THE IMPORTANCE OF DIVERSITY IN THE DIET OF MOOSE

Dale G. Miquelle and Peter A. Jordan

Department of Entomology, Fisheries and Wildlife

University of Minnesota

The array of plant species eaten by moose (Alces alces) has been well documented; however, whether their dietary diversity reflects a basic feeding strategy or simply a scarcity of preferred species has not been tested. Closely observed moose on Isle Royale in summer consumed a number of species during each period of sustained feeding ($\overline{X}$ = 56 ± 4.8 min). To determine preferences when preferred species are not limited, captive moose were offered common, preferred browse species *ad libitum*. While showing distinct preferences, the experimental animals did not select a monotypic diet. Vegetation analysis revealed that, given the availability of browse on Isle Royale, moose could fulfill their quantitative needs (21.6 kg/day) by feeding on one preferred species; however, they selected for more than one species, suggesting that diversity was an objective. Preferred foods of captive and wild moose were not the same, suggesting that previous experience and/or diet may affect preference. Speculations on the relationship between availability of various species and the nutritional implications of selecting a diverse diet are made.

It is well documented that moose (Alces alces) feed on a wide array of plant species (Dodds 1960, Peterson 1955, Houston 1968, Peek et al. 1976, Aldous and Krefting 1946). LeResche and Davis (1973) noted that variety in the diet, especially in summer, may be even greater than that determined by traditional methods. However, the nutritional significance of di-

versity per se has not been investigated. It has been shown that mule deer (Odocoileus hemionus) benefit from a mixed diet (Longhurst et al. 1969). Single-species diets may be refused to the point of death (Milchunas et al. 1978) or taken only under special circumstances (Bissell et al. 1955); however, these studies focused on single species which were noted for having inhibitory, secondary compounds. Oldemeyer et al. (1977) showed that five species could better meet the needs of moose on the Kenai Peninsula than any one of these species alone. It was hypothesized by Westoby (1974) that large, generalist herbivores, limited primarily by the rate they can process food, must select food items that will provide a high qualitative level and an appropriate balance of nutrients, given their relatively fixed quantitative intake. Belovsky (1978) has developed a diet optimization model for moose based on energy and sodium requirements, but this only considers food classes--browse, forbs, and aquatic vegetation--rather than species.

Sensitivity to nutrient content by taste or by a "long-delay learning" mechanism (Westoby 1974) could lead to selection of the one species or a combination of several species that would provide the best possible diet from available vegetation. On the other hand, moose may not recognize or be able to respond to specific nutrient deficiencies; instead, natural selection may simply have favored those animals which fed on several rather than one palatable species, thus raising the probability of their consistently meeting all nutritional requirements.

Given that moose do feed on a variety of plants and that such variety may be nutritionally beneficial, it is important to document whether moose are selecting for diversity. However, if one observes that moose select a mixed diet, it is difficult to assign whether this is due to their inability to obtain more of a single, most-preferred species, or whether they are actually seeking to combine two or more items.

If diversity is nutritionally important to moose, it is likely this will be demonstrated most clearly in summer when the highest ecological metabolism occurs (Moen 1978). Studies on deer (Odocoileus spp.) show reproductive success is directly related to summer-range conditions (Swank 1958, Arnold and Verme 1963, Julander et al. 1961, Longhurst 1951, and Robinette et al. 1955). While diversity in the diet may also be important in winter, as in low-quality forage habitats on the Kenai (LeResche and Davis 1973), the nutritional demands of winter maintenance are not as great.

In an attempt to determine whether moose do select for a diverse diet, we measured food intake by species in the field, and we made the same measurements on captive moose offered some of the same browse species *ad libitum.* Measurements included amounts taken, time spent feeding on each item, and space covered by free-ranging animals while foraging. From these data we are attempting to reconstruct general patterns of food selection in moose while asking whether animals will select for a single most-preferred species or, if not, how they allocate their preferences among two or more species. From these results, speculations can be made about the relationship between availability of various species and the nutritional implications of selecting a diverse diet. This paper summarizes the data and progress to date.

ACKNOWLEDGEMENTS

We thank Murry Lankester for the use of the captive moose, and Steve Dudzinski for facilitating the experiments at his game farm;

assistants deserve special thanks for their long hours of tedious work: Peter Berglund, Dean Faber, Gary Heimark, Tim Olson, Kathy Preece, Tom Remington, Jean Sularz, and Richard Yeates. We thank personnel of Isle Royale National Park for logistic support, particularly District Ranger Noel Poe. Funding was provided primarily by the National Park Service but also by the Minnesota Agricultural Experiment Station[1] and the Big Game Club of Minneapolis.

