SIXTEEN YEARS OF MOOSE BROWSE SURVEYS IN ONTARIO

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ABSTRACT

This paper summarizes 51 moose (Alces alces) browse surveys totalling 3,834 plots that were carried out by district staffs across the moose range of Ontario from 1955-1970. The purpose was to answer questions asked by moose managers concerning food availability and use. In 13 surveys, percentages of twigs browsed were estimated for all species; in the remainder, stems of 10 species were recorded as either browsed or not browsed. Twenty two of 33 recorded plant species were browsed by moose. Beaked hazel and mountain maple provided most food; mountain-ash, alternate-leaved dogwood and juneberry were preferred species but contributed less because of low availability. Balsam generally ranked low in availability and use, but contributed over 90% of the browse on an island. Browsing might have seriously affected the vegetation in 3 of 32 studies, two of them on islands. Since in most of these areas, moose populations were stable and hunting light, moose densities appeared to be regulated naturally below levels that would result in starvation or substantially reduced food supplies. The moose appeared to be generalists relative to major food species within the context of optimal foraging, but constraints imposed by chemical defenses greatly reduced or eliminated availability of some plant species.

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A review of moose (*Alces alces*) food habit studies by Peek (1974) reported only one browse survey for Ontario (Peterson, 1953). Since that time some additional browse studies in Ontario have been reported (Hamilton and Drysdale 1975; Kearney 1975; McNicol and Gilbert 1980; McNicol, Timmermann, and Gollat 1980; Todesco et al. 1985), but a relatively-large body of information concerning winter foods of moose



126

remains unpublished. In this paper I have collated and presented these data.

The field work began in 1955 and continued as an organized program until 1970. It was initiated because the Ontario moose herd was perceived to be of value, but too little information was available for rational management programs. Since early reports from Isle Royale (Aldous and Krefting 1946, Krefting 1951) and Newfoundland (Pimloti 1953) suggested that moose might overbrowse their range in ways similar to the widely feared overbrowsing by white-tailed deer (Odocoileus virginianus), the people responsible for managing moose in Ontario were very concerned about what moose might be eating and how great their impact might be on the browse species, both because of the implications for other forest users and for the future of the moose themselves. Little information on moose foods was available from elsewhere. Following the initial work on Isle Royale (Aldous and Krefting 1946), Hosley (1949) summarized a few studies in the United States and several provinces of Canada; Krening (1951) reported again on Isle Royale; and Peterson (1953) examined moose foods on St. Ignace Island, Lake Superior. The popularity of moose hunting was increasing in Ontario (Cumming 1972), and the moose herd appeared to be growing in size and expanding its range (Peterson, 1955). More information about food habits of moose became a priority for managers, especially information about winter foods which were considered most important because winter is widely acknowledged to be the critical time of year (e.g. Bryant and Kuropat 1980). After a few initial browse surveys to establish methods, the staff in forest districts were instructed to begin surveys to answer the most important questions. (1) How many plant species do moose eat during winter? (2) Which plants are most important in their diet? (3) Which species do moose prefer? (4) How great are variations in availability and preferences across northern Ontario? Most importantly, (5) are moose over-browsing their range or likely to do so in the near future?

STUDY AREA

Northern Ontario stretches about 1000 km east to west. Typical boreal forest grows over the Precambrian shield. Temperatures frequently range to -40⁰C and precipitation averages about 70 cm of water per year. Snow depths exceed 1 m only in exceptional winters. Spruce species (*Picea mariana* and *P. glauca*) dominate the overstory in many areas but in some places are replaced by, or mixed with, jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*). Disturbances include cutting, burning and infestations of spruce budworm (*Choristoneura fumiferana* Clem.) (Appendix Table 1). The only major variation in soil types resulted from glacial deposits of clay, sand and gravel in the eastern half of northern Ontario, that is, east of approximately 86⁰ longitude (Appendix Table 1).

METHODS

Surveys were carried out by district staffs of the Ontario Department of Lands and Forests under the direction and coordination of head office supervisors (H. G, Lumsden1955-59; H. G. Curming 1959-62, 66-70; J. B. Dawson 1962-66). Since one of the questions to be answered concerned the possibility of over-browsing, district staffs were instructed to choose places with the highest known moose densities. In all but 2 cases, where a deliberate effort was made to find why moose densities were low, these instructions were followed. Each survey was independently organized and carried out; therefore, the results cannot be considered a series of sample plots in a carefully controlled experiment. Personnel varied from highly competent district biologists to temporary employees hired as untrained casuals. Despite all efforts toward standardization of methods, instructions were not always followed exactly. Variations in site, forest type and forest disturbance (Appendix Table 1) would be expected to produce

128

differing results even on nearby areas, and the surveys extended over most of the 1000 km wide area (Fig. 1). Varying moose densities would also be expected to affect browsing rates in different areas. To clean the data as much as possible for calculations the following steps were taken: 2 surveys were omitted entirely because data were not collected in standard ways; 6 surveys that had been surveyed by the same method on the same area at another time were set aside (surveys with most plots or least disturbance to the moose population were included). Except for 3 areas that were surveyed in 2 different ways and thus analysed separately, all surveys in the analyses were on different areas.

A complete analysis of large herbivore food habits requires an estimate of forage availability as actually encountered by the animals (e.g. Wetzel et al. 1975), biomass used, and chemical composition of the browse, but these methods are time consuming and costly. They would have been inappropriate for the kind of extensive initial surveys required in Ontario. A method was needed that would provide a reasonable approximation of availability and use but that would be relatively fast and inexpensive. In Ontario a method had been developed by Passmore and Hepburn (1955) for surveying winter range of deer that seemed promising for moose also. They suggested that surveys to estimate winter browsing should be timed as soon as possible after snow-melt and before leaf-out. Plots should be arranged in parallel pairs of transects (to facilitate easy return to point of access) across the topography so as to sample systematically all important habitat types within the study area. Plots 1 chain (20 m) long and 2 feet (0.6 m) wide would be much easier to count than round or square ones and they should be located at 5 chain (100 m) intervals. Their rule-of-thumb minimum of 64 plots on any study area (or 64 times the square root of the area, in square miles, for areas greater than 1 square mile) was based on the variability in data collected during early deer browse studies (on advice

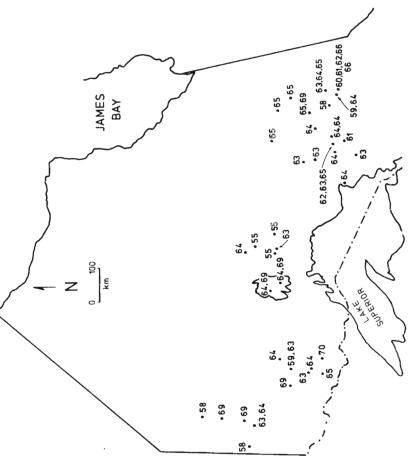
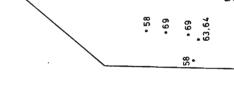


Fig. 1. Locations and dates of moose browse





of D. B. Delury, Director, Department of Mathematical Statistics, Ontario Research Foundation; Hepburn, pers. comm.). On each plot, they tallied by species the number of living stems arising from within the plot and providing twigs available to deer under average winter conditions (i.e. between 1.5 feet (0.45 m) and 6.5 feet (2 m) above ground level). The percentages of twigs that had some part of their length removed by deer were estimated (counted on every 10th plot) as mid-points of percentage ranges (e.g. 50 for 40-60%). The number of living stems on each plot would be multiplied by the degree of browsing to determine the number of "browse units", defined as "the quantity of food consumed when one percent of the twigs of one stem is removed by browsing". The average percentage of twigs browsed could then be calculated by dividing the number of browse units by the number of living stems for each species. The numbers of stems killed and mutilated by browsing were also recorded in each survey, along with descriptive data on the site, topography, and the forest overstory.

