WINTER HABITAT STRUCTURE OF THE SNOWSHOE HARE

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ABSTRACT

WINTER HABITAT STRUCTURE OF THE SNOWSHOE HARE

By

Michael James Conroy

Snowshoe hare habitat structure was studied on diverse, partially clearcut areas in northern Michigan during January through March, 1976. Utilization, habitat, and weather variables were intensively measured on a 61 ha study area in order to develop a descriptive and predictive model; predictions from this model were tested during March, 1976 by surveying two 23 km^2 extensive study areas. Results from the intensive study indicate that hare activity centered around lowland coniferous and alder (*Alnus*) types, but dispersed into adjacent upland coniferous-hardwood and clearcut hardwood communities where habitat interspersion was high. Distance from lowland coniferous-hardwood types and habitat interspersion were the two most important factors determining hare utilization. Utilization was heavy along several clearcut-conifer edges. Red maple (*Acer rubrum*) and speckled alder (*Alnus rugosa*) were the most frequently browsed species. Browse selection shifted to aspen (*Populus* spp.), pine (*Pinus* spp.), and blackberry (*Rubus* spp.) as these became available.

The extensive surveys supported the conclusions about hare utilization made from the intensive study. Hare utilization decreased drastically farther than 200 m from lowland coniferous canopy cover, in both cut and uncut areas. Clearcuttings near lowland coniferous cover were utilized heavily, primarily along the edges. Clearcut communities very distant from lowland conifers were essentially

non-utilized by hares. Cuttings managed for hares should be small or shaped so that canopy cover is within 100 m of all parts of the cutting. Slash left from cutting operations may act as supplemental cover if strategically concentrated along likely feeding and travel lanes.

WINTER HABITAT STRUCTURE OF THE SNOWSHOE HARE

By

Michael James Conroy

A THESIS

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INTRODUCTION

The niche of a species may be defined in theory by its coordinates in *n*-dimensional space, each coordinate corresponding to a measurable environmental parameter (Hutchinson, 1957). Problems of applying this concept to field data include redundancy, non-additivity, and non-linearity among the parameters (Green, 1971). Analytical approaches to overcome these difficulties have included discriminant analysis and principal component analysis (Green, 1971; James, 1971; Whitmore, 1975).

In a very general sense, the niche of the snowshoe hare (*Lepus americanus*) is known. Grange (1932) described several types of habitats in Wisconsin in which hares were commonly found; hare utilization of these habitats varied seasonally, but included aspen (*Populus* spp.) stands of moderate age adjacent to conifer swamps, alder (*Alnus* spp.) swamps, old burns, young jackpine (*Pinus banksiana*) stands, and hardwood stands near conifer cover. In Minnesota, Aldous (1937) noted that during inclement weather hares remained close to forms or resting spots consisting of hollow logs, willow (*Salix* spp.) clumps, or fallen trees. Based on pellet surveys in Montana, Adams (1959) found that hares occurred in the greatest concentrations where woody vegetation was thick, but there apparently is an optimum density of vegetation beyond which increasing density will diminish hare use of the habitat.

More recent workers have attempted to isolate specific important factors in habitat structure. Bider (1961) showed that vegetation structure plays an important part in determining the size of home ranges in Quebec hares, and that climatic and physical factors may dampen or activate movements within those ranges. Brocke (1975) found that continuity of coniferous canopy seems to be essential for snowshoe hares in the Adirondack region of New York. Hares spend the day in "base cover" consisting of conifers averaging 3.5 m tall; "travel cover" (conifers 8.3 m tall) provides travel lanes when adjacent to base cover, but has no value in the absence of the latter. Hardwood browse was the most important winter food source. Keith (1974) felt that specific vegetative parameters, particularly stems less than 3 mm in diameter, are a critical part of a hare-grouse-predator system of cyclic abundance.