STUDY AREA

Field studies were conducted at the southwest end of Isle Royale National Park, Michigan, in Lake Superior (Fig. 1). Two vegetation sampling sites, "Coastal" and "Yellow Birch," each 1/4 km^2, were used; these were previously described by Belovsky et al. (1973). Direct observations on free-ranging moose were made in the region of Washington Harbor and Grace Creek (Fig. 1), areas typical of the Yellow Birch Forest type (Belovsky et al. 1973). Captive-moose feeding trials were conducted near Kakabeka Falls, Thunder Bay District, Ontario, some 70 km from Isle Royale and in a similar climatic zone. Browse for these trials was collected near Kakabeka Falls.

METHODS

Feeding Trials

Trials of 3-6 days each were conducted in September of 1977 and in June, July, August, and September of 1978 using three captive moose.

---

[1]Scientific Journal Series No. 10,827, Project 86. Agricultural Experiment Station, University of Minnesota, St. Paul, MN. 55108

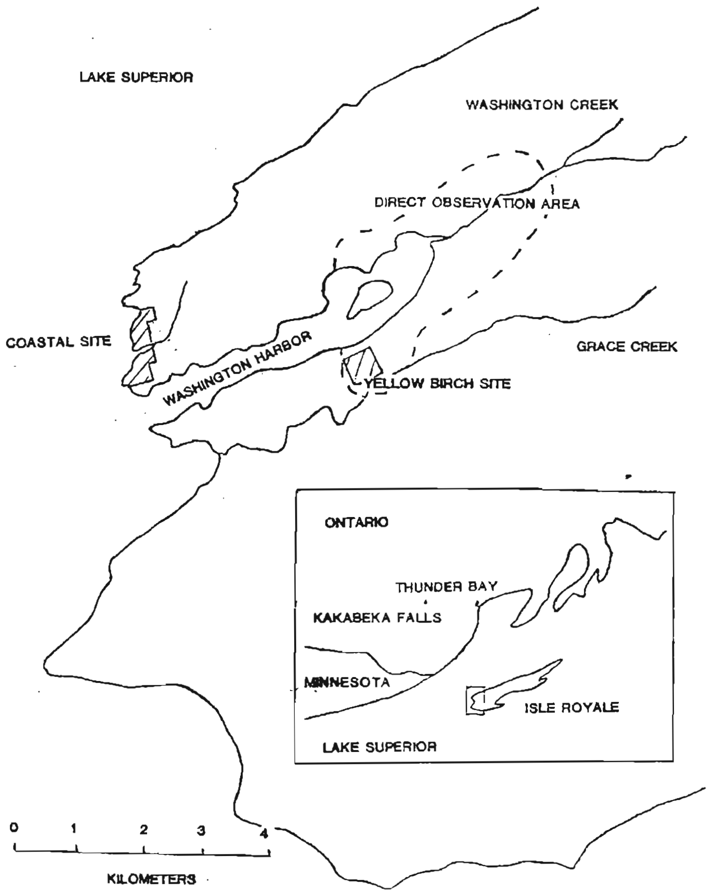

FIGURE 1. Study area.

Two animals, a female and male referred to as #1 and #2 respectively, were acquired as abandoned calves in the Thunder Bay region in early summer 1977. They were raised together in a small enclosure, being fed both milk and browse throughout the summer; at the first trial, September 6-9, 1977, they were 3 to 3 1/2 months old. These two were also used as yearlings in 1978; the female appeared unhealthy during the July trial and died shortly afterward, apparently from a respiratory infection. Data from her July trial are not included. A new male calf, #3, also picked up in that region, was used for the August and September 1978 trials.

During the trials, animals were kept in separate, 10 x 20-m enclosures and provided with shade and water. Between trials in 1978, the yearlings were kept in a larger enclosure containing small amounts of speckled alder (*Alnus rugosa*) and balsam poplar (*Populus balsamea*) which the animals quickly depleted. The bulk of their diet between trials was a mixture of crushed oats, beet pulp, grass and clover. Male calf #3 was housed in a small pen and supplied with cut browse for the first half of the summer; he was later moved to a large enclosure where he fed freely on available browse. All calves were fed a quart of milk twice daily, even during the trials, into the fall of their first year.

Experimental forages, which were woody, deciduous species, were cut as 0.5 - 1.5-m stems containing ample foliage and stored under shade, often with the cut ends inserted in water. No browse of wilted appearance was offered to moose; new stems were gathered as often as necessary (2-5 times/day) to insure a fresh supply. Each stem was firmly affixed to the woven-wire enclosure fence so moose could readily pull off leaves without freeing the stems (a moose cannot strip leaves from an unattached stem).

