sup> )		6.3			
No. sample points		25			
Biomass remaining after feeding (g) <sup>b</sup>		148.2			
Consumption (kg/pond/summer)		580.1			

<sup>a</sup> The consumption is measured for deciduous leaves, herbaceous plants, and aquatic plants.

<sup>b</sup> Only pertains to the open water of the pond, since moose restrict their feeding to these areas.

plants were later weighed after drying to estimate production (Table I). Although this may seem like a very small sample size from which to estimate herbaceous production, we find a very small variance in the amount of vegetation present in the plots (the 95% confidence interval is within 30% of the mean), and any larger sample size would have been prohibitive with respect to the required time. The same 20 2-m-radius plots were searched by the observer for stalks remaining from herbs fed upon by moose. When one such stalk was found, a plant of the same species was picked and saved for later weighing. The dry weights of all such plants provide an estimate of herb removal (Table II).

The estimate of aquatic production and removal by moose is more difficult since moose remove large quantities of these plants, leaving no historical reference which can be observed (i.e., petioles, scars, stalks, etc.). Therefore, two exclosures (120 m<sup>2</sup> each) were established in the only pond in the Yellow Birch study area during 1973. Both beaver and muskrat, the only other aquatic herbivores, were also excluded from the exclosures. Their consumption of aquatic plants is assumed to be small since they appeared to feed most frequently on hummock vegetation when feeding on aquatics, while moose fed almost entirely in open water. At the end of the aquatic growing season, mid-September, the vegetation was sampled by clipping all plants within 47  $\frac{1}{4}$ -m<sup>2</sup> plots located in the exclosures. Also, 25  $\frac{1}{4}$ -m<sup>2</sup> plots outside of the exclosures were clipped to determine how much vegetation remained after moose feeding. By drying and weighing the vegetation clipped within the exclosures, we have an estimate of aquatic production (Table I); from the difference between this value and the dry weight of vegetation outside of the exclosures, we have an estimate of the amount of vegetation cropped by moose (Table II). This was accomplished by assuming that moose feed only in open water areas of the pond, rather than on grassy hummocks; this appeared to be the case from observation.

### *Moose Density*

The density of moose was measured by means of feces counts. In the same plot centers used for measuring the quantity of food removed by moose, the number of feces (amorphous wet "pies") was counted approximately every 2 weeks, and they were cleared from the plot to avoid later recounting. Only terrestrial plots were examined for feces since in 65 hours of observing moose in ponds, defecation was never seen, while in 48 hours of observing moose on land, defecations were frequently observed. The plots were examined every 2 weeks to avoid missing overly decomposed feces. Between 1972 and 1973, the plots examined for feces had a 4.57-m radius, while in 1974 the radius was increased to 7.62 m in an attempt to determine whether the earlier plots had been too small. Also, to ensure a minimum of missed feces, the observers made the counts on hands and knees, searching between plants. Using the observed daily defecation rate per moose (5.66 feces/moose/day, see section on

daily activity), one can estimate the number of moose/km<sup>2</sup> (Table III). Although these estimates have fairly large confidence intervals, it will be shown later that the observed means can be used to compute other known parameters and provide very good estimates of these other parameters. Finally, further sampling could not be used in our study to reduce the confidence intervals, since the present feces counts required almost 150 man-hours per summer.

TABLE III

The Measurement of Moose Population Densities for Two Forest Types at Isle Royale National Park from Feces Counts (adult moose/km<sup>2</sup>/summer)<sup>a</sup>

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
No. feces counted	4.0	3.5	12.0	1.5	13.0
Area sampled (m <sup>2</sup> )	1313.4	1313.4	5472.4	656.7	1824.2
No. sample points	20	20	30	10	10
Feces/km <sup>2</sup>	3045.5	2664.8	2192.8	2284.2	7126.4
Feces/moose/day	5.66	5.66	5.66	5.66	5.66
Days of deposition	124	124	124	124	124
Moose/km <sup>2</sup> /summer	4.3 (1.9)	3.8 (1.7)	3.1 (0.7)	3.3 (2.3)	10.2 (3.0)

<sup>a</sup> The values in parentheses are the standard errors.

#### *Plant Species Composing a Moose's Diet*

To determine the selection of deciduous leaves by 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 or stakes put out during his first run. Each summer's total transect sampling, combining 12 separate runs of individual transects, covered some 16.5 km. The observer walked the transect, counting within 2 m on either side all individual instances of leaf removal by moose during the previous 10 days. We restricted this counting to recent removals because of our interest in comparing the composition of a moose's diet at different periods of the summer (Table IV, Figs. 1a-e). Criteria for recent removal, a critical aspect of the technique, were developed through the study of the cut surfaces of petioles or new leaders. A scablike structure soon forms on newly cut surfaces,

TABLE IV

The Percentage Species Composition of the Deciduous Leaves Consumed by Moose for Two Forest Types at Isle Royale National Park

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
Sample size (g)	3480.3	4516.3	823.9	3991.6	843.0
<i>Sorbus americana</i>	60.2	51.7	32.0	77.7	59.3
<i>Acer spicatum</i>	20.3	25.7	53.5	15.3	35.8
<i>Betula alleghamiensis</i>	6.5	8.6	5.5	3.6	0.0
<i>Betula papyrifera</i>	2.9	4.6	4.0	2.4	1.8
Other species	10.1	9.4	5.0	1.1	3.1
Total	100.0	100.0	100.0	100.0	100.0