The objectives of this study were to, on diverse and partially clearcut areas: (1) built a descriptive and predictive model about hare utilization based on intensively measured utilization and habitat variables, (2) use this model to generate predictions about hare utilization on similar areas, (3) make a preliminary test of these predictions, using data from extensively surveyed areas, and (4) tentatively evaluate the effects of certain types of clearcut situations, based on the data collected above.

METHODS

Intensive Study Area

Vegetative data were collected during the summer of 1975 and hare utilization data during January-March, 1976, on a 61 ha study area located in southeastern Roscommon County, Michigan. This part of Michigan is characterized by a relatively mild climate, with normal annual average temperatures of around $5^{\circ}C$ and total annual precipitation of about 71 cm. The study area is part of a 23 km^2 research unit (designated the Lanes Lake Unit by the Michigan Department of Natural Resources) that was partially clearcut in 1973 for a deer range management study. The geology of the area is primarily of glacial morainic origin. Three major soil types have been mapped (Veatch, 1929). Well-drained, low fertility Grayling sand on level to gently rolling terrain supports upland types in the southwestern third of the study area. A strip of Rubicon sand running from the northwest corner to the southcentral end of the area supports upland types in which small pockets of lowland types are interspersed. The east half of the area is predominately Newton loamy sand on level to gently sloping terrain, with many flat, low areas prevalent; large areas are very swampy, and some standing water occurs seasonally.

The study area was surveyed during June, 1975, noting species compositions, canopy heights, and basal areas for the overstories and species compositions, heights, and percentages of cover for the understories (Figure 1). Overstory canopy heights were estimated using an altimeter, and basal areas were estimated using an angle gauge; several readings were taken in each community to get a rough range for each parameter. Understory heights and coverages were estimated by eye.

Five major groups of vegetative communities occur on the study area (Figure 1). Communities IVa to IVe, formerly composed of oak (*Quercus* spp.), aspen, and pines (*Pinus* spp.) 12 m to 15 m tall were clearcut between January and April, 1973; they thus had three complete growing seasons as of the commencement of this study. Moderate to heavy reproduction of aspen, red maple (*Acer rubrum*), oak, cherry (*Prunus* spp.), and juneberry (*Amelanchier* sp.) dominates these communities. Large slashpiles left from the cutting operations are scattered throughout. Although Figure 1 indicates that the overall percentages of low cover are similar for all five of the clearcut communities, the distributions of low woody cover and slash are quite heterogeneous. Communities IVa and IVd, particularly the former, have many rather open patches, and cover tends to be relatively sparse near the edges. Communities IVb, IVc, and IVe, while having some open areas toward the centers of the communities, tend to be more densely covered toward the edges. These latter communities also tend to have a higher density of slash, especially around the edges, than do communities IVa and IVd.

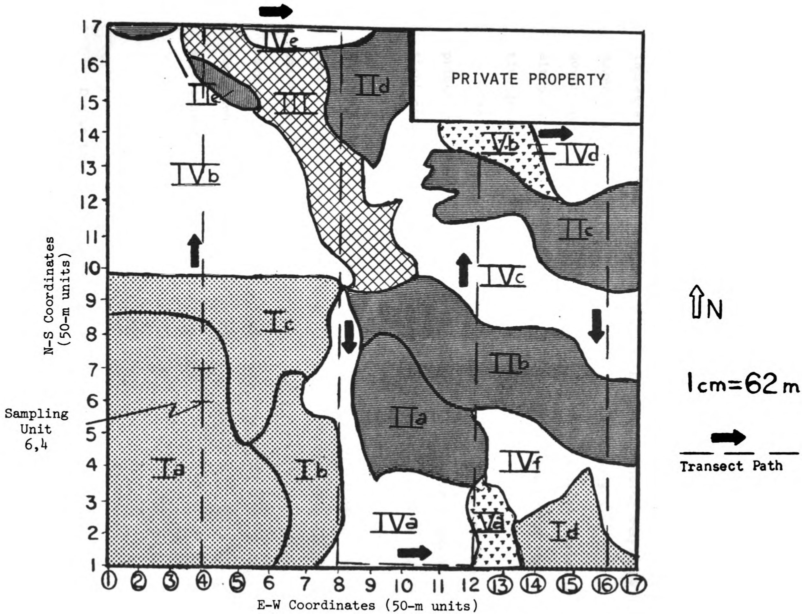
Forestry records indicate that community IVf was commercially cut for oak in 1961; although there are no further records, it appears to have been burned about five years prior to the time of the study. Scattered 10 cm to 20 cm diameter fir (*Abies balsamea*), aspen, red

Figure 1. Description of vegetative communities and illustration of transect method.