Method 1

Since browse species in northern Ontario were fewer (Soper and Heimburger 1982) and unlikely to be more abundant, the minimum figure of 64 plots on any study area was thought to be conservative and was adopted for the moose browse studies. The only modification that seemed necessary for surveying moose browse was raising the plot boundaries: (1) lower boundaries were raised to 2 feet (0.6m) because of the generally higher prolonged snow depths in northern Ontario and (2) upper boundaries to 10 ft (3 m) because of the greater heights of moose. This slightly revised method became the standard and continued to be used until 1962 (Appendix Table 1). However, there were problems. The heights to which moose browse are more variable than those reached by deer; in some cases moose break down stems well above 3 m. Thus the 3 m maximum height was at best a very rough approximation of the height to which twigs were

available. Additionally, the Passmore and Hepburn (1955) method was designed for use by expert deer biologists who would compare methods and ensure that the estimated percentages of twigs browsed correlated well among observers. This standardization became difficult to ensure for the many people carrying out moose surveys in different districts.

Method 2

In 1960 Stephenson (pers. comm.) suggested that stems be tallied simply as living or browsed. The percentage of browsed stems would then become the major statistic. This modification was found to have the advantages of simplicity, speed of operation, ease of understanding, reduced subjectivity and fewer training requirements. Dawson (pers. comm.) examined the results of surveys from 1958-62 and found that 93% of all browse units (Passmore and Hepburn 1955) consumed by moose occurred on 10 plant species. In 7 of the 10 surveys, these species contributed over 97% of the total browse. He suggested that only those species be tallied. With these modifications a further series of surveys was carried out (Appendix Table 1).

All surveys were carried out during the month of May. Peile? group counts were on plots with the same centres but with 6 foot (2 m) widths. A deposition rate of 13 (Joyal and Richard 1986) was used to calculate moose densities for comparisons between areas (but not necessarily establishing actual densities). Some aerial counts were also available for comparison (Appendix table 1).

Despite the fact that samples were systematically located, I followed common practice and treated them as if they had been located randomly. Prior to combining data for generalizations, analyses of variance of stems per hectare were carried out.

Calculations of preference and electivity followed Petrides (1975). T-tests, analyses of variance and regression analyses were carried out using Statview512 on a Macintosh

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132

computer.

RESULTS

Method 1

In 13 browse surveys using method 1, plants were tallied and browsed twigs estimated on 998 plots (Appendix table 2). Twenty-two of the 33 recorded plant species were browsed by moose (Table 1). Beaked hazel and mountain maple each contributed over 10% of the total browse units. Additional species contributing over 1% to the diet included balsam fir, willow, trembling aspen, white birch, mountain-ash, pin cherry, juneberry, and alternate-leafed dogwood. (These species became the ones surveyed in method 2.) Jack pine, black spruce, eastern white cedar, balsam popular, speckled alder, green alder, red maple, black ash, raspberry, rose, honey suckle and viburnum, though commonly present, each contributed <1% to the total diet.

Stem counts by species (transformed log (x+1)) did not vary more among surveys than within surveys (F=1.468, p=0.1329). Browse unit variability was greater and significant at =0.05 (F=1.929, p=0.0345); however, this amount of variability was not considered great enough to prevent pooling for presentation of over-all averages. Heaviest browsing was on alternate-leafed dogwood at 53% average percentage of twigs browsed, followed by beaked hazel at 24%, juneberry at 23% and willow at 20%. Among the species that were browsed, use appeared to follow availability, e.g. hazel constituted 23% of the available browse and contributed 43% of the total browse units (Table 2). An obvious exception was speckled alder which made up 13% of the available browse but only 1% of the browse units. Raspberry and black spruce comprised over 4% of the available stems each, but only 0.1% of the browse units. Preferences cannot be calculated from these data because the "number of living stems" used for calculating average percentage of stems browsed on a plot would cancel out with

Table 1. Plant species available and used for food by moose, recorded

Table 1. Plant species available a	ind used for lood by moose, recorded	
during 13 surveys of all species		
COMMON NAME	LATIN NAME	USE CATEGORY
Red pine	Pinus resinosa Ait.	
Eastern white pine	Pinus strobus L.	
Jack pine	Pinus banksiana Lamb.	#
Tamarack	Larix laricina (Du Roi) K. Koch	
White spruce	Picea glauca (Moench) Voss	
Black spruce	Picea mariana (Mill.) B. S. P.	#
Eastern white cedar	Thuja occidentalis L.	#
Balsam fir	Abies balsamea (L.) Mill.	# #
Ground hemlock	Taxus canadensis Marsh.	
Willow	Salix spp.	# #
Balsam poplar	Populus balsamifera L.	#
Trembling aspen	Populus tremuloides Michx.	# #
Yellow birch	Betual alleghaniensis Britton	
White birch	Betual papyrifera Marsh.	# #
Beaked hazel	Corylus cornuta Marsh.*	###
Speckled alder	Alnus incana rugosa*	#
Green alder	Alnus viridis crispa*	#
Mountain-ash	Sorbus spp. L.	# #
Choke cherry	Prunus virginiana L.	
Pin cherry	Prunus pensylvanica L.f.	# #
Sugar maple	Acer saccharum Marsh.	
Red maple	Acer rubrum L.	#
Mountain maple	Acer spicatum Lam.	###
Black ash	Fraxinus nigra Marsh.	#
Elderberry	Sambucus spp. L*	
Ribes	Ribes spp. L.*	
Juneberry	Amelanchier spp. Medik.*	# #
Raspberry	Rubus spp. L.*	#
Rose	Rosa spp. L.*	#
Alternate-leaved dogwood	Cornus stolonifera Michx.*	# #
Honeysuckle	Lonicera spp. L.*	#
Viburnum	Viburnum spp. L.*	#
Ground juniper	Juniperus communis L.	
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Sources

Hosie, R. C. 1973. Native trees of Canada. Canadian Forestry Service, Department of the Environment, Ottawa.
*Soper, J. H. and M. L. Heimburger. 1982. Shrubs of Ontario.
Royal Ontario Museum. Toronto.
<1% of total browse units

1-10% of total browse units
>10% of total browse units

134

Table 2. Total numbers of stems and browse units (number of stems times average percentage of twigs browsed) tailled for all species in 13 surveys using method 1.

	TOTAL LIVING	TOTAL	AVERAGE	PERCENT TOTAL	PERCENT
SPECIES	STEMS	ESTIMATED		STEMS AVAILABLE	
	TALLIED	BROWSE UNITS	BY SPECIES	BY SPECIES	BY SPECIES
White birch	1851	18553	10.0	7.2	5.6
Balsam fir	1503	13619	9.1	5.9	4.1
Mountain-ash	1150	19702	17.1	4.5	5.9
Willow	727	14858	20.4	2.8	4.5
Mountain maple	3676	60764	16.5	14.4	18.3
Alternate-leaved dogwood	386	20396	52.8	1.5	6.
Pincherry	1597	5942	3.7	6.3	1.8
Juneberry	529	12297	23.2	2.1	3.7
Trembling aspen	847	13619	16.1	3.3	4.1
Beaked hazel	5942	142979	24.1	23.3	43.0
Red maple	220	1862	8.5	0.9	0.6
Sugar maple	2	0	0.0	0.0	0.0
Balsam poplar	9	140	15.6	0.0	0.0
Ground hemlock	4	0	0.0	0.0	0.0
White spruce	47	0	0.0	0.2	0.0
Tamarack	23	0	0.0	0.1	0.0
Jackpine	697	73	0.1	2.7	0.0
White cedar	228	70	0.3	0.9	0.
Speckled alder	3277	4796	1.5	12.8	1.4
Mountain alder	114	560	4.9	0.4	0.:
Ribes	9	0	0.0	0.0	0.0
Raspberry	1022	335	0.3	4.0	0.
Rosa	238	1071	4.5	0.9	0.3
Horieysuckle	49	159	3.2	0.2	0.
Black spruce	1160	2	0.0	4.5	0.0
Viburnum	96	428	4.5	0.4	0.
Black ash	10	190	19.0	0.0	
White pine	10	0	0.0	0.0	
Yellow birch	1	0	0.0	0.0	
Choke cherry	90	201	2.2	0.4	
Red pine	1	0	0.0	0.0	
Elder	13	0	0.0	6.1	0.
	11	0		0.0	
Ground juniper	[]	U	0.0	0.0	0.