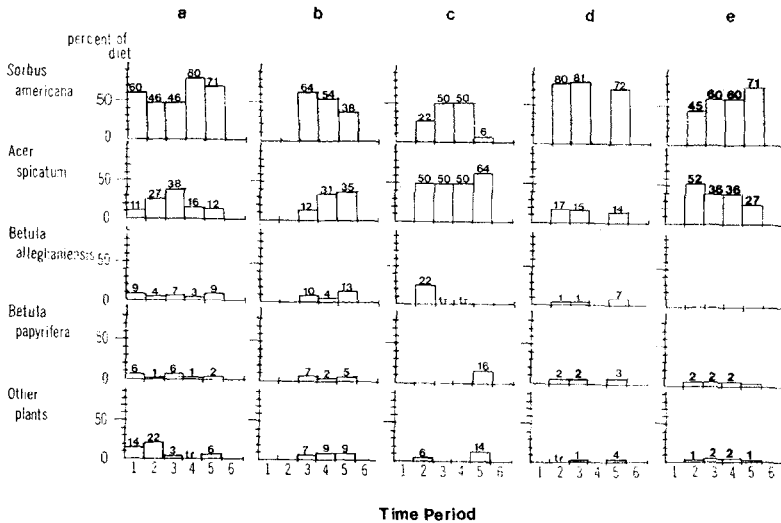


FIG. 1. Histograms of the moose's consumption of different deciduous plant species (percentage of diet by weight) at various times during the summer. (a) The Yellow Birch Forest in 1972, (b) the 1973 Yellow Birch Forest, (c) the 1974 Yellow Birch Forest, (d) the 1972 Coastal Forest, and (e) the 1974 Coastal Forest. The time periods are: (1) June 1-21; (2) June 22-July 12; (3) July 13-August 3; (4) August 4-August 25; (5) August 25-September 15; and (6) September 15-October 5.



and after 10 days or so, it becomes recognizably different in color and thickness. From observations of control specimens, we concluded that our criteria of freshness, under the existing environmental conditions, provide a reliable means of distinguishing recent removals.

The incidence of herbaceous species in a moose's diet was determined by placing 2-m-radius plots along the transects and searching the ground for the remaining herb stalks. This required careful examination by the observers on their hands and knees. These plots were examined only once during the summer, owing to the time required to search them. Seventy of these plots were searched in 1973 for herbaceous plant removal (Table V) in the Yellow Birch forest only.

TABLE V  
The Species Composition of a Moose's Herbaceous Diet for the  
Yellow Birch Forest in 1973<sup>a</sup>

	Percentage available	Percentage in diet
Sample size (g)	435.3	150.6
Sample size (plots)	$20 \times \frac{1}{4} \text{ m}^2$	$70 \times 12.57 \text{ m}^2$
<i>Streptopus roseus</i>	3.8	17.5
<i>Dryopteris spinulosa</i>	11.4	50.6
<i>Aralia nudicaulis</i>	4.6	7.0
<i>Poa</i> sp.	14.6	0.7
<i>Cornus canadensis</i>	6.6	11.2
<i>Lycopodium</i> sp.	41.0	0.0
<i>Equisetum</i> sp.	3.0	3.5
<i>Clintonia borealis</i>	3.7	0.0
Other species	11.3	9.5
Total	100.0	100.0

<sup>a</sup> The percentage availability of each herb species was obtained by breaking down the cumulative value of herbaceous production presented in Table I.

The determination of leaves and herbs composing the moose's diet requires that we distinguish between those items fed upon by moose and those consumed by insects and snowshoe hare, the only other terrestrial herbivores on Isle Royale. When hare feed they cut the leaf's petiole or the herb's stalk at a neat 45° angle; insects, on the other hand, seldom consume the entire plant or leaf. Therefore, those leaves or herbs broken off in a tearing manner have been

TABLE VI

The Species Composition of the Aquatic Plants Consumed by Moose in Two Forest Types at Isle Royale National Park during the Summer of 1973<sup>a</sup>

Study area	Yellow Birch Forest		Coastal Forest	
	% Available % in diet		% Available % in diet	
Sample size (g)	1587.1	684.5		3.4
<i>Carex</i> sp.	61.1	9.2	100.0	1.0
<i>Nitella</i> sp. and <i>Chara</i> sp.	11.4	58.4		
<i>Potamogeton</i> sp.	6.8	15.5		
<i>Equisetum fluviatile</i>	6.2	9.7		
<i>Eleocharis</i> sp.	tr. <sup>b</sup>	5.8		
<i>Spirogyra</i> sp.			tr.	99.0
Other species	14.5	1.4		
Total	100.0	100.0	100.0	100.0

<sup>a</sup> The species compositions of available aquatic plants are also presented and are based upon the total production values presented in Table I.

<sup>b</sup> tr.: trace in sample.

consumed by moose, and we can identify the items as having been fed upon by moose.

The selection of aquatic plants by moose (Table VI) was determined by a feeding simulation, which is discussed in the section on cropping rates.

### Cropping Rate

To determine the intake of deciduous leaves per minute, we observed animals through  $7 \times 35$  binoculars at distances no greater than 15 m. Two sets of data were collected: bites per unit time and leaves per bite. The product of these two values provides an estimate of the intake of deciduous leaves per minute of feeding. The same approach was used for herbaceous plants since the plants selected by moose were large enough to be easily observed. If we know the number of leaves on a branch or herbs in a given area, the above method can be tested by counting the number of leaves or herbaceous plants missing after a moose was observed feeding on the known branch or area. In this way, the observation estimates could be compared with the actual counts of removals; the result is an error no greater than 25% and averaging  $12 \pm 6\%$  ( $N = 12$ ), with no bias for over- or underestimation.

The above approach could not be applied for aquatic cropping rates, since moose feed with their heads submerged, as are the plants. Several techniques have been reported in the literature for measuring aquatic consumption by moose:

- (1) Observe and identify plants in the moose's mouth when it surfaces.
- (2) Record plants floating in the water which the moose has dropped or uprooted.
- (3) Mark off areas in a pond dominated by certain plants and assume that the incidence of feeding at each site is equal to the proportion of each dominant plant in the diet. Although these methods estimate the proportion of each species in the diet, they do not measure the quantity of food consumed. Also, the first technique is biased by the size and texture of plants which affects the moose's ability to handle plants; the second is biased by the fact that some aquatic plants sink and some might be preferentially dropped; and the third is biased by the fact that many species of aquatic plants grow together. Therefore, a better technique is needed.

In response to these difficulties, it was decided that a better estimate of aquatic consumption could be made by:

- (1) measuring the width of a moose's incisors and toothless upper palate, the region used for cropping ( $13.0 \pm 3.0$  cm for adult moose,  $N = 7$ ) and then simulating this surface (the observer's hands, working like jaws);
- (2) using the simulator, aquatic plants could be cropped in areas of the pond known to be used by moose;
- (3) timing each simulation so that cropping occurred over the average time moose were observed to remain submerged. Also, during the feeding simulations, cropped aquatic plants were compressed to account for the compacting effect of the moose's tongue. These samples can then be separated according to species to estimate the fraction of each in the diet according to dry weight. Also, the total weight of plants in each simulation divided by the collection time estimates the cropping rate.