A set of stems of one species was weighed to the nearest gram before being offered. When most of the foliage had been eaten or when it appeared wilted, the set was removed for reweighing, and a new set was immediately put out. At the end of each 24 hours all browse was replaced so that daily totals were uniformly measured. Controls of each species were regularly weighed to estimate rate of water loss or gain.

One observer was always stationed on the outside of the enclosure near the stems where he/she recorded all bites and the total number of seconds the animal spent feeding on each species. Activity patterns, including length of resting and feeding periods, were also recorded. Night observations were aided by lanterns. Biomass intake was recorded for both animals; the activity records were made on only one animal for each 24 hour period.

Prescribed sets of species or "menus" were offered *ad libitum* for one or more 24-hour period.

Direct Observations

During June-August 1977 and 1978, free-ranging moose at Isle Royale were followed by one or two observers for as long a continuous span as possible to record details of feeding. New observers replaced those following the moose every 6-8 hours, contact being maintained by 2-way radios.

Feeding data were grouped according to "feeding periods," defined as any span greater than 15 minutes during which a moose feeds continuously. More than 95% of all bites recorded occurred during such continuous bouts. Feeding time within a period was the sum of seconds spent in biting, chewing, swallowing (but not in ruminating), and moving

between bites. Short interruptions due to human disturbance, alert posturing, comfort activities, urination, or defecation were not included. Aquatic feeding was not included.

Observers recorded number of bites of each species, leaves per bite, and steps taken in a feeding period. Duration of feeding period was recorded to the nearest second and of other major activities-- rest and extended movements-- to the nearest minute. Where possible, sample measures of length of step and the distance a moose reached laterally and vertically to remove leaves were made.

In the study area many moose appeared well-habituated to humans. Initial flight distance was often less than 25 m, and after an hour or so of having observers that close, moose would tolerate them at 3-5 m. This included cows with calves at heel. At these distances, an experienced observer could identify browse species being eaten with reasonable consistency, although circumstances never permitted continuous visual contact with the moose's head due to intervening vegetation or the position of the animal. Therefore, counts of bites really were a subsample of 30 to 100% of the total feeding time.

Moose were followed through the night with the aid of a flashlight, and this had no visible effect on the animals. Activity patterns were recorded at night, and, in some instances, animals could be approached close enough with a flashlight to permit plant-species identification and bite counts.

Biomass intake is calculated as bites x weight/bite, where weight/bite is leaves/bite x weight/leaf. Leaf weights for all species consumed were determined from 15 samples of a known number of leaves weighed both wet and oven-dry (65° C, 24 h). Terrestrial browse consumption by Isle Royale moose, as determined by direct observations, was calculated from the sum of observations on all moose. Individual variation is not reported here.

Vegetation Analysis

Vegetation was measured at Isle Royale in summer 1978 on 155 (66 in the Yellow Birch site and 89 in the Coastal site), 7.5-m^2 plots. Plots were spaced at 50 m along parallel transects. On each plot foliage and herbaceous vegetation between 15 cm and 2.8 m above ground, the zone considered available to moose, was removed. Since moose, in general, take bites consisting only of bunches of leaves, not all foliage is equally "available." We employed a sampling scheme designed to simulate moose browsing so as to best estimate actual forage availability. The rational and applicability of this method will be more fully discussed in a later paper.

At each plot, available browse was removed and later weighed; a correction factor was used for all species to adjust for moisture loss between removal and weighing. We assumed that subsequent regrowth during the same season produced insufficient browse to warrant a separate measurement. Regrowth following early-summer browsing will be treated in another paper.

To determine removal of browse by moose, 24 semi-permanent, 30 x 2.5-m plots were established along the same transects. All leaves removed by moose within each plot were counted at 10-day intervals. Each "moose bite" was flagged to prevent subsequent recountings; Belovsky and Jordan (1978) had stated that leaf removals within less than 10 days could be

distinguished from older removals by the appearance of the cut petioles or leader, but we found this to be unreliable.

Removal of herbs could not be reliably measured by the removal-evidence method, so we used direct observations on feeding moose for that estimate.

RESULTS

Forage consumption by captive animals and browse available at Isle Royale are expressed as wet weights. We are concerned that forage volume may limit intake, and water content here--a minimum 58-80%--exceeds that considered critical to intake (Duckworth and Shirlaw 1958). Dry weights were also determined, and a basis for conversion is provided (Table 1).

Throughout the report results are accompanied by confidence intervals at the 95% level.