Table 1) and for percentage of total browsed stems supplied by each species compared

with percentage of browse units supplied by each species (R2=0.99, Vozeh 1961;

the "number of living stems" used when calculating preference. However, inspection of a comparative graph (Fig. 2) suggests that beaked hazel and mountain maple are used more than mere presence would warrant, while jack pine, speckled alder and black spruce were browsed less. These surveys including all browse species are of particular interest for establishing the species that were not browsed. Twenty three species constituting 28.5% of the total stems were not browsed at all or browsed on less than 1% of the stems

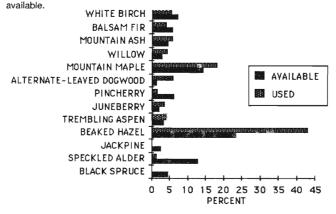
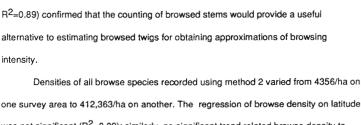


Fig. 2. Stems available and twigs used (in browse units) for 13 surveys tallying all species. (Only those contributing >1% are shown.)

Method 2.

In 32 surveys using method 2, stems were counted on 2836 plots (Appendix Table 3). On two early surveys, results were tallied by both method 1 (estimating percentages of twigs browsed in browse units) and method 2 (counting percentages of stems browsed); these results made comparison of the methods possible. The correlation coefficients for percentage of stems browsed by species compared with average browse units per species (R²=0.999 for Vozeh 1961; R²=0.976 for Vozeh 1962, Appendix



one survey area to 412,363/ha on another. The regression of browse density on latitude was not significant (R2=0.09); similarly, no significant trend related browse density to longitude (R2=0.03). A 1-way ANOVA of living stems/ha by species in all studies showed evidence of some variability (F=1.663, p=0.0178). However, removing from the data the surveys on two islands in Lake Nipigon reduced the variation to insignificance (F=1.259, p=0.1757). Browsed stems showed more variability (F=2.525,p=0.0001). Most variation was in the eastern half of northern Ontario (F=2.437, p=0.0021) where 5 surveys had to be eliminated (on the basis of high numbers of differences shown by paired LSD tests) to reduce variability to non-significance (F=1.795, 0.0565). In the western half, overall variation was significant (F=2.291, p=0.0094) but elimination of the two islands eliminated all significance (F=1.344, p=0.2103); in fact, eliminating only one mainland study was enough to render variation insignificant (F=1.695, p=0.0764). In all these cases the F-values were low, and, apart from the islands, there seemed to be no reason to eliminate surveys that were slightly different; therefore surveys have been combined to allow presentations of average conditions in this fairly homogeneous boreal forest region.

The value of preference data has been questioned by several recent authors, usually with reference to optimal foraging theory. Nudds (1980), for example, pointed out that if use is correlated with availability, as predicted by optimal foraging theory for



general foragers, then "preference ratios" may not really indicate preference. The percentage of food contributed by different plant species was indeed positively correlated (R²=0.807, Fig. 3). Several observations fell outside the 99% confidence bands. Although there remains a small probability that they do belong, these outliers raise questions about the completeness of generalized foraging by moose. Some species recorded in method 1 were also clearly not eaten in the porportions encountered (especially, speckled alder).

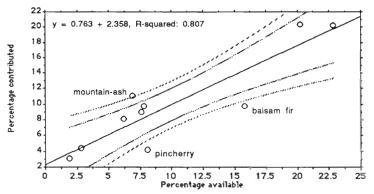


Fig. 3. Regression of percentage contributed on percentage available for 10 browse species (method 2). Bands represent 95% and 99% confidence limits on y.

Since the status of moose as specialist or generalist has not been firmly established, I have presented calculations of preference for method 2 in the traditional form (i.e. as described by Petrides 1975) to facilitate comparison with other studies.

The importance of mountain maple and beaked hazel as staple foods (Leopold 1933) was apparent from their contributions of over 20% each to the moose diet (Table 3).

Mountain-ash, alternate-leaved dogwood and juneberry, on the other hand, although rating high in the preference index, and so possibly worthy of the designation



138

Table 3. Preference ratings and electivity Indices from 38 moose browse surveys where total stems

	Amo	ounts	Per	centages	S	Indi	ces
Browse species	Stems	Sterns	Stems		Browsing		
	available	removed	available	Diet	on stems	Preference	Electivity
White birch	3054	1041	7.6	9.0	34.1	1.18	0.1
Balsam fir	6383	1133	15.8	9.8	17.8	0.62	-0.2
Mountain ash	2774	1286	6.9	11.1	46.4	1.61	0.2
Willow	3133	1134	7.8	9.8	36.2	1.26	0.1
Mountain mape	8153	2360	20.2	20.3	28.9	1.01	0.0
Alternate-leaved dogwood	1144	515	2.8	4.4	45.0	1,56	0.2
Pincherry	3250	483	8.1	4.2	14.9	0.52	-0.3
Juneberry	757	362	1.9	3.1	47.8	1.66	0.2
Trembling aspen	2505	938	6.2	8.1	37.4	1.30	0.1
Beaked hazel	9197	2349	22.8	20.2	25.5	0.89	-0.1

used less than their availability would suggest. White birch, willow and aspen were intermediate in preference rating and in availability.

Perhaps a better approach is to look at the distribution of percentages browsed for each species. Mountain ash was generally most heavily browsed (Fig.4) and balsam fir was among the least. Dogwood and juneberry, rated highly by mean percentage browsed, were among the less browsed species in the box plots, indicating that the high mean percentage browse was due to heavy browsing in 2-3 locations where these species were also abundant (indicated by the higher individual values in Fig. 4).

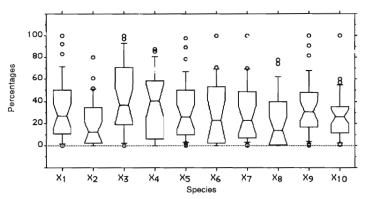


Fig. 4. Percentage browsing recorded by species in 32 surveys of 10 browse species (method 2). The 10th, 25th, 50th, 75th, and 90th percentiles are shown.

None of the species was browsed on average above 50% of the stems (Table 3). Looking at individual species over the whole range of studies, the 90th percentile exceeded 75% browsing only for mountain ash and willow (Fig. 4). Individual species showed browsing on 100% of the available stems only in



140

reported overall browse levels above 80%; one reported just under 80%; and 4 reported 40-50%. All others reported fewer than 40% of the stems showing any browsing. Thus, only in 3 of the 32 studies could browsing be seriously affecting the vegetation.

Combining all results from method 2 allows a generalized picture of the staple moose foods of northern Ontario (Fig. 5).

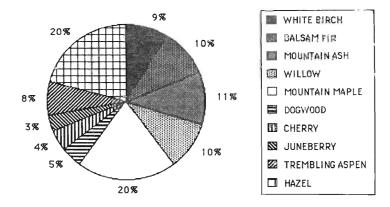


Fig. 5. Staple foods of moose in northern Ontario as determined by 32 surveys of 10 browse species (method 2).

Comparisons of stem counts on either side of 86° longitude showed no significant difference for total living stems/ha (transformed log (x+1), t=-0.185, d.f.=30, p=0.855) and only 1 species with a significant difference between numbers of stems/ha, mountain ash (t=3.860, d.f.=30, p=0.0006), with about twice as many stems per hectare in the east. However, significantly more browsed stems per hectare were recorded in the western portion (t=-4.754, d.f.=30, p=0.0001), and 2 individual species differed significantly in numbers of brwosed stems/ha, mountain-ash higher in the east (t=2.361, d.f.=30, p=0.025), and juneberry, higher in the west (t=-3.669, d.f.=30, p=0.001). The difference between total numbers of stems per hectare browsed

may have related to the generally higher densities of moose in the west (t=-2.089, d.f.=29, p=0.0456).