To determine the accuracy of this aquatic cropping rate measurement:

- (1) The volume of a moose's mouth was measured (mean width  $\times$  mean length  $\times$  mean height).
- (2) The volume was halved to account for the size of a moose's tongue.
- (3) The mouth's capacity for aquatic plants was determined by multiplying the volume by 0.95, the density of the plants.
- (4) Using the estimated cropping rate, the time required to fill the mouth can be compared to the observed average submergence time. Using an average

volume of  $416 \pm 53 \text{ cm}^3$  ( $N = 7$ ), it was found that the predicted submergence time, if a moose is assumed to remain submerged until its mouth is full, is very close to the average observed submergence time (Fig. 2). This suggests that the cropping rate measurement is very good. To make this comparison, however, it is assumed that moose are not selective for particular aquatic plant species. From observing what moose have in their mouths when they surface, it appears that they crop many different aquatic species. Also, we find it difficult to explain how they could distinguish very small filamentous plants under water. Therefore, we believe that moose seek specific feeding sites which contain large amounts of the desired plants and are then unselective while submerged. It is for this reason that the simulation was carried out only in regions of the pond known to be favored by moose.

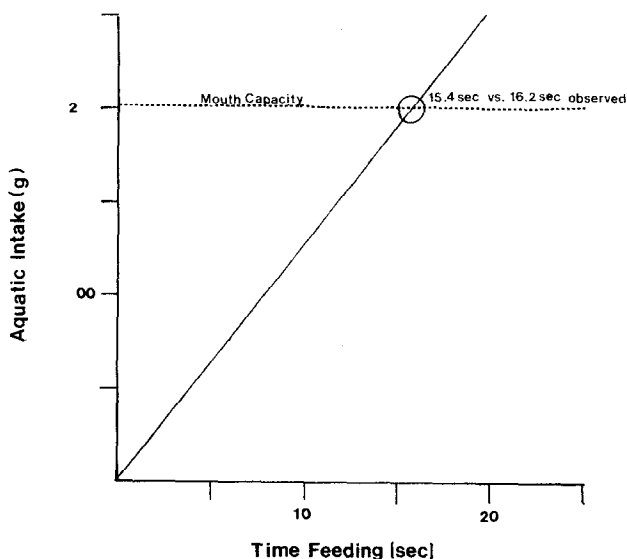


FIG. 2. This graph presents a plot of a moose's time-intake of aquatics (g-dry wt/feeding time in seconds) with the moose's mouth capacity for aquatics (g-dry wt) to determine how long a moose should remain submerged cropping aquatics (sec). The intersection of the time-intake and mouth capacity lines predicts the length of time a moose should remain submerged, if it feeds until its mouth is full, 15.4 sec. This compares favorably with the observed time,  $16.2 \pm 8.1$  sec (see text for details).

In the Coastal forest study area pond, moose were observed to "slurp" up filamentous algae, *Spirogyra* sp. To simulate this aquatic feeding, the mouth width, as measured above, was used to shape a squeeze bottle with a moose's mouth volume ( $416 \text{ cm}^3$ ). The bottle was used to "slurp" up algae by skimming the pond's surface until the bottle was full of algae and water; the algae collected was then dried and weighed. The number of times a moose placed its head

down to "slurp" per minute (determined by observation) was multiplied by the weight of algae collected in the squeeze bottle simulator to estimate the cropping rate.

The cropping rate measurements are presented in Table VII for deciduous leaves, herbaceous plants, and aquatic feeding.

TABLE VII  
The Cropping Rates of Moose Measured for Deciduous Leaves,  
Herbaceous Plants and Aquatic Plants

	Leaves or plants cropped per minute	Sample size		Weight per item (g)	Grams consumed/ minute
		No.	Duration (hr)		
Deciduous leaves	73.0 ± 30.1	35	12	0.23	16.7 ± 4.2
Herbaceous plants	27.7 ± 7.0	13	2	0.31	8.3 ± 1.6
Aquatic plants					
Yellow Birch Forest		33 Simulations			20.3 ± 3.1
Coastal Forest		21 Simulations			4.7 ± 2.4

*A Moose's Daily Activity Cycle, Feeding Time, Rate of Movement,  
and Distance Moved*

To determine activity cycles in moose, we made a series of 24-hour activity observations from fixed vantage points in the forest and at ponds. A pair of observers recorded all feeding 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: 15 24-hour records (360 hours) from a point allowing a radial coverage of 100 to 150 m provided a large amount of data on individual animals (194 individuals). We believe the sample was adequate for us to reconstruct the daily activity cycle (Fig. 3).

The daily feeding time was measured by following individual moose for periods exceeding 12 hours. During these observations, the observer recorded the length of time a moose was active, the fraction of this time that was devoted to cropping food, and the average daily temperature, since thermal parameters were thought to determine feeding time. Seven measurements of daily activity time multiplied by the fraction of time actually spent cropping food (not ruminating or searching:  $48 \pm 13\%$  of the time) are plotted against the mean daily air temperature in Fig. 4 ( $r^2 = 0.92$ ,  $p \leq 0.001$ ). The daily activity time is computed by multiplying 24 hours by the fraction of time the moose were observed to be active while we followed them. The mean daily air tem-

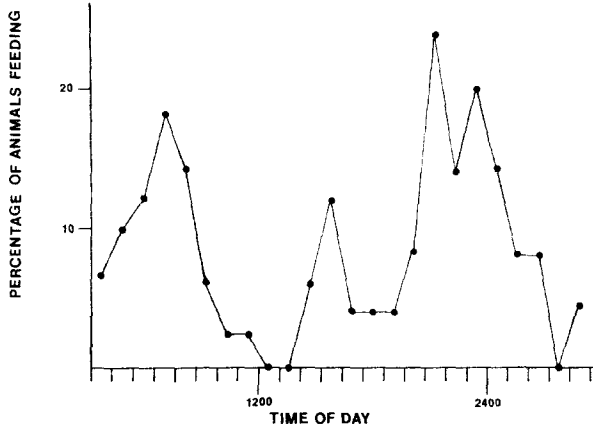


FIG. 3. A plot of the moose activity cycle based upon 194 observations of feeding moose. At each hour, the percentage of the 194 moose observed to be feeding is presented. Three definite feeding peaks appear: (1) dawn and just after; (2) late afternoon aquatic feeding; and (3) sunset and just after.