Table 1. Wet Weight To Dry Weight Conversion Factors

Mountain Ash (*Sorbus americana*)	.345	Choke Cherry (*Prunus virginiana*)	.385
Mountain Maple (*Acer spicatum*)	.289	Hazel (*Corylus cornuta*)	.421
Paper Birch (*Betula papyrifera*)	.400	Sugar Maple (*Acer saccharum*)	.361
Yellow Birch (*Betula lutea*)	.347	Red Osier Dogwood (*Cornus stolonifera*)	.316
Pin Cherry (*Prunus pennsylvanica*)	.295	Herbaceous Vegetation	.253

Feeding Trials

A three-species menu of mountain ash, mountain maple, and paper birch was presented to all animals sometime during each set of trials except in September 1977. These three browse plants occur in reasonable abundance at Isle Royale, and all were found frequently eaten in the observation areas. Yellow birch (*Betula lutea*) would also have been included because of its abundance and frequent use, but it was not available around the Kakabeka Game Farm. Other menus included pin cherry, choke cherry and red osier dogwood, which were less abundant on the island but regularly used, and hazel and sugar maple which were relatively abundant but little used. Feeding results are shown in Tables 2 and 3.

Mountain ash was the most preferred item, constituting more than 50% of all multi-species diets except in one instance. Paper birch was next in preference, although in the seven-species experiments there was no significant difference in intake between pin cherry and birch ($p > .1$). Sugar maple and hazel made up only a minor portion of the diet (except for animal #3 who took significant quantities of hazel). It is important to note, however, that a measurable quantity of every species offered was always taken.

Animals #1 and #2 generally had similar preferences; in contrast, animal #3 took far more birch, less ash and more hazel than the other two. There was not a significant difference between intake of ash and of birch in the multi-species trial for animal #3 ($p > .1$). Variation among animals is, therefore, an important factor.

Part of the variation among animals and within a single animal may be due to previous conditioning. Animals #1 and #2, when fed a 5-species diet as calves in 1977, showed a strong preference for mountain maple, it being

Table 2. Mean daily wet-weight biomass intake (kg) by captive moose offered various menus; species not offered indicated by dash (95% confidence interval reported).

	Date of Trial	Age	# Days	Mountain ash	Mountain maple	Paper birch	Sugar maple	Pin cherry	Choke cherry	Hazel	Red Osier dogwood	Total wet weight
Animal #1	Sept 1977	C[1]	2	4.106 ± 1.232	1.209 ± 1.135	.420 ± .302	-	-	-	.074 ± .092	.844 ± 1.146	6.662 ± 1.523
	June 1978	Y[2]	3	11.689 ± .678	1.599 ± .743	2.819 ± 1.349	-	-	-	-	-	16.108 ± 2.514
Animal #2	Sept 1977	C	2	3.593 ± 1.888	1.949 ± .207	.672 ± .026	-	-	-	.046 ± .046	.668 ± .218	6.930 ± 2.377
	Jun-Jul Aug-Sept 1978	Y	10	14.270 ± 2.511	1.299 ± .303	6.368 ± .954	-	-	-	-	-	21.939 ± 2.054
	Aug-Sept 1978	Y	4	14.127 ± 2.766	1.233 ± 1.551	3.992 ± 2.021	.240 ± .200	3.982 ± 1.837	2.714 ± 1.555	.502 ± .514	-	26.790 ± 2.302
	Jul-Aug 1978	Y	4	21.519 ± 2.355	-	-	-	-	-	-	-	21.519 ± 2.355
	Sept 1978	Y	2	-	17.412 ± 9.614	-	-	-	-	-	-	17.412 ± 9.614
Animal #3	Aug-Sept 1978	C	4	6.602 ± 1.404	.310 ± .185	4.975 ± .781	-	-	-	-	-	11.888 ± 2.200
	Aug-Sept 1978	C	4	5.109 ± 2.579	.691 ± .858	4.343 ± .422	.291 ± .301	2.722 ± 1.102	.571 ± .485	.989 ± .510	-	14.768 ± 2.058
	Sept 1978	C	2	-	12.034 ± 5.847	-	-	-	-	-	-	12.034 ± 5.847

[1] C = calf. [2] Y = yearling

Table 3. Percentage intake by menu and animal, calculated from average intake for all days in which a particular menu was presented to an animal.

	Mountain ash	Mountain maple	Paper birch	Sugar maple	Pin cherry	Choke cherry	Hazel	Red Osier dogwood
5-Species Menu								
animal #1	61.6	18.1	6.4	-	-	-	1.1	12.8
animal #2	51.8	28.1	9.7	-	-	-	.7	9.6
3-Species Menu								
animal #1	72.6	9.9	17.6	-	-	-	-	-
animal #2	65.1	5.9	29.0	-	-	-	-	-
animal #3	55.5	2.7	41.8	-	-	-	-	-
7-Species Menu								
animal #2	52.7	4.6	14.9	.9	14.9	10.1	1.9	-
animal #3	34.6	4.7	29.4	2.0	18.8	3.8	6.7	-

For monotypic diets, one species obviously constitutes 100% of the diet.