Two repeated surveys by Gibson (Appendix Table 1) showed similar browsing differences related to moose densities. Shakespeare Island in Lake Nipigon during 1964 had an estimated population of 1.27moose/km² counted from the air (3.85/km² estimated from pellet groups) and nearby Kelvin Island supported 0.48/km² seen from the air (3.24/km² from pellet groups). Prior to 1965 no hunting had been allowed on these islands for many years, but after the first surveys the season was opened. During the next 5 years, 300 moose were shot from the islands and nearby mainland, reducing populations on Shakespeare to 0.05/km² (0.14/km²) and Kelvin to 0.09/km² (1.91/km²). The total living stems increased on Shakespeare between 1964 and the second survey in 1969 (4992 to 6432 stems/ha) and decreased only slightly on Kelvin (8266 to 7259 stems/ha) but the number of stems browsed was reduced on both islands by about half (Shakespeare 4073 to 2802 stems/ha; Kelvin 6521 to 3286 stems/ha). Shakespeare Island also showed unusual species composition with 93% of the counted stems balsam fir (30% on Kelvin). Balsam fir constituted 92% of the diet on Shakespeare Island in 1964, decreasing to 89% in 1969; on Kelvin Island balsam fir made up only 19% of the diet in 1964, perhaps because of higher availability of alternate browse species, but it increased to 69% by 1969. The decreased moose densities changed some other aspects of browse data as well. Browsing on birch, mountain-ash and mountain maple also decreased. On Kelvin the living stems per hectare of balsam fir, birch, and mountain maple dropped. Thus some relationships exist between moose densities and percentages browsed. Efforts to find similar correlations across northern Ontario were not successful.



142

DISCUSSION.

The most important information derived from these surveys was that moose at current population densities in Ontario were not overbrowsing the range to an extent that would interfere with other forest users or seriously reduce the productivity of the forest for moose. Furthermore, the population would have to increase substantially before any real danger to the food supply would be forthcoming. This information began to change the emphasis in Ontario moose range management from concern over food to concern for cover and interspersion of food and cover (Euler 1981).

This finding was also of theoretical interest because these surveys were conducted at a time when moose populations in Ontario were relatively stable and little altered by hunting except in the most accessible areas (Cumming 1974). Thus moose in most places were naturally regulated below the limit that would be imposed by food shortage and starvation. Food supplies cannot be written off as of no importance, for moose populations have been commonly observed to increase following disturbance of a virgin forest (e.g. Cumming 1980); presumably the major change after disturbance is an increase in food abundance. Possibly food shortages limit moose populations at the low levels of availability in mature forests but outstrip increasing moose populations following disturbance. Most of the studies reported here were in disturbed areas and could therefore be seen as examples of food supplies increasing faster than moose populations. However, in Ontario we have never seen evidence of moose populations catching up, to the extent that shortage of food could be limiting, even in parks where no hunting is permitted (e.g. McNicol et. al. 1980, though the reduced availability of browse in this case might mean that the moose numbers would become limited by food eventually). Moose managers in Ontario speculated about other possible limiting factors - predation, social behaviour,, or perhaps some combination of factors, but no evidence was available at the time these

surveys were completed. Bergerud (1981) and Bergerud et al. (1983) have supported the idea that predation alone could be controlling moose numbers. Further work will be required to find if that is true generally throughout unhunted portions of Ontario.

As predicted by optimal foraging theory (e.g. Pyke et al. 1977, Nudds 1980), moose followed the foraging pattern of a generalist eating a wide variety of the plant species available (66.7%), many at rates that varied with availability. But the model does not fit completely. Looking at the reverse side of these results, one third of the plant species were not eaten at all and among those that were eaten the linear relationship between use and availability only held for some. Apparently moose are generalists only among plant species that constitute major foods. The most likely explanation would seem to be plant defenses (Bryant and Kuropat 1980). Belovsky (1978) suggested that resins of species like birch and alder may be toxic to rumen microbes. He concluded that subarctic browsing animals do not select their diet on the basis of proximal nutrient content, but avoid feeding on plants that contain high concentrations of secondary chemical constituents. This idea of generalization within constraints imposed by plant defenses seems to fit the results of the surveys reported here for moose of the boreal forest better than the idea of a more complete generalization proposed by Nudds (1980) for white-tailed deer in southerly forest types. If such constraints actually exist, they must substantially reduce the carrying capacity of an area (in these studies by 1/3). Additional application of optimal foraging theory to the examination of these data could be undertaken but are beyond the scope of this paper.

Nudds (1980) cautioned about calculation of food preferences and some of his reservations certainly apply to the methods used in these studies. A systematic survey may not reveal availability of browse to a moose wandering from one patch to another; also food use to some extent varied with availability as discussed above. However, at least

the most extreme results obtained from the preference indices agree with field observations and with reports from elsewhere (e.g. Peek 1974). As pointed out by Trottier (1981) for western moose ranges, hazel was a key species, with mountain maple nearly of equal importance. Not so well known is the high preference for mountain-ash. One of the greatest surprises was the relative low importance of balsam fir. The only information available at the time these surveys were commenced (Aldous and Krefting 1946, Dyer 1948, Hosley 1949, Krefting 1951, Peterson 1953, Pimlott 1953) suggested that balsam fir was a major food item. In fact, conventional opinion held that moose differed from white-tailed deer in preferring balsam fir, rather than eastern white cedar. Therefore, the finding that balsam fir rated very low in preference and amount used was quite unexpected. The only really high values for occurrence and use of balsam fir came from Shakespeare Island in Lake Nipigon. This observation recalled two early studies showing high use of balsam that were also conducted on islands (Isle Royale, Krefting 1951 and St. Ignace Island, Peterson 1955). What circumstances cause moose on islands to eat more balsam than those on the mainland? In each island study the density of moose was high and balsam constituted a high proportion of the browse species available. Perhaps, moose use balsam as a staple food, rather than preferred, and turn to it for a major portion of the diet only when more preferred foods are scarce.