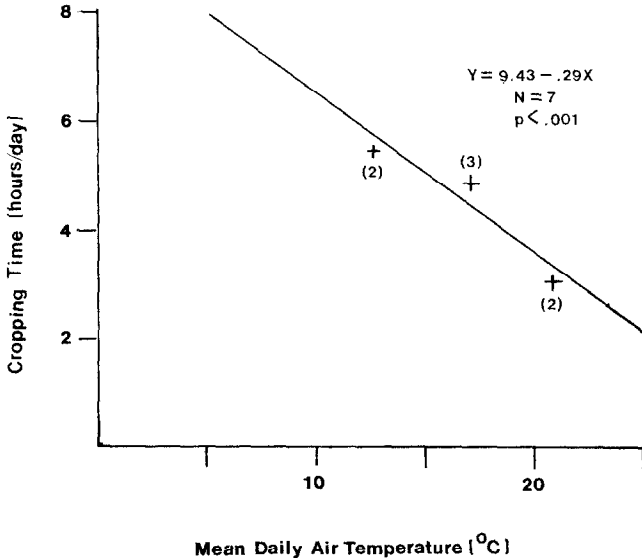


FIG. 4. A plot of mean daily air temperature ( $^{\circ}\text{C}$ ) against a moose's observed time spent cropping food (hr/day). The number in parentheses is the number of moose observed at that air temperature; these observations are combined because they represent a group of moose observed at the same time, and all appeared to feed equally. The graph also contains the regression of these points, which demonstrates that moose feeding is negatively correlated with the temperature. The total moose activity time is 2.08 times the cropping time (see text).

perature is the average of the day's maximum and minimum air temperatures.

During the observations of daily activity time, the distance walked by the animal was measured by marking plants fed upon and returning later to measure the distances between plants. Since the observer was also recording the time, one can estimate the speed of movement. Finally, the number of defecations was recorded, to estimate the daily output of feces (used to estimate population density), 5.66 defecations/day (95% conf. int. 1.82).

For aquatic feeding, the observer recorded the length of time an animal visited a pond each day. This was possible because individuals were identifiable from distinguishing traits (notches in ears, length of the neck's skin flap, antler shape, scars, etc.) and the ponds were the only ones available to our moose, since the nearest neighboring pond was approximately 3.3 km away. The distance between ponds may seem very small, but moose have a very small summer home range (approx. 1 to 10 km<sup>2</sup> (unpublished data from this study; Phillips *et al.*, 1973; Houston, 1968), with the average around 2 to 5 km<sup>2</sup>). In addition, it appears that this home range may be set by the limited time moose have to be active during each summer day and their energy requirements (Belovsky, unpublished ms.). Also, the observer recorded the fraction of time moose spent submerged and the distance traveled by moose per unit of time. The distance was measured by locating moose in relation to an established grid system (flags at known distances).

### *Cost of Locomotion*

Using data on the weight-specific cost of locomotion presented by Taylor (1973), we calculated that a 358-kg average adult moose (Jordan *et al.*, 1971) would expend 0.09 kcal/m in addition to its nonmoving metabolism. To apply this energy value to aquatic movement, one must also know the energy required by a moose to extract itself from a soft pond bottom. First, by measuring the surface area of moose hooves from impressions in soft mud, we found that the 358-kg moose would have an average load force of 190 g/cm<sup>2</sup> (95% conf. int. 47;  $N = 10$ ). Applying this force to a rod of known area and measuring the depth it sinks into the mud, one can measure the work required to extract the rod from the mud, as the distance times the force measured on a spring scale. Assuming that moose are as efficient as farm draft animals in performing work, 35% (Brody, 1945), one can multiply the work done in extracting the rod by the inverse of the efficiency to compute the "realized" work performed. And then using Brody's (1945) value for energy expended by animals in performing a unit of work, 0.00234 kcal/kg-m, we can compute the energy expended by a moose. Table VIII presents the values used in calculating the energetic cost of locomotion and this cost in relation to a gram dry weight intake of food.

TABLE VIII

The Values Used to Calculate the Energy Expended by a Moose to Crop a Gram of Each of the Three Summer Foods at Isle Royale National Park

	Speed (m/min)	Sample		Energy (kcal/m)	Food consumed (g/min)	Energy expended in cropping (kcal/g)
		No.	Duration (hr)			
Deciduous	2.7 ± 1.3	35	12	0.087	16.7	0.01
Herbaceous	1.1 ± 0.8	13	2	0.087	8.3	0.01
Aquatic	2.6 ± 1.9	11	40	0.087	20.3	0.01
Additional extraction cost for aquatic feeding						
	Strides/min	Extraction force (kg/stride)		Efficiency of work (%)		
	2.6 ± 1.9	24.1 ± 7.2		35		0.02
	Total aquatic expenditure					0.03

#### *Wet Weight, Dry Weight, Digestibility, and Caloric Value of Plants*

Plants of each species consumed by moose were collected and weighed while fresh and again after drying (80°C for 98 hr). The percentage of water by weight in these plants is 75% (range: 73–78%) for deciduous leaves, 77% (range 70–90%) for herbaceous plants and 95% (range: 81–99%) for aquatics.

The plant samples were also measured for dry matter digestibility using a two-stage *in vitro* digestion process (Tilly and Terry, 1963): rumen fluid and pepsin. The rumen fluid was collected from freshly killed moose that were eating the plants to be tested. Knorre (1959) measured *in vivo* dry matter digestion of deciduous leaves to be 72%. If we know the ratio of *in vitro* digestibilities for other food types to that measured for deciduous leaves, the product of the ratio and 72% estimates the *in vivo* digestion (Table IX). Johnson and Dehority (1968) have found *in vitro* digestibilities to be linearly correlated ( $r^2 = 0.81$ ) to *in vivo* digestion for domestic cattle, which suggests that the ratio conversion used in this study is appropriate.

The gross caloric content of plants was taken from bomb calorimetric measurements in the literature: 4.2 kcal/g-dry wt for deciduous leaves (Golley, 1961), 4.8 kcal/g-dry wt for herbaceous plants (Golley, 1961) and 4.1 kcal/g-dry wt for aquatics (Boyd, 1970). Interspecies variations in gross caloric content were not considered because they are very small (Golley, 1961), and since we are examining only summer feeding, we need not concern ourselves with seasonal variations.