18-28% of their diet and their second most preferred species. Previous to this trial these animals had been given, in addition to their commercial feed and milk, browse consisting largely of mountain maple. Then, during the intervening fall through spring prior to the 1978 trials, these animals were on a commercial feed with little browse and no maple. When in July 1978 #2 was put on a maple-only menu, its intake dropped dramatically on the first day, and it was observed kneeling to feed on clover growing in the pen, the only record of such behavior. On the second day of the maple-only menu, however, #2's biomass consumption returned to normal. Animal #3, the 1978 calf, had not been previously exposed to mountain maple either, and it responded exactly as #2 during the July 1978 trial. The large standard deviations in consumption while on the maple-only menu reflect these initial rejections.

In contrast, when all three animals were presented with mountain ash for the first time, there was no initial rejection; it immediately became a major component of their intake. The differences shown suggest that preferences for some species vary over time even for the same animals, due perhaps to previous experience or diet. Thus, predicting preferences in wild moose from captive-feeding results requires caution. Given differences in availability of certain species, moose in the wild may actually feed on and prefer foods that would not be taken initially in free-choice experiments by naïve animals.

We wished to determine whether captive moose were selecting for a monotypic diet focusing on mountain ash, the species clearly most-preferred. An analysis of variance was run for #2, the only animal for which summer-long data were collected.

We first tested to determine if total biomass consumption increased as the number of species in the diet increased. There did not appear to be any difference in total consumption between an ash-only and a 3-species menu ($p > .25$) or between a 3-species and a 7-species menu ($p > .25$), but there was a significant increase from an ash-only to a 7-species menu ($p < .05$). Although not conclusive, we believe this suggests that the total eaten was more when there was a greater variety of species present.

Next we tested whether lesser quantities of mountain ash were consumed when a greater variety of species was offered (Table 2). In contrast to an ash-only menu, intake was significantly less with a 3-species ($p < .025$), and a 7-species ($p < .05$) menu. However, intake of ash in a 3-species menu was not significantly different from that in a 7-species menu ($p > .25$), suggesting there may be a threshold level above which intake of a highly preferred food such as mountain ash will not decline as more species are offered.

Finally, we compared the rates of consumption (biomass/time) among the species in a 3-species trial (Table 4).

Table 4. Frequency distribtuion (percentage) of biomass intake and time allocation by captive moose #1 and #2 from 10, 24-h experimental feeding periods in which three species comprised the menu.

	Mountain ash	Mountain maple	Paper birch
Average biomass intake (wet weight)	66 $\pm$ 6.1	6 $\pm$ 1.2	28 $\pm$ 5.8
Average time allocation	58 $\pm$ 7.3	4 $\pm$ 1.2	38 $\pm$ 6.9

More mountain ash was eaten per unit time than paper birch. A t-test shows that the proportional intake of birch was less than the time allotted to feeding on it ($p < .001$) suggesting that there is sufficient advantage for including birch so as to compensate for the slower intake rate.

In summary, the feeding trials showed that while there are distinct preferences among the species offered, moose do not exclusively choose the most preferred item. Additional species are sought even when inclusion of a less-preferred species requires a lowering of feeding efficiency.

Direct Observations on Free-Ranging Moose

During June-August 1977 and 1978, 388 h of observation time, including 113 h of feeding-periods, were recorded for free-ranging moose. It is not possible to know how many individuals were involved, but we estimate at least 14 were followed for a total of 20 observation sets (2 animals were definitely followed more than once). All were adult females, and all but two were without calves. Earlier work by Belovsky (1978) demonstrated that there was no difference in diet between adult females with calves and those without, so we combined data from all animals. Length of observations varied from 50 min to 7 days, with most records being for more than 3 h.

Feeding periods averaged 56 $\pm$ 4.8 min, with 7-8 periods/24 h. Time/24 h spent in feeding, estimated from the overall proportion of feeding recorded by all direct observations, was 6.74 $\pm$ 1.00 h. This estimate is higher than those of Belovsky and Jordan (1978) and Geist (1963), perhaps partly because our definition of feeding time included time of travel between bites.

Moose averaged 142.2 $\pm$ 5.6 steps per feeding period, the length of each step being 1.35 ± .05 m. The radius of reach, measured at 90° angle to the body, was 1.18 ± .16 m. From these measurements we calculated that a moose was feeding over 3,276 ± 134 m^2/day. This does not include ground covered during non-feeding movements.

Intake per 24 h averaged 4,987 ± 1,465 bites. Weight per bite, determined from measurements on leaves per bite and weight per leaf (Table 5), varied by species.