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146

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AUTHORS OF SURVEY REPORTS	LOCATION	LAIIIUDE	LUNGILUD	LATITUDE LONGITUDE FOREST DISTRICT	SIZE OF AREA (KMAZ) MOOSE/KMAZ) MOOSE/KM^2
METHOD 1. COUNTS OF STEMS AND ESTIMATES OF BROWSE UNITS FOR ALL SPECIES	OF BROWSE UNITS FOR ALL SPECIES		23	ACTO 14 DEC	•	
COMMING, T. G. 1955s	TAGE CHARE		2 2	GERALDION	9.7	6.1
COMMING, H. G. 19550	EASI SHORE LONG LANE		8 8	GENALDION	7.0	
CUMMING, H. G. 1955c	FLEMING LAKE, EXION IMP.		8	GERALDION	2.6	
JOHNSTON, F. 1962	MARSHALL TWP.		83 28	CHAPLEAU	4.5	NA.
MACFIE, J. A. 1958	CARTER AND STETHAM TWPS.		93	GOGAMA	2.6	1.5;0.8A
D'SHAUGHNESSY, T. 1961	12E TWP.		83 18	CHAPLEAU	1.0	N.A.
SIMKIN, D. W. 1958a	OAK LAKE		2	SIOUX LOOKOUT	20.7	6.1;1.6A; DEER4.9
SIMKIN, D. W. 1958b	UPPER GOOSE LAKE		83 40	STOUX LOOKOUT	11.7	2.0;1.7A
SIMKIN, D. W. 1959	24 KM W. OF IGNACE		91 40	SIOUX LOOKOUT	7.8	2.6;1.4A; DEER 0.4
FOZEH, G. E. A. ZIMMERMAN 1959	TOGO TWP.		81 31	GOGAMA	2.6	0.5A
VOZEH, G. E. 1960	NABAKWASI 3		12 18	GOGAMA	. 6	1.8:1.64
VOZEM. G. E. 1961	NABAKWASI SW	47 33	81 27	GOGAMA	2.8	2.3 (1.8-2.7):1.7A
VOZEH, G. E. 1962	NABAKWASI 11	47 33	12 18	GOGAMA	a.	0.5 (0.3-0.8)
WETHOD 2. COUNTS OF STEMS ONLY FOR 10 SPECIES	CIES		2	1000	,	
AMMENIACING, A. E.1804	COLOR OF THE CONTROL OF THE COLOR OF THE COL		8 8	SACUA LOOKOOI	n. (1.5(1.1-1.9);0.ZA
BHOWN, P. R. 1965	CIRRUS LAKE, 23 KM S. W. ATHROKAN		2 5	FORI PRANCES	2.8	1.5(0.7-2.2)
BUSCH, D. & GAGNE, D. 1969	26 MI, N.E. RED LAKE	2 5	2 2	SOUX LOOKOUT	38.8	6.1(3.7-7.9);3.4A
CLOSE, R.W. 1966a ("= VOZEH 1960)	NABAKWASI LAKE 3		/2 15	GOGAMA	9.0	2.1
CLUSE, M. W. 1968B ("= VOZEM 1962)	NABAKWASI LAKE 11		2 5	GOLDANA	3	8.0
CORNELL, F. 1964	RUPERT TWP.	2 1	20 / 02	GEHALDION	2.6	2.5
CREIGHTON, W. A. 1965a	SYDERE TWP.		45	COCHHANE	2.6	0.8(0.1-1.4)
CREIGHTON, W. A. 1985b	CARNEGIE TWP	48 45	81 24	COCHRANE	2.6	2.9(1.9.3.8)
CRICHTON, V. 1963a	STOVER		83 67	CHAPLEAU	6.5	1.2
CRICHTON, V. 1963b	MARSHALL		83 28	CHAPLEAU	33	2.0
CRICHTON, V. 1963c	MILDRED		83 55	CHAPLEAU	13	4.1
GIBSON, B. H. 1963	SALSBERG TWP.		67 01	GERALDTON	2.6	6.9
GIBSON, B. H. 1964a	SHAKESPEARE IS. (56 KM-2, 6 KM TO MAINLAND)	49 38	88 25	GERALDTON	2.6	3.8(2.5-5.2), 1.3A
21BSON, B. H. 1964b	KELVIN IS. (68 KM-2, 10 KM TO MAINLAND)		28 24 24 25	GERALDTON	2.6	3.2(2.0-4.5), 0.5A
#ALL,R. B. 1963	MAYNARD LAKE		93 24	KENORA	4.7	E.3
HENDRY, G. M. 1965	PARNELL AND ECCLESTONE TWPS.	49 23	8	KAPUSKASING	11.4	4.5(3.6-5.5);3.3-4.8A
LUCKING, E. M. 1963a	MOFFAT TWP		83 54	GOGAMA	1.3	
LUCKING, E. H. 1964a	TOGO TWP		91 31	GOGAMA	2.6	0.8(0.1-1.4)
LUCKING, E. H. 1964b	CARTY TWP		2 2 3	GOGAMA	2.6	1.5(0.8-2.5)
LUCKING, E. H. 1965a	REEVES TWP.	48 16	82 08 23	GOGAMA	-	1.2(0.7-1.7)
LUCKING, E. H. 1965b	KEMP TWPGRASSY LAKE		81 19	GOGAMA	1.1	0.3
MACFADYEN, A. L. 1964	OLD WOMAN RIVER (L. SUPERIOR PROV. PARK.)		20	SAULT STE. MARIE	3.7	2.0
MILLER, J. 1963	CROW ROCK LAKE		5 5	FORT FRANCES	K.A.	KA.
MONK, C. E. 1963 ("=SIMKIN 1959)	24 KM W. KGNACE	48 25	91 40	SIOUX LOOKOUT	7.1	9.1
D'SHAUGNESSY, T. AND W. KEAN 1965	N. E. CORNER MARSHALL TWP.		83 38	CHAPLEAU	2.6	8.0
D'SHAUGNESSY, T. J. 1964a	BORDEN TWP. I	47 54	23	CHAPLEAU	2.6	7.0
D'SHAUGNESSY, T. J. 1964b	BORDEN TWP, 2		-	CHAPLEAU	2.6	9.0
D'SHAUGNESSY, T. J. 1964c	STRATHEARN TWP.		E .	CHAPLEAU	2.6	1.7
STASUS, A. 1970	PICKEREL LAKE, QUETICO PARK	3 5	8 6	FORT FRANCES	5.5	1.5(1.2-1.8);0.5A
SWIFI, E. J. 1964	TURILE LAKE	6 5	2 2	KENOBA	8. °	0.8(0.4-1.8)
TUDINGON, N. C. 1909	PICON LANE	8 8	2 2	KENOBA	9.4	
REPEATED SURVEYS			1		•	
GIBSON, B. H. 1969a(*; GIBSON 1964a)	SHAKESPEARE IS. (56 KM-2, 6 KM TO MAINLAND)	40 30	98 28	GERALDTON	2.6	6.1. 0.05A
GIBSON, B. H. 1969b(*= GIBSON 1964b)	KELVIN IS. (168 KM^2, 10 KM TO MAINLAND)	49 61	88 40	GERALDTON	2.8	1.9. 0.09A
HALL, R. B. 1964(*= HALL 1963)	MAYNARD LAKE	22 23	93 EF	KENOBA	4.7	4.8(3.2-6.8); DEER 15.0
HERRON, G., & P. CARTER 1969 ("= LUCKING 1965& REEVES TWP.	965a REEVES TWP.	49 16	82 06	CHAPLEAU	2.6	¥.
.UCKING, E. H. 1963b (*= LUCKING 1965b)	KEMP TWP -GRASSY LAKE	47 48	81 19	GOGAMA		1.2
.UCKING, E. H. 1964c("= LUCKING 1963b)	KEMP TWP -GRASSY LAKE	47 49	81 19	GOGAMA	1.1	6.8 (0.4-0.8)
= INDICATES ANOTHER SURVEY ON THE SAME SI	INDICATES ANOTHER SURVEY ON THE SAME SITE, SURVEYS WITH MOST PLOTS OR LEAST DISTURBANCE TO THE MOOSE HERD WERE CHOSEN TO BE INCLUDED.	E TO THE M	NOOSE HER	WERE CHOSEN TO B	E INCLUDED.	