TABLE IX

The Percentage Dry Matter Digestibility of a Number of Plant Species Available for Moose to Consume, as Determined by a Two-Stage *in Vitro* Simulation of Ruminant Digestion<sup>a</sup>

	% Digestion		Ratio of <i>in vitro</i> to deciduous <i>in vitro</i>	Predicted <i>in vivo</i> (%)
	<i>In vitro</i>	<i>In vivo</i>		
<b>Deciduous</b>				
<i>Sorbus americana</i>	48 ± 1.5			
<i>Diervilla lonicera</i>	22 ± 0.9			
<i>Acer spicatum</i>	42 ± 1.2			
<i>Betula alleghamiensis</i>	34 ± 1.0			
<i>Betula papyrifera</i>	26 ± 1.0			
<i>Corylus cornuta</i>	29 ± 0.2			
<i>Populus tremuloides</i>	52 ± 4.2			
<i>Rubus parviflorus</i> <sup>b</sup>	28 ± 1.0			
<i>Alnus rugosa</i> <sup>b</sup>	30 ± 1.2			
<i>Lonicera canadensis</i> <sup>b</sup>	5 ± 0.4			
Average	36.1 ± 11.4	72	1.0	72
<b>Herbaceous</b>				
<i>Streptopus roseus</i>	42 ± 0.7			
<i>Dryopteris spinulosa</i>	44 ± 0.8			
<i>Aralia nudicaulis</i> <sup>b</sup>	1 ± 0.1			
<i>Clintonia borealis</i> <sup>b</sup>	-1 ± 0.3			
Average	43 ± 1.4		1.19	86
<b>Aquatic</b>				
<i>Nitella</i> sp.	43 ± 1.1			
<i>Potomegeton</i> sp.	62 ± 1.7			
<i>Sparganium</i> sp.	47			
<i>Carex</i> sp.	58 ± 1.3			
<i>Equisetum fluviatile</i>	23 ± 1.1			
<i>Elodea</i> sp.	50 ± 4.0			
Average	47.2 ± 13.8		1.31	94
<b>Mix</b>				
Mixed species sample	38 ± 0.3		1.06	76
Weighted average of individual components	41.4		1.15	82

<sup>a</sup> Based upon a study of *in vivo* digestion by moose (Knorre, 1959), these *in vitro* values are used to estimate an *in vivo* value (see text).

<sup>b</sup> Species not consumed by moose to any major extent, so they are not included in the computation of the food class's average *in vitro* digestion.

## DISCUSSION

*Daily Food Consumption per Moose*

One can estimate the daily consumption ( $C$  in g-dry wt/day) of food per average moose, by

$$C = R/D/124 \text{ days,}$$

where  $R$  is the biomass removed by moose (Table II) per summer,  $D$  is the density of moose (Table III), and 124 days is the duration of the summer period. Table X presents the calculated daily dry weight consumption for deciduous leaves, herbaceous plants, and aquatics, showing a very consistent

TABLE X

Calculation of the Daily Summer Intake of Deciduous Leaves, Herbaceous Plants, and Aquatic Plants by an Average Adult Moose in Two Forest Types at Isle Royale National Park

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
<b>Deciduous</b>					
Food removed (kg/km <sup>2</sup> /summer)	1980.0	1680.3	1439.9	1990.0	5508.5
Moose density (no./km <sup>2</sup> )	4.3	3.8	3.1	3.3	10.2
Days of feeding	124	124	124	124	124
Consumption (g/day/moose)	3679	3566	3722	4863	4355
Average		3556 ± 81		4609 ± 359	
<b>Herbaceous</b>					
Food removed (kg/km <sup>2</sup> /summer)		176.3			
Moose density (no./km <sup>2</sup> )		3.8			
Days		124			
Consumption (g/day/moose)		375			
Average		375			
<b>Aquatic</b>					
Food removed (kg/pond/summer)		562.7			
Moose density (no./pond)		6			
Days of feeding		108			
Consumption (g/day/moose)		868		161 <sup>a</sup>	
Average		868		161	

<sup>a</sup> This value is calculated as the time that an average moose feeds (34.1 min/day) times the cropping rate (4.72 g/min).

level of consumption between years (less than an 8% coefficient of variation in the Coastal forest and 2% in the Yellow Birch). In total, a Yellow Birch moose consumes 4898 g-dry wt/day and a Coastal moose 4770 g-dry wt/day. Although we can only calculate confidence intervals for deciduous leaf consumption, we find even with what might seem to be crude measurements very consistent consumption values which are significantly different between the two forest types. The daily intake is apportioned in the Yellow Birch forest 74.6–7.6–17.7% for deciduous leaves, herbaceous plants, and aquatics; a similar breakdown for the Coastal forest is 96.6–3.4% for deciduous leaves and aquatics, since herbaceous consumption was not measured here.

Using the average percentage of water in each of the three plant classes' tissues, the observers computed the wet weight consumption of food each day (Table X) to be 33.6 kg/day in the Yellow Birch area and 33.2 kg/day in the Coastal region (this is a minimum value since no herb consumption was measured in the Coastal region). Kellum (1941) found that captive, adult moose from Isle Royale, when fed fresh-cut browse *ad lib.*, consumed 23 to 27 kg/day. It could be that our figure lies at Kellum's upper limit because free-living animals require a greater intake of energy than captive animals and because the water content of aquatic vegetation is higher than that of fresh-cut browse. Knorre (1959), however, working with captive Siberian moose, found that they consume between 30 and 40 kg-wet wt per day. Therefore, it appears that this method of computing daily food consumption is quite adequate.

#### *Energy Intake per Moose per Day*

The daily energy intake by a moose ( $E$ ) can be computed as

$$E = \sum_i C_i(K_i D_i - L_i),$$

where  $K_i$  is the gross caloric content of food type  $i$ ,  $C_i$  is the consumption of food class  $i$  (Table X),  $D_i$  is the dry matter digestibility of food  $i$  (Table IX), and  $L_i$  is the cost of searching for a gram of food  $i$  (cost of locomotion, Table VIII). The caloric intake estimates for the Yellow Birch and Coastal areas range between 15,610 and 14,488 kcal/day.