Table 5. Species composition of diet for free-ranging moose on Isle Royale recorded as percentage biomass taken, and the measures used for calculating biomass intake from field observation.

	% of intake	Leaves/ bites	Wet weight/ leaf (g)
Mountain ash	18.8	5.7 ± 3.4	.90 ± .04
Mountain maple	57.1	7.3 ± 6.1	.59 ± .08
Paper birch	3.6	6.9 ± 5.0	.53 ± .04
Sugar maple[2]	> .1	-	.51 ± .03
Pin Cherry	.9	17.9 ± 16.9	.30 ± .02
Choke cherry	> .1	12.2 ± 8.3	.31 ± .02
Hazel	1.6	5.6 ± 2.4	.57 ± .03
Yellow birch	8.1	10.8 ± 5.9	.35 ± .03
Other woody vegetation	6.6	-	-
Herbaceous vegetation	1.5	-	-
Unknown[1]	1.8	-	-

[1]Unknown = Bites that are recorded, but due to limited visibility, species identification was not possible.

[2]No observations for leaves/bite for sugar maple were recorded. For calculations we used leaves/bite for mountain maple.

From these data and the distribution of bites by species, we calculated that the daily consumption of deciduous leaves and forbs averaged 21.6 kg. Belovsky and Jordan (1978) reported a wet-weight intake of 33.63 kg. per day, but only 16.27 kg was terrestrial vegetation, the rest being aquatic.

Biomass intake by species, recorded as percentage of diet, is presented in Table 5.

Vegetation Analysis

Mountain maple made up 65% of the diet in the Yellow Birch forest while mountain ash made up 66% in the Coastal area (Table 6). In each case, the most common species in the forest was also the most common in the overall diet of moose in the area, as reflected by leaf removal. A greater proportion of mountain maple was removed than mountain ash in both forest types, suggesting maple was being selected more intensely. The primary difference in summer diets between these two forest types is that the dominant role of maple and ash are switched.

Removal of herbaceous material was estimated for the Yellow Birch forest from direct observations. Because feeding observations were not made in coastal-forest types, the degree to which herbaceous plants are used there is unknown.

While only a few moose were followed within the Yellow Birch site where vegetation was actually analyzed, nearly all observations were within yellow birch forests, of which the site is representative, thus permitting comparison between vegetation analysis and direct observations. Species composition in the diet of observed animals (Table 5) fits closely with the distribution of species removals measured on the transect plots (Table 6). In general, this indicates that our vegetation measurements were quite representative for moose removals.

Table 6. Availability and removal of browse species in the Yellow Birch and Coastal vegetation analysis sites.

	Yellow Birch (n = 66)[1]			Coastal (n = 89)[1]		
	Density g/m^2	% removed	% in diet	Density g/m^2	% removed	% in diet
Mountain ash	6.1 ± 1.9	20.2	15.8	17.1 ± 2.9	47.0	66.1
Mountain maple	10.4 ± 3.5	48.9	64.8	3.7 ± 1.5	64.0	19.3
Paper birch	.3 ± .4	96.5	3.4	4.4 ± 2.0	21.3	7.7
Pin cherry	> .1 ± .1	.1	> .1	.3 ± .4	42.0	1.0
Choke cherry	.3 ± .4	.4	> .1	0	0	0
Hazel	3.7 ± 2.6	2.5	1.2	0	0	0
Yellow birch	6.7 ± 2.7	13.9	11.9	-[3]	-[3]	> .1
Other woody veg.	2.2 ± 1.7	1.3	.3	6.3 ± 2.7	11.2	5.5
Herbaceous veg.	10.2 ± 6.4	1.5[2]	1.5	5.0 ± 4.0	?[4]	?[4]
Total	40.5 ± 12.5	19.4	100.0	36.4 ± 10.1	33.4	100.0

[1]= # plots sampled.

[2]From observation data.

[3]Yellow birch not encountered on sampling plots

[4]No reliable estimate of removal of herbaceous vegetation.

DISCUSSION

Using our estimates of available biomass by species and the area covered by moose while feeding, we estimate whether a moose can meet its quantitive needs if it selectes only one species. We observed moose cover an average area of 3,276 m^2 a day while feeding; in the Coastal area this would bring them in contact with an average of 56 kg/day of mountain ash if the animals were moving at random with no duplication of ground covered. Belovský and Jordan (1978) reported a summer adult-moose density of 3.3/km^2 for the Coastal area in 1972; since then various population measurements strongly indicate that density had declined by 1976-77. Thus, even if calves are included, the equivalent browsing pressure would not be as great as 3.3 adults: we did, however, calculate on the basis of 3.3/km^2 and found that over the 92-day season of leaf browsing, moose would in their daily feeding not quite cover the whole area once. Thus competition for ash as a declining food supply is theoretically not a factor because each day each animal encounters more than twice the ash it could consume. An ash-only intake would account for 21.6 kg/animal-day, yet animals were actually taking only 14 kg/day. Ash availability is greater than demand, at least in the Coastal area, yet this species comprised only 66% of the mooses' intake there. By eating only one-fourth the available ash (14 vs. 56 kg/day), these moose are demonstrating they probably could easily afford to raise their ash intake if such were their nutritional inclination.