SOIL AND TOPOGRAPHY	FOREST TYPE	DISTURBANCE
LOAM.PEAT 17CM-0.7M	BLACK SPRUCE, WHITE BIRCH, BALSAM	BUDWORM 1940
LOAM, PEAT 17CM-0.7M, LOW AND ROLLING	ASPEN, WHITE BIRCH, BALSAM	SPRUCE CUT 1940
SANDY HILLS WITH LOAMY SECTIONS AND SWAMPS	ASPEN, WHITE BIRCH, WILLOW, PIN CHERRY	BURNED 1936, 1945
SANDY WITH ROCK OUTCROPS	WHITE BIRCH, JACK PINE, BLACK SPRUCE, TREMBLING ASPEN	CUT 1956-57
GENTLY ROLLING, SANDY LOAM	MATURE BW, SB, SW	EARLY SELECTIVE LOGGING, BUDWO
FLAT SANDS, BEDROCK, SWAMPS	TREMBLING ASPEN, WHITE BIRCH, JACKPINE, BLACK SPRUCE	BURNED 1930'S, CUT 1950'S, BLOW
PRECAMBRIAN ROCK WITH PEAT 17cm-7m.	TREMBLING ASPEN, WHITE BIRCH, BLACK SPRUCE, BALSAM FIRBURNED 1933	R BURNED 1933
ROCK, 50% SAND WITH PEAT	JACKPINE, TREMBLING ASPEN, WHITE BIRCH, BLACK SPRUCE	BURNED ABOUT 1930
PRECAMBRIAN OUTCROPS OVERLAIN WITH 1-6" PEAT	JACKPINE, WHITE BIRCH, TREMBLING ASPEN, BLACK SPHUCE	BUHNED 1922
HIGH RIDGE SLOPING TO SWAMP	MIXED YOUNG GROWTH, SPRUCE SWAMPS	BURNED 1941
ROLLING SANDY LOAM >0.7m	YOUNG MIXED WOOD WITH CONIFER PAICHES	BURNED 1941
ROLLING SANDY LOAM >0.7m	MIXED WOOD WITH CONIFER SWAMPS	BURNED 1941
ROLLING SAND PLAIN-6.7M DRY	HARDWOODS WITH JACKPINE	BURNED 1941
N. A.	BALSAM, JACKPINE, WHITE BIRCH, WILLOW, MOUNTAIN ASH	LOGGED 1952
ROCK RIDGES, SWAMPS	BLACK SPRUCE, WHITE BIRCH, TREMBLING ASPEN, JACKPINE	NONE
BOULDER MORAINE	TREMBLING ASPEN, WHITE BIRCH, JACKPINE REGENERATION	BURNED 1961
SANDY LOAM 6-8' DEPTH	MIXED CONIFER, HARDWOODS 30-40	CUT, THEN BURNED IN 1941
SAND, SANDY LOAM, 2	JACKPINE, TREMBLING ASPEN	BURNED 1941
LIGHT SAND TO CLAY	TREMBLING ASPEN, WHITE SPROCE, JACKPINE	
WELL DRAINED CLAY	MIXED CONIFER, HARDWOODS, BLACK SPRUCE	CUT 1948-49
WELL DRAINED CLAY	WHITE BIRCH, BALSAM, BLACK SPRUCE, BALSAM POPLAR	EARLY SELECTION CUT
N. A.		BURNED 1955
ROLLING TERRAIN WITH SANDY, GRAVELLY SOILS AND BEDROCK	WHITE BIRCH, JACK PINE, SPRUCE, TREMBLING ASPEN,	HALF CUT
χ. Α.	N. A.	CURRENTLY BEING LOGGED
DUMP TILL, FINE TO COARSE GRAVEL, DAMP	BALSAM, JACKPINE, WHITE BIRCH	CUT 1943, 1951, 1952
ARCHEAN, 300 FT BLUFFS, SILTY SAND AND FROM OUTWASH PLAIPOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	INOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	BUDWORK 1843, BLOWDOWN
ARCHEAN, 300 FT BLUFFS, SILTY SAND AND FROM OUTWASH PLAILOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	INOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	BUDWORM 1943, BLOWDOWN
CLAY LOAM, GRANITE OUTCROPS, ROLLING, WELL DRAINED	WHITE BIRCH, TREMBLING ASPEN, JACKPINE, BLACK SPRUCE	BUDWORM, BLOWDOWN
HIGH LIME SILTY CLA Y WITH SOME PEAT	ALDER, BIRCH, MOUNTAIN MAPLE	CUT 1946-55
PEAT OVER SAND WITH MUSKEG AREAS	TREMBLING ASPEN, WHITE BIRCH, TAMARACK	BURNED 1934
ROLLING TOPOGRAPH, STEEP CLIFFS	JACKPINE, TREMBLING ASPEN	BURNED 1941,1951
MAINLY PEAT WITH SOME SHALLOW SAND, ROCK	JACKPINE, TREMBLING ASPEN, BALSAM FIR, BLACK SPRUCE	NONE
THIN SOIL OVER BED ROCK, CEDAR SWAMPS	MIXED CONIFER, HARDWOODS, MATURE	NONE
BARE ROCK, SHARP CONTOURS	TREMBLING ASPEN, WHITE BIRCH	BURNED 1951
VERY RUGGED AND HILLY	OVERMATURE YELLOW BIRCH, HARD MAPLE, BALSAM, SPRUCE	NONE
ROLLING WITH ROCKY OUTCROPS	BLACK SPRUCE, MIXED	CUT DURING 1940'S
18" SOIL OVER PRECAMRIAN, MODERATE HILLS, ALDER SWALES		BURNED 1922
ROLLING TERRAIN WITH SANDY, GRAVELLY SOILS AND BEDROCK	_	LIMITED CUTTING SINCE 1962
N. A.	HEAVY BALSAM REGENERATION	LOGGED 1950'S, BLOWDOWN
ж. А.	TREMBLING ASPEN, BALSAM REGENERATION	BURNED EARLY 1940'S
х. А.	TREMBLING ASPEN, WHITE BIRCH REGENERATION	EARLY LOGGING, BLOWDOWN
SAND, GRAVEL, PEAK POCKETS. RELIEF 33M	WHITE BIRCH, TREMBLING ASPEN	BLACK SPRUCE, JACKPINE CUT 10
ROLLING, JACKPINE SAND FLATS, BLACK SPRUCE SWAMPS	JACKPINE, BLACK SPRUCE, BALSAM	COT 1946-47
SHALLOW SANDY TILL OVER BED ROCK	JACKPINE, BLACK SPRUCE, TREMBLING ASPEN, BALSAM	NONE
SHALLOW SANDY TILL OVER BED ROCK	JACKPINE, BLACK SPRUCE, INEMBLING ASPER, BALSAM	MOME
ARCHEAN, 300 FT BLUFFS, SHITY SAND AND FROM OUTWASH PLABOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	BOVERNATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	BUDWORM 1943, BLOWDOWN
ARCHEAN, 300 FT BLUFFS, SILTY SAND AND FROM OUTWASH PLANOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	HOVERMATURE BLACK SPRUCE, WHITE SPRUCE, WHITE BIRCH	BUDWORM 1943, BLOWDOWN
CLAY LOAM, GRANITE OUTCROPS, ROLLING, WELL DRAINED	WHITE BIRCH, TREMBLING ASPEN, JACKPINE, BLACK SPRUCE	BUDWORM, BLOWDOWN
YULU GOLI OVER DED BOOK OFFIAR SWIAMOS	SCHOOL MACING THIS VOICE WHOCK CAN INSTRUCT	DISCUSSION TO SE ATT. CITTING SPESS.



							ALIEKNAIE				
STEMS COUNTED BY SPECIES	NUMBER WHITE	WHITE	BALSAM MOUNTAIN	UNTAIN-		MOUNTAIN LEAVED	LEAVED		T	TREMBLING BEAKED	BEAKED
АОТНОВ	OF PLOTS BIRCH	ВІВСН	FIR ASH	Ŧ	WILLOW	MAPLE	DOGWOOD	PINCHERRY J	PINCHERRY JUNEBERRY ASPEN	SPEN	HAZEL
CUMMING, H. G. 1955a	6 4	114	108	3.7	0	377	6	0	0	0	0
CUMMING, H. G. 1955b	6 4	2 8		-	12	104	7.2	-	7	4 6	•
CUMMING, H. G. 1955c	6 4	190		0	-		•	182	6	9	10
JOHNSTON, F. 1962	6 4	5 5	179	7 9		432	13	11	4	36	116
MACFIE, J. A. 1958	6.4	89		186			•	80	4 3	0	171
O'SHAUGHNESSY, T. 1961	6.4	3.4		-	32		•	10	4	8	260
SIMKIN, D. W. 1958a	110	201	310	0	0	1073	212	3.4	179	176	2544
SIMKIN, D. W. 1958b	110	638		0	324	•	•	0	0	229	0
SIMKIN, D. W. 1959	110	5 1	132	18			•	7	2	e	110
VOZEH, G. E & A. ZIMMERMAN 15		8 7		219	4 2		•	337	5 6	4 9	323
VOZEH, G. E. 1960		126		419	4 6	214	4	396	80	8	615
VOZEH, G. E. 1961	6 4	128	37	6 2	5.5	169	5.4	182	9 9	116	570
VOZEH, G. E. 1962	06	110	43	108	96	150	28	434	8 1	3	1223
BROWSE UNITS RECORDED BY SPECIES	CIES										
CUMMING, H. G. 1955a		3340	734	1304		5800	_				
CUMMING, H. G. 1955b		5 1				210	1925				
CUMMING, H. G. 1955c		1027			721			2730		163	
JOHNSTON, F. 1962		235	2.1	1439		587				110	538
MACFIE, J. 1958		176		4535		2642		30	417		863
O'SHAUGHNESSY, T. 1961		1495		300	180	7634					954
SIMKIN, D. W. 1958a		7161	80			39896	16301	1595	9870	8992	135351
SIMKIN, D. W. 1958b		2883	440		6149					3370	
SIMKIN, D. W. 1958c		586		250		2921					825
VOZEH, G. 1959		332		4219	2710		_	454	240	395	402
VOZEH, G. 1960		211	215	4345		584		367		8	890
VOZEH, G. 1961		936	-	1530	2570		7	730	1220	415	1901
2001		4 2 2	9 7 7	. 100	•			96	0 4 5	•	