Gasaway and Coady (1974) and Moen (1974) claim that the metabolism of an animal ( $M$ : kcal/day) can be presented as

$$M = aW^{0.75},$$

where  $W$  is the animal's weight in kilograms, and  $a$  is a constant dependent upon the animal's activity. Using the measurements of  $a$  for a white-tailed deer (*Odocoileus virginianus*) and sheep (*Ovis aries*) presented by Gasaway and Coady (1974) and Moen (1974), we estimated a moose's  $a$  value to be

140 for a bull or barren cow and 193 for a cow with calf. The  $a$  value was arrived at by assuming that  $a$  is a weight-independent constant for closely related species (see Kleiber (1961) and Hemmingsen (1960) for justification) and taking the average of various  $a$  measurements made on taxonomically related species that were in environmental and reproductive states similar to those of our moose. If the moose population is composed of 57% bulls and barren cows, 31% cows with single calves, and 12% cows with twins (Jordan *et al.*, 1971), the average moose would have an  $a$  value of 170 or an  $M$  expenditure of approximately 14,000 kcal/day. This means that moose in the Yellow Birch Forest have 1670 kcal/day above their  $M$  expenditure after feeding, while the moose in the Coastal Forest have 488 kcal/day more. These values represent surplus energy above that required for the moose's growth, reproduction, and maintenance. Although moose do have a surplus of energy from feeding, it is not a very large amount, leaving little room for the moose's error or changes in its environment.

TABLE XI

The Wet Weight Intake of Food per Day during the Summer by an Average Adult Moose for Two Forest Types at Isle Royale National Park Based Upon the Average Diet Values in Table X and the Percentage of Water in Each Food Class<sup>a</sup>

	Yellow Birch Forest	Coastal Forest
Deciduous	14,624	18,436
Herbaceous	1,646	?
Aquatic	17,360	14,771
Total	33,630	33,207

<sup>a</sup> Intake is given in grams. See text for discussion.

### *A Moose's Daily Time Budget*

The daily activity cycle for moose (Fig. 3) suggests that moose are primarily active from just prior to sunset through slightly after dawn, with peaks of activity centered at sunset and dawn. However, there exists a slight peak of activity during the late afternoon which is restricted to aquatic feeding. Nevertheless, moose appear to be largely nocturnal during the summer, which Knorre (1959) claimed in the only other published study of moose activity that was concerned with the entire 24-hour period of a summer day. This observation combined with the high correlation ( $r^2 = 0.92$ ) between average daily air temperature and feeding time (Fig. 4) suggests that moose might be limited in their activity by thermal conditions. The importance of thermal

conditions on summer moose activity is documented elsewhere (Belovsky, 1977).

Using the regression between mean daily air temperature and feeding time (Fig. 4), we can compute how long a moose will feed on an average summer day when the average air temperature is 15.4°C. This predicted value of 302 min/day can then be compared with the estimated time for food acquisition, using the observed cropping rates and predicted food consumption, to determine whether the consumption of food is consistent with the amount of time spent feeding (Table XII). Deviations between these two measures of feeding time

TABLE XII

The Time Expenditure of an Average Adult Moose for Feeding in Two Forest Types at Isle Royale National Park Based on the Average Diet in Table X and the Cropping Rates in Table VII

Study area	Yellow Birch Forest		Coastal Forest	
	g-consumed/day	min/day	g-consumed/day	min/day
Deciduous	3656	218.9	4609	276.0
Herbaceous	374	45.1	?	?
Aquatics	868	42.8	161	34.0
Total	4898	306.8	4770	310.0
Amount of time spent feeding each day based upon the regression in Fig. 4 and an average summer day of 15.4°C		301.6		301.6

range from 5 to 8 minutes, or approximately 3% of the daily feeding time based upon the regression with air temperature. This is a rather close agreement. We can now conclude, since a moose's energy intake does not exceed its requirements by a large margin, that something is limiting food consumption, and perhaps this feeding element is the amount of thermally suitable time during each day.

Feeding time was also used to partially demonstrate differences between the diets chosen by cows and bulls (Table XIII). This was accomplished by solving the simultaneous equations:

$$C = 0.5M + 0.5F \quad \text{and} \quad F = xM,$$

where  $C$  is the average daily consumption for an average moose,  $M$  is the average bull moose's diet,  $F$  is the average cow's diet, and  $x$  is the ratio of

observed time spent feeding by bull moose to that spent by cows. The 0.5 value in the above equations is the observed sex ratio. The results of this apportionment show that cows consume more herbaceous and aquatic vegetation per day than do bulls. Deciduous leaf consumption, however, could not be apportioned, since there was no way to estimate  $x$  when this feeding primarily

TABLE XIII

Differences in the Diets of Bulls and Cows Based Upon the Relative Amounts of Time Spent by Each Sex Feeding on the Foods in Two Forest Types at Isle Royale National Park<sup>a</sup>

Study area	Yellow Birch Forest				Coastal Forest			
	Bulls		Cows		Bulls		Cows	
	g/day	min/day	g/day	min/day	g/day	min/day	g/day	min/day
Deciduous <sup>b</sup>	—	—	—	—	—	—	—	—
Herbaceous <sup>c</sup>	150	18.1	598	72.1	—	—	—	—
Aquatics <sup>d</sup>	655	32.3	1081	53.3	112.2	23.5	214.2	44.7

<sup>a</sup> There appeared in this study to be no statistically significant differences between cows with and without calves.

<sup>b</sup> There exists no way to apportion the consumption of deciduous leaves between the sexes since this feeding primarily occurs at night.

<sup>c</sup> Cows were observed feeding on herbs four times more frequently than bulls.

<sup>d</sup> Cows were observed feeding on aquatics 1.65 times more frequently than bulls in the Yellow Birch Forest and 1.93 times more frequently in the Coastal Forest.

occurred at night. Finally, barren cows were not separated from cows with young since there did not appear to be any differences in feeding time; this suggests that barren cows may anticipate future pregnancies and store needed nutritional components.