It is interesting that in the Coastal area frequency in diet of mountain ash (66%), mountain maple (19%), and paper birch (7.7%), together totalling 92.7%, match closely the three proportions when these same three species comprised the whole menu in the *ab libitum* feeding trial (Table 2); however in the latter the ratios of maple and birch were reversed from the former. In the Coastal area, percent of available maple removed was higher than in either the Yellow Birch area or the trials suggesting that this species was the most preferred in the Coastal area, and its intake may have been limited by availability.

In both the Coastal area and the feeding trials, relatively high to unlimited availability of ash leads to high utilization of it, but in both cases two other species contributed importantly to the diet. As suggested earlier, there may be a threshold level above which ash will not be taken, no matter what its availability. It seems then that there is not a purely hierarchical order of preference in which the most preferred is taken to the exclusion of all others. Rather, some combination of species is being selected for. It also appears that the ordering of species in the mixed diet will not be consistent among individuals nor among environments.

In the Yellow Birch forest, mountain ash makes up only 16% (vegetation analysis) to 19% (observation data) of the total intake. Yet our calculations indicate the density of ash there would permit moose to take 20 kg/day or 93% of their diet. Such intense selection would, however, soon remove all ash foliage, and, incidentally, severely depress future production and survival of the species. Also, moose prefer to select food from particular vertical strata of the vegetation (McMillan 1953). Despite this, moose in the Yellow Birch forest could feed on greater quantities of ash than they did. In contrast, moose in the Coastal forest are in fact removing some 47% of available ash.

Nearly half (49%) of the available mountain maple was removed from the Yellow Birch study area, and it comprised 57% (observation data) to 65%

(vegetation analysis) of the diet for animals in this area. With the densities of maple on this site, 34 kg of foliage are available per day, enough to meet quantitative needs. Thus while mountain maple was not preferred in the feeding trials, moose on Isle Royale utilized large quantities of it and, in some cases, were selecting strongly for it. There seems to be a clear difference between the captive and free-living animals in their preference for maple. Yet, even though maple appears preferred at Isle Royale and is adequately available to provide all the summer browse eaten by moose in the Yellow Birch area, it is not taken to the exclusion of other forage species.

Moose on Isle Royale and in the feeding trials tend to select heavily for a single species, though choice of that species, at least for Isle Royale animals, seems partially dependent on availability. It is equally clear that additional species are sought. It seems that moose are selecting for a limited diversity in their diet, and that species actually used are in part dependent on availability as well as on palatability. While we have not yet run the tests to verify this, we present a working hypothesis on how moose determine their dietary regime under given environmental restrictions.

Our studies show that moose, given the opportunity, will concentrate on one species up to 60-70%. While selection for this species is obviously related to availability -- the species must be readily available in sufficient quantities, it may also be an efficient feeding strategy. Perhaps an increased efficiency in seeking food through use of a search image (Tinbergen 1960), or an increase in digestive efficiency (Mellenberger et al. 1971) may make specilization on a limited basis a favorable strategy to employ. Such specialization might occur only on a short-term basis since availability of certain types of foods varies seasonally and annually. However, microflora of the rumen are capable of making changes in population structure in response to diet so as to make efficient use of the available substrate (Schwartz and Gilchrist 1975).

Despite potential advantages of a specialized diet, it is unlikely that any one native plant will meet all the nutritional requirements of moose. Selective pressures would tend to diminish any plant from being a complete diet (Longhurst et al. 1968). Therefore, moose must incorporate more than one species into their diet to meet nutritional demands. Thus complete specialization is an impossibility, and diversity must be sought.

It seems that the plant species which is most highly preferred and most capable of meeting the quantitative needs of moose will become the key item in the diet on a seasonal basis. In the Yellow Birch forest of Isle Royale, this plant is apparently mountain maple, while in the Coastal area it appears to be mountain ash. Interestingly, Belovsky and Jordan (1978) reported that between 1972 and 1974, utilization of mountain ash dropped from 60 to 32% in yellow birch forests. Apparently availability of this important food item has decreased to the point where moose had to shift to mountain maple.