APPENDIX TABLE 2 CONTINUED

	30	40	SUGAR BALSAM GROUND	OND.	WII E			MILE	WHILE SPECKLED MOUNIAIN	CONTAIN		
	MAPLE MA	PLE PO	PULAR HEA	MLOCK SF	RUCE TAI	MAPLE MAPLE POPULAR HEMLOCK SPRUCE TAMARACK JACKPINE	- 1	CEDAR ALDER		ALDER. F	RIBES RASPBERRY	PBERRY
CUMMING, H. G. 1955a	0	0	-	٥	0	0	0	7.7	2 6		٥	4
CUMMING, H. G. 1955b	0	0	4	0	0	-	-	10	267		9	7
CUMMING, H. G. 1955c	٥	0	က	0	0	•	5 8	-	8.4		0	18
JOHNSTON, F. 1962	S	0	0	٥	0	•		6	7.2		8	6.4
MACFIE, J. A. 1958	36	0	0	0	14	•	0	7 0	214		0	٥
O'SHAUGHNESSY, T. 1961	0 9	0	-	-	0	•	0	8	5.7		0	e
SIMKIN, D. W. 1958a	0	0	0	0	0	0	0	0	315		0	833
SIMKIN, D. W. 1958b	0	٥	0	0	0	22	32	0	624		0	0
SIMKIN, D. W. 1959	36	0	0	0	0	0	0	0	542		-	18
VOZEH, G. E. & A. ZIMMERMAN 1959	6	8	0	~	ĸ	0	4 3	4	347		0	4
VOZEH, G. E. 1960	2 0	0	0	0	12	0	7.7	-	137		0	0
VOZEH, G. E. 1961	3.2	0	0	-	1.0	0	5 9	1.5	383	8 2	0	0
VOZEH, G. E. 1962	22	0	0	0	-	0	427	3 9	209	32	0	٥
BROWSE UNITS RECORDED BY SPECIES	6											
CUMMING, H. G. 1955a									-			
CUMMING, H. G. 1955b												
CUMMING, H. G. 1955c			0 6				6.4	7 0				
JOHNSTON, F. 1962												0 6
MACFIE, J. 1958	165								4 5			
O'SHAUGHNESSY, T. 1961	455		20						1336			
SIMKIN, D. W. 1958a									2153			245
SIMKIN, D. W. 1958b							0		897			
SIMKIN, D. W. 1958c	1020								244			
VOZEH, G. 1959									0 9			
VOZEH, G. 1960	9											
VOZEH, G. 1961	216								30	560		
VOZEH. G. 1962									3.0			



		BLACK	_	BLACK	WHITE	YELLOW	BLACK WHITE YELLOW CHOKE RED	e	9	GROUND
DSE HONES	HONESUCKLE	SPRUCE	SPRUCE VIBURNUM ASH	- 1	PINE	ВІЯСН	CHERRY PINE	- 1	DER J	ELDER JUNIPER
2 CUMMING, H. G. 1955a	-	1.0	-	•	0	٥				
2.7 CUMMING, H. G. 1955b	80	3	•	0	0	0	-			
1 CUMMING, H. G. 1955c	•	3.9	8	٥	0	•				
0 JOHNSTON, F. 1962	•	3.4	•	•	0	0	-		-	
0 MACFIE, J. A. 1958	'n	5.6	8	0	0	٥				
0 O'SHAUGHNESSY, T. 1961	•	•	•	0	٥	0	10		*	Ξ
203 SIMKIN, D. W. 1958a	-	34	7.5	o	0	•				
0 SIMKIN, D. W. 1958b	0	755	11	0	٥	•				
۵	80	9	•	-	0	0				
0 VOZEH, G. E. & A. ZIMMERMAN 1959	60	28	•	0	-	-	6		4	
<u>а</u>	0	36	•	0	0	٥				
0 VOZEH, G. E. 1961	0	2.5	•	0	80	0	6 4	-	4	
4 VOZEH, G. E. 1962	0	34	•	0	-	•	=			
BROWSE UNITS RECORDED BY SPECIES										
CUMMING, H. G. 1955a	-									
CUMMING, H. G. 1955b										
CUMMING, H. G. 1955c										
JOHNSTON, F. 1962										
MACFIE, J. 1958										
O'SHAUGHNESSY, T. 1961							31			
1071 SIMKIN, D. W. 1958a	158	~	428	190						
SIMKIN, D. W. 1958b										
SIMKIN, D. W. 1958c										
VOZEH, G. 1959										
VOZEH, G. 1960										
VOZEH, G. 1961							170			

TABLE	MBERS OF	LIVING STEMS	3a. TOTAL NUMBERS OF LIVING STEMS RECORDED IN SURVEYS OF 10 SPECIES (METHOD	SURVEYS OF	10 SPECIES (METHOD 2)
AUTHORS	PLOTS WH	WHITE BIRCH BAL	BALSAM FIR MOUNTAIN ASH	TAIN ASH	WILLOW MO	MOUNTAIN MAPLE
ARMSTRONG 1964	113	292	238	424	840	541
BROWN 1965	6 4	9 2	-1	0	6 1	2 6
BUSCH & GAGNE 1969	6 4	166	0	0	4 7	8 1
CLOSE1966a	8 0	8 0	ις	170	5 6	169
CLOSE 1966b	8 4	117	16	4 5	3.1	103
CORNELL1964	6.4	2 8	155	12	7	166
CREIGHTON 1965a	6.4	186	135	244	446	465
CREIGHTON 1965b	6 4	181	289	83	3 1	110
CRICHTON 1963a	6 4	o	356	33	100	161
CRICHTON 1963b	120	139		217	106	784
CRICHTON 1963c	108	131		146	3 9	774
GIBSON 1963	6.4	141	398	7 0	391	9 1
GIBSON 1964a	6 4	10	364	8	0	14
GIBSON 1964b	6 4	146	194	99	00	186
HALL 1963	7 9	147	339	0	က	314
HENDRY 1965	136	199	938	111	150	419
LUCKING 1963a	6 4	26	3.1	2.7	9	187
LUCKING 1964a	ъ Б	36	က	264	9	119
LUCKING 1964b	6 4	8 4	458		7	408
LUCKING 1965a	120	80	670		7.1	330
LUCKING 1965b	128	8 2	16		209	
MACFADYEN 1964	6.4	9 1	234		0	ø
	6 4	229	6 1	2 6	•••	œ
MONK 1963	106	2 3		6 4	238	
O'SHAUGNESSY 1964a	6.4	4.7		6 4	12	0
O'SHAUGNESSY 1964b	6.4	ĸ	7.2	က	4	4
O'SHAUGNESSY 1964c	6.4	7.4	262	112	S.	ø
O'SHAUGNESSY & KEAN 1965	6.4	38	83	4	4 2	9
STASUS 1970	6 9	4 4	0	33	96	230
SWIFT 1964	6.4	3 55	0	0	8 4	4 2
THOMPSON 1969a	6 9	124		-	7	
THOMPSON 1969b	63	7	180	-	က	550
REPEATED SURVEYS						
GIBSON 1969a	6.4	2.7		2 8	8	2
GIBSON 1969b	6.4	199	324	16	-	13
HALL 1954	6	407	1076	10	2 2	327
HERRON & CARTER 1969	6.4	33	191	59	7.1	8 1
LUCKING 1963b	6.4	4 1	0	4	6 9	-
LUCKING 1964c	6.4	5.4	0	2.7	7.7	18