#### *Moose Diets in Relation to Available Browse*

The terrestrial browse species available differed between the Coastal and Yellow Birch study areas (Table XIV), with the relative abundances of all species differing significantly in 1974 and all but *Sorbus americana* in 1972 ( $\chi^2$  contingency table with  $P \leq 0.05$ ). These vegetation differences no doubt reflect the sharp climatic differences between coastal and inland zones. Between-year differences in species availability within each study area were also tested using a  $\chi^2$  contingency table. Significant differences are presented in Table XIV. Changes in relative species abundance are most likely due to consumption-

TABLE XIV

The Percentage Availability of Deciduous Leaves by Weight Based upon the Total Production Values in Table I for Two Forest Types at Isle Royale National Park<sup>a</sup>

Study area	Yellow Birch Forest			Coastal Forest	
	1972	1973	1974	1972	1974
Year					
Sample size (g)	16,137.9	18,459.7	3,334.7	5,522.3	4,203.8
<i>Sorbus americana</i>	16.1 <sup>b,d</sup>	14.1 <sup>b</sup>	13.8 <sup>d</sup>	12.8	12.7
<i>Acer spicatum</i>	6.9 <sup>b,d</sup>	12.1 <sup>b,c</sup>	53.4 <sup>c,d</sup>	29.8 <sup>d</sup>	36.1 <sup>d</sup>
<i>Betula alleghaniensis</i>	37.4 <sup>b,d</sup>	29.8 <sup>b,c</sup>	12.3 <sup>c,d</sup>	0.5 <sup>d</sup>	1.4 <sup>d</sup>
<i>Betula papyrifera</i>	2.8 <sup>b</sup>	1.6 <sup>b,c</sup>	2.4 <sup>c</sup>	15.6 <sup>d</sup>	7.0 <sup>d</sup>
Other species	36.8 <sup>b,d</sup>	42.4 <sup>b,c</sup>	18.1 <sup>c,d</sup>	41.3	42.8
Total	100.0	100.0	100.0	100.0	100.0

<sup>a</sup> Significant differences— $\chi^2$  contingency table:  $P \leq 0.05$ . All  $\chi^2$  tests were done by using the number of leaves counted rather than the biomass since a  $\chi^2$  test requires discrete measurements.

<sup>b</sup> 1972 vs 1973.

<sup>c</sup> 1972 vs 1973.

<sup>d</sup> 1972 vs 1974.

induced productivity declines and competitive release arising from this predation: i.e., *Sorbus americana*, the major deciduous component of a moose's diet, consistently declines in abundance, while *Acer spicatum*, a less heavily used plant, increases in abundance. This is even more apparent when one realizes that the total production (Table I) does not change drastically between years. One change in relative species abundance which does not appear to fit this hypothesis is the change in the abundance of *Betula alleghaniensis*. Although this species is not heavily used by moose, its abundance has declined. Perhaps this observation results from successional changes; for example, *Betula alleghaniensis* plants have grown above the 2.8-m limit for moose feeding and we no longer count them in our browse surveys. The effect of moose consumption on these forests will be examined in depth in a later paper.

The summer diets of moose are, we believe, well represented by the relative proportions of leaf removals accounted for on the transects: Table IV shows the averages of all transect runs in the two study area forest types for each year. Comparing Tables XIV and IV, one notes that in 1972 deciduous diets are more alike between the two study areas than are the sets of browse available in those areas. During 1974, the diets and food availability are equally similar. Similarity was determined using Schoener's (1970) measure of percentage

similarity. The 1972 dissimilarities in diet, however, suggest that in feeding moose make selections which are not merely related to what is available. The same appears to be the case for herbaceous plants (Table V) and aquatics (Table VI). Table XV presents a list of plant species which were found to be chosen more frequently, at the same frequency and less frequently than the species' availability, as determined by  $\chi^2$  contingency tests.

TABLE XV

Moose Preferences (% in Diet vs % Available) for Various Food Plant Species Based Upon a  $\chi^2$  Contingency Analysis ( $P < 0.05$ )<sup>a</sup>

	Preferred	Indifferent	Avoided
Deciduous	<i>Sorbus americana</i> <i>Populus tremuloides</i> <i>Acer spicatum</i> <i>Diervilla lonicera</i>	<i>Betula papyrifera</i>	<i>Betula alleghamiensis</i> <i>Corylus cornuta</i> <i>Sambucus pubescens</i> <i>Rubus parviflorus</i> <i>Lonicera canadensis</i>
Herbaceous	<i>Streptopus roseus</i> <i>Dryopteris spinulosa</i>	<i>Cornus canadensis</i> <i>Aralia nudicaulis</i> <i>Equisetum</i> sp.	<i>Poa</i> sp. <i>Lycopodium</i> sp. <i>Clintonia borealis</i>
Aquatics	<i>Nitella</i> sp. <i>Chara</i> sp. <i>Potomegeton</i> sp. <i>Spyrogyra</i> sp.	<i>Equisetum fluviatile</i>	<i>Carex</i> sp.

<sup>a</sup> All  $\chi^2$  tests were done by using the number of leaves counted as being removed, since a  $\chi^2$  test requires discrete measurements.

The apparent selectivity of plants by moose fits our impression that moose distinguish and select among species according to a hierarchy of preferences; the diets from given areas and years are more similar than would be expected from availability alone (except for a 1974 comparison of Coastal with Yellow Birch). Therefore, the differences between these diets reflect the degree to which these preferences can be satisfied. In addition to specific preferences, moose might seek to combine the intake of two or more species during a given period to avoid overintake of specific plant toxins and to take advantage of synergistic chemical combinations for digestion (Freeland and Janzen, 1974). This suggests that a diverse diet should be more digestible than monophagy. The *in vitro* digestion values in Table IX include a sample of mixed plant species (14 species) and the digestion value estimated from the frequency of each species in the sample; no apparent advantage for diet diversity was



found since the digestion values are very similar (76% for the mixed diet vs 82% from the component frequencies).

The actual digestibility of the moose's summer diet, based upon the weight of feces and forage removed, appears in Table XVI (79% digestible). Consequently, there appears to be no digestion advantage of a mixed diet, but this does not preclude the need for diversity to supply diverse mineral requirements.

TABLE XVI

Calculation of the Dry Matter Digestibility of the Summer Diet Chosen by Moose in Two Different Forest Types at Isle Royale National Park, Based upon the Average Consumption in Table X

Study area	Yellow Birch Forest	Coastal Forest
Dry matter consumption (g/day/moose)	4898	4770
Dry weight of feces (5.66 defecations/day × g/pie) <sup>a</sup>	1010	1004
Dry matter digestibility (%)	79.4	79.0

<sup>a</sup> 178.3 g/pie ± 34.8 in the Yellow Birch ( $N = 35$ ). 177.4 g/pie ± 42.3 in the Coastal Forest ( $N = 11$ ).