In summary, our results suggest that, at least in summer, moose can nutritionally afford neither to specialize by selecting a monotypic diet nor to generalize by selecting a randomly diverse diet. Rather, their strategy can be viewed as a compromise or balance between specialization and diversification.

LITERATURE CITED

Aldous, S. E. and L. W. Krefting. 1946. The present status of moose on Isle Royale. Trans. N. Amer. Wildl. Conf. 11: 296-306.

Arnold, D. A. and L. J. Verme. 1963. Ten years' observations of an enclosed deer herd in northern Michigan. Trans. N. Amer. Wildl. and Nat. Res. Conf. 28: 422-430.

Belovsky, G. E., P. A. Jordan and D. B. Botkin. 1973. Summer browsing by moose in relation to preference and animal density. N. Amer. Moose Conf. and Workshop Proc. 9: 101-122.

Belovsky, G. E. and P. A. Jordan. 1978. The time energy budget of a moose. Theoretical Pop. Biol. 14: 76-104.

Belovsky, G. E. 1978. Diet optimization in a generalist herbivore: the moose. Theoretical Pop. Biol. 14: 105-134.

Bissell, H. D., B. Harris, H. Strong and F. James. 1955. The digestibility of certain natural and artificial foods eaten by deer in California. Calif. Fish and Game. 41: 57-78.

Dodds, D. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. J. Wildl. Mgmt. 24: 52-60.

Duckworth, J. E. and D. W. Shirlaw. 1958. A study of factors affecting feed intake and the eating behavior of cattle. Animal Behav. 6: 147-154.

Geist, V. 1963. On the behaviour of the North American moose (Alces alces andersoni Peterson 1950) in British Columbia. Behaviour 20: 377-416.

Houston, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Tech. Bull. Grand Teton Nat. Hist. Assoc., No. 1. 110 pp.

Julander, O., W. L. Robinette and D. A. Jones. 1961. Relation of summer range condition to mule deer herd productivity. J. Wildl. Mgmt. 25: 54-60

LeResche, R. E. and J. L. Davis. 1973. Importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska. J. Wildl. Mgmt. 37: 279-287.

Longhurst, W. M. 1951. Range conditions as an influence in big game productivity. Proc. 31st Ann. Conf. West. Assoc. State Game Fish Comm. pp. 190-194.

Longhurst, W. H., H. K. Oh, M. B. Jones and R. E. Kepner. 1968. A basis for the palatibility of deer forage plants. Trans. N. Amer. Wildl. and Nat. Res. Conf. 33: 181-192.

_____. 1969. Deer forage palatability, digestibility, and management complications. Trans. 16th Ann. Meet. Calif-Nev. Sect. Wildl. Soc. p. 1-7.

McMillan, G. F. 1953. Some feeding habits of moose in Yellowstone National Park. Ecology 34(1): 102-110.

Mellenberger, R. W., L. D. Satter, M. A. Millet and A. J. Baker. 1971. Digestion of aspen, alkali treated aspen, and aspen bark by goats. J. Anim. Sci. 32(4): 756-763.

Milchunas, D. G., M. I. Dyer, O. C. Wallmo and D. E. Johnson. 1978. In vivo/in vitro relationships of Colorado mule deer forages. Colorado Division of Wildlife. Special Report No. 43. 44 pp.

Moen, A. N. 1978. Seasonal changes in heart rates, activity, metabolism, and forage intake of white-tailed deer. J. Wildl. Mgmt. 42: 715-738.

Oldemeyer, J. L., A. W. Franzmann, A. L. Brundage, P. D. Arneson and A. Flynn. 1977. Browse quality and the Kenai moose populations. J. Wildl. Mgmt. 41: 533-542.

Peek, J. M., D. L. Urich and R. J. Mackie. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildl. Monogr. 48. 65 pp.

Peterson, R. L. 1955. North American moose. University of Toronto Press. 280 pp.

Robinette, W. L., J. S. Gashweiler, D. A. Jones and H. S. Crane. 1955. Fertility of male deer in Utah. J. Wildl. Mgmt. 19: 115-135.

Schwartz, H. M., and F. M. C. Gilchrist. 1975. Microbial interaction with the diet and the host animal. pp. 165-179 in: I. W. McDonald, A.C.I. Warner eds. Int'l. Symp. on Ruminant Physiology, IV, Digestion and metabolism in the ruminant, Armidale, Austr: Univ. of New England Publishing Unit. 602 pp.

Swank, W. G. 1958. The mule deer in Arizona chaparral and an analysis of other important deer herds. Arizona Game and Fish Dept. Wildl. Bull. 3. 109 pp.

Tinbergen, L. 1960. The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by songbirds. Arch. Neer. Zool. 13: 265-343.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Natur. 108: 290-304.