	TABLE 3a	D. TOTAL	CONTINUED. TOTAL NUMBERS OF LIVING STEMS RECORDED (METHOD 2).	LIVING S	TEMS REC	ORDED (METHO	2)
	- 1	DOGWOOD	CHERRY JUNEBERRY TREMBLING	NEBERRY	TREMBLI	NG ASPEN		HAZE
	×	4 5	9 8	233	_	_	9	-
***	BROWN 1965	2	10	0		(7)	3.1	10
	BUSCH & GAGNE1969	0	357	63		100	91	19
	CLOSE 1966a	0	143	_		_	7	15
	CLOSE 1966b	12	126	9			89	2
	CORNELL1964	2	0	0		-	29	4
	CREIGHTON 1965a	8 6	159	4		1	0 1	27
	CREIGHTON 1965b	132	0	80		7	7	2
	CRICHTON 1963a	0	10	0		4	7	9
	CRICHTON 1963b	6	39	7		4	9	9
	CRICHTON 1963c	17	4 5	1.5		9	63	6 9
	GIBSON 1963	219	83	1.5		4	58	12
	GIBSON 1964a	0	0	_			-	
	GIBSON 1964b	3 3	0	LG.		-	-	
	HALL 1963	6 2	31	8	•	-	3.1	155
	HENDRY 1965	365	3 1	0		2	2	17
	LUCKING 1963a	14	112	0		_	က	-
	LUCKING 1964a	0	124	~	_		7	13
	•	9	13	8			7	3 2
	LUCKING 1965a	0	96	e		7	9	4 9
	LUCKING 1965b	6	556	-		30	9	5 4
	~	0	80	14	_		0	œ
	Œ	0	136	'n		~	2 4	4
	MONK 1963	0	-1	236		6	9	14
	O'SHAUGNESSY 1964a	0	7	8		e	3.7	13
	O'SHAUGNESSY 1964b	0	9	0		e	0	12
		0	œ	0		_	co	5 4
	O'SHAUGNESSY & KEAN 1965	30	2 5	-		9	80	38
	ເກ	က	931	2 0	_	2	4	69
	4	0	47	0		~	8	4 8
	THOMPSON 1969a	က	2 0	18	_	~	0	20
	THOMPSON 1969b	13	0	10	_	-	0	38
	REPEATED SURVEYS							
	GIBSON 1969a	0	0	1 4			ဗ	
	GIBSON 1969b	0	0	-			2	
	HALL 1964	256	4 4	7 3	_	4	4	178
	HERRON & CARTER 1969	114	9.7	0		7	0	4 7
	LUCKING 1963b	4 9	323	0		12	21	17
	LUCKING 1964c	=	299	•		7	27	16

APPENDIX TABLE 35. NUMBERS OF BROWSED STEMS RECORDED IN SURVEYS OF 10 SPECIES (METHOD 2)	ERS OF BROWSED S	TEMS RECORDE	IN SURVEYS OF 10 SPEC	SIES (METHOD 2).	
AUTHORS	NO. OF PLOTS WH	IITE BIRCH BAL	NO. OF PLOTS WHITE BIRCH BALSAM FIR MOUNTAIN-ASH	WILLOW MOUNTAIN MAPL	MAPLE
ARMSTRONG 1964	113	5 2	79 346	211	180
BROWN 1965	6.4	17	4	36	12
BUSCH & GAGNE 1969	6.4	138	0	4 4	13
CLOSE 1966a	8 0	19	0 139	4.9	2 8
CLOSE 1966b	8 4	11	0 15	1.9	10
CORNELL1964	6.4	0	11 6	9	8 7
CREIGHTON 1965a	6.4	10	18 78	23	3 6
CREIGHTON 1965b	6.4	3.4	68 41	9	3 5
CRICHTON 1963a	8 4	9	23 13	ຕ	4 2
CRICHTON 1963b	120	4 2	28 91	4 4	205
CRICHTON 1963c	108	63	42 77	2.8	2 8
GIBSON 1963	6.4	8 2	176 37	230	5.7
GIBSON 1964a	6.4	10	293 2	0	-
GIBSON 1964b	6.4	135	96 64	7	166
HALL 1963	4 7	20	7.2 0	2	141
HENDRY 1965	136	86	64 67	98	172
LUCKING 1963a	6.4	12	19 9	0	8 6
LUCKING 1964a	6 9	0	0 42	0	-
LUCKING 1964b	6.4	-	7 11	0	2 4
LUCKING 1965a	120	o	8 22	5	2 5
LUCKING 1965b	128	4	1 12	6-	0
MACFADYEN 1964	6.4	3.4	4 28	0	4 0
MILLER 1963	6.4	7 3	1 47	-	142
MONK 1963	106	13	27 64	183	263
O'SHAUGNESSY 1964a	6.4	8	1 13	0	œ
O'SHAUGNESSY 1964b	6.4	-	0	-	2 6
O'SHAUGNESSY 1964c	6.4	14	2 23	0	63
O'SHAUGNESSY & KEAN 1965	5 6.4	9	11 11	18	9
STASUS 1970	69	2 2	0 28	4 9	7
SWIFT 1964	6.4	2 0	0	33	-
THOMPSON 1969a	6 9	63	24 0	-	224
THOMPSON 1969b	63	0	5.4	0	166
REPEATED SURVEYS					
GIBSON 1969a	6.4	12	196	0	8
GIBSON 1969b	6.4	6.4	177 2	-	œ
HALL 1964	6 9 3	2 9	8 2 1	9	109
HERRON & CARTER 1969	6.4	8	3 13	15	ဗ
LUCKING 1963b	6 4	13	0	1.8	0



APPENDIX TABLE 3b CONTINUED. NUMBERS OF BROWSED STEMS RECORDED IN SURVEYS OF 10 SPECIES (METHOD 2),	D. NUMBERS O	OF BROWSE	D STEMS RECORDED	IN SURVEY	S OF 10 SPECIES (METHOD 2).
AUTHORS	DOGWOOD	CHERRY JL	CHERRY JUNEBERRY TREMBLING ASPEN	IG ASPEN	HAZEL
ARMSTRONG 1964	3.2	4	9.5	2.7	5.1
BROWN 1965	0	7	0	o	6.2
BUSCH & GAGNE 1969	0	122	7	100	9 9
CLOSE 1966a	0	2.7	0	2	4.8
CLOSE 1966b	0	4	-	-	2.2
CORNELL1964	-	0	0	5 8	26
CREIGHTON 1965a	2 8	15	0	12	-
CREIGHTON 1965b	2 6	0	က	2 4	1.4
CRICHTON 1963a	0	က	0	1 9	19
CRICHTON 1963b	-	18	8	10	212
CRICHTON 1963c	-	1 5	က	2 8	163
GIBSON 1963	120	33	9	255	29
GIBSON 1964a	0	0	0	-	0
GIBSON 1964b	33	0	-	10	0
HALL 1963	2.7	9	4 4	7.7	525
HENDRY 1965	214	1 9	0	7.1	73
LUCKING 1963a	က	30	0	4	4.7
LUCKING 1964a	0	4	0	8	1.5
LUCKING 1964b	0	8	0	-	3.4
LUCKING 1965a	0	4	0	က	91
LUCKING 1965b	-	6	0	-	8
MACFADYEN 1964	0	-	0	0	15
MILLER 1963	0	3 1	4	1 4	13
MONK 1963	0	11	175	16	149
O'SHAUGNESSY 1964a	0	0	0	8	-
O'SHAUGNESSY 1964b	0	4	0	6	17
O'SHAUGNESSY 1964c	0	4	0	က	2.8
O'SHAUGNESSY & KEAN 1965	13	-	-	4	6
STASUS 1970	84	4 8	80	104	247
SWIFT 1964	0	33	0	18	89
THOMPSON 1969a	0	2 8	-1-	S	228
THOMPSON 1969b	က	0	-	0	102
REPEATED SURVEYS					
GIBSON 1969a	0	0	80	0	0
GIBSON 1969b	0	0	8	က	0
HALL 1964	83	1 4	3.2	144	848
HERRON & CARTER 1969	2 5	1 2	0	2	7.1
LUCKING 1963b	13	2 8	0	-	10