### *Changes in Diet over the Summer*

The diets of the moose changed as summer progressed (Figs. 1a-e); we found significant differences in the relative frequency with which species were taken between consecutive 2-week periods ( $\chi^2$  contingency table,  $P \leq 0.05$ ). Diversity in diets, as interpreted from the transect data, was examined by computing for each biweekly average of species removed along the transects a Shannon-Weaver diversity index (Pielou, 1969):

$$H' = -\sum_i p_i \ln p_i,$$

where  $p_i$  is the relative occurrence of the  $i$ th species in the moose's diet. This single index,  $H'$ , reflects both the number of species taken and the frequency of their consumption.

Figure 5 traces dietary diversity throughout the summer. We believe the higher values in early summer for the Yellow Birch area, when total production of new plant growth is still low, reflect the generally 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, moose may find more species

of browse attractive during the period of early leaf growth than later, when leaves are maturing. The midsummer minimum in diversity of deciduous leaves in the diet may also reflect increased use of aquatics—comprising up to 18% of the diet according to our measurements. In late summer, coincident with a dropping-off of aquatic feeding and the desiccation of leaves, diversity in the diet begins to rise again.

Diversity changes in the Coastal diet over the summer are much smaller than those in the Yellow Birch, and they do not show a marked trend. Also, the diversity of the Coastal diet is much lower than that for the Yellow Birch

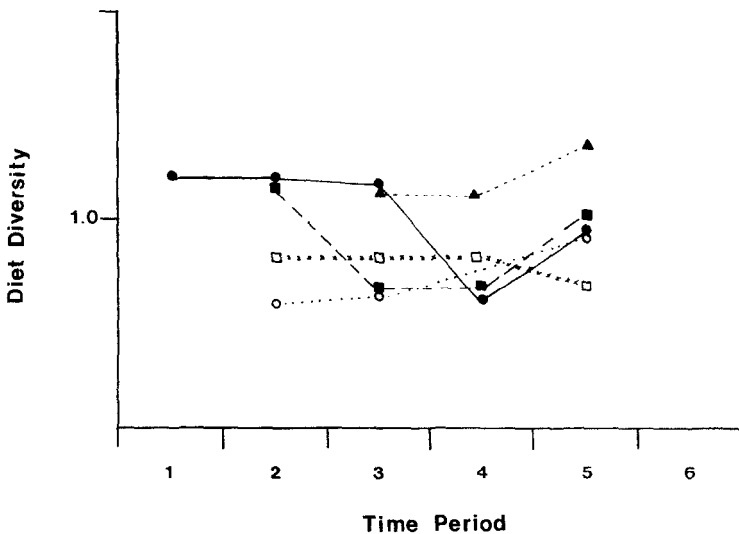


FIG. 5. A plot of the moose's diet diversity at a series of different times during the summer. The time periods are defined in Fig. 1 and the different symbols represent: ●, Yellow Birch Forest 1972; ▲, Yellow Birch Forest 1973; ■, Yellow Birch Forest 1974; ○, Coastal Forest 1972; and □, Coastal Forest 1974. See the text for further details on these diversity values.

(0.80 vs 1.18), even though both possess nearly equal diversities of the species available (1.28 vs 1.30). Therefore, Coastal moose must have a greater abundance of highly palatable foods; for example, the Coastal area does not have the large availability of *Betula alleghaniensis*, which is not preferred.

#### *Moose Abundance*

It would be advantageous to be able to predict the density of moose in the two study areas from some feeding parameter. The first parameter to come to mind is plant production, especially the production of deciduous plants

since they provide the bulk of the diet. Plant production, however, was not found to be correlated with moose numbers ( $r^2 = 0.01$ ,  $N = 5$ ,  $P \geq 0.10$ ). 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. This suggests that moose densities might be related to forage diversity. Although a better correlation was found ( $r^2 = 0.46$ ,  $N = 5$ ,  $P \geq 0.10$ ) using diversity, the correlation is still not very good and further research suggests that moose do not choose their diets for diversity (Belovsky, in preparation). Therefore, there appears to be no simple measurement which predicts moose density.

Several other parameters might act as determinants of moose population density. First, forest production might be important, but the production of each species should be weighted by some palatability measure to achieve a more relevant measure. This seems like a possible avenue since the Yellow Birch area has a lower moose density than the Coastal area and also has a large production of food plants of low palatability, i.e., *Betula alleghaniensis*. This, however, requires some estimate of palatability which we do not have at present.

Another alternative is the distribution of forest production in usable patches; i.e., the food might be distributed very uniformly so that time and energy limitations prevent its use by moose. This means that regions with equal productivities might support very different numbers of moose because of the distributions of plants.

Botkin *et al.* (1973) and Jordan *et al.* (1973) found that the Isle Royale moose are potentially limited by sodium availability, since aquatic plants are the only source of sodium. This might mean that the abundance of aquatic vegetation determines moose densities. Finally, the availability of winter foods (twigs and conifer needles) might determine moose densities. We suspect, however, that winter survival is dependent to a large extent upon the storage of fat during the summer. Therefore, we return to deciduous plant production as the main determinant of moose densities either through species composition, distribution over the region, or the moose's ability to utilize leaves and still satisfy its sodium requirements at beaver ponds. Each of these parameters will be examined in detail in future papers.

## CONCLUSION

We believe our integrated approach of various methods for the study of moose browsing has produced promising results. Although it requires a considerable input of time and effort by the observers, it provides feeding estimates which do not suffer from the biases involved in studies based entirely on direct observations of feeding animals. Therefore, the diet estimate is not biased by differential abilities to count certain foods being fed upon by an animal

or the different accessibilities for the observer to watch animals of different sexes and reproductive classes. This is particularly helpful since moose are primarily nocturnal in the summer and many of their forest habitats are so thickly vegetated that close observation is difficult. We now possess very sound estimates of a moose's diet and time-energy budget from these measurements, which can be employed in mineral-energy flow studies of the Isle Royale ecosystem and detailed evolutionary ecology studies of moose feeding.

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