Daily routes start at south end of area (at one of circled coordinates). Example route begins at coordinate 1,4 and ends at 1,16.

LEGEND

	Overstory	Ht. (m)	Basal area (m^2)	Understory Species	Ht. (m)	% Cover
I.	Upland Hardwood-Conifer					
	a. Red oak, red pine, jackpine	12-18	7-8	Aspen, oak, cherry, maple, juneberry	1-5	15-20
	b. Red oak, red pine, jackpine, aspen, red maple	12-15	5-6	Aspen, oak, cherry, maple, juneberry	1-5	20-30
	c. Red pine, jackpine, aspen, red maple	12-15	5-6	Aspen, oak, cherry, maple, juneberry	1-5	25-40
	d. Jackpine, red pine, red oak	12-18	4-5	Aspen, oak, maple, hazelnut (*Corylus* spp.), alder	1-5	50-60
II.	Lowland Conifer-Hardwood					
	a. Balsam fir, white cedar, red maple, black ash	15-20	12-13	Alder, ash, maple, cherry, cedar, fir	1-3	0-5
	b,c,d,e. Balsam fir, white cedar, red maple, black ash	12-17	8-11	Alder, ash, maple, cherry, cedar, fir	1-3	5-15
III.	Lowland Hardwood					
	American elm, black ash	12-14	1-2	Alder, dogwood (*Cornus* spp.), elm	1-3	5-30
IV.	Clearcut Oak-Aspen					
	a-e.			Aspen, oak, maple, cherry, juneberry	1-4	60-75
	f. Scattered red pine, red oak, balsam fir	12-15		Aspen, oak, maple, cherry, juneberry	2-7	60-70
V.	Alders					
	a-b.			Alder, dogwood, elm	1-7	30-60


PRIVATE PROPERTY
N-S Coordinates (50-m units)
E-W Coordinates (50-m units)
Sampling Unit 6,4
IVb
IVe
IIe
III
IId
Vb
IVd
IIc
IVc
Ic
Ia
Ib
IIa
IIb
IVf
IVa
Va
Id
1cm=62 m
N
Transect Path

pine (*Pinus resinosa*), and jackpine remain; otherwise the community is similar to, although more advanced than, communities IVb, IVc, and IVe.

Prior to clearcutting, the study area was fairly continuously canopied, with the exception of the ash (*Fraxinus nigra*), elm (*Ulmus americana*) and alder (*Alnus rugosa*) communities (communities III, Va, and Vb; Figure 1). It appears that the clearcuttings have extensively increased the habitat interspersion on the area, creating many more edges than previously existed. There is an increased amount of low cover available toward the clearcut edges of most canopied communities, although this was not reflected in community-wide measures of vegetative density.

The oak-pine group was classified into four communities, based primarily on the amount of low cover present. Community Ia has a tight canopy and consequently relatively sparse low cover, while communities Ib and Ic, having more open overstories, have denser understories. Understory densities in both the latter communities tend to be highest near the edges of the clearcuttings. Community Id has a much more open canopy than Ia, Ib, or Ic and appears to have been partially burned at about the same time that community IVf was. Consequently the understory density in this community is quite high, approaching that of the clearcut communities.

Estimates of Vegetative Parameters

Due to time constraints, it was necessary to take vegetative samples during summer, 1975, for all communities except Va and Vb, which were sampled during winter, 1976. It was assumed that relative differences in vegetative parameters between communities were constant from summer to winter. Based on a trail sample of 84 variously sized circular plots in 7 communities, it was determined that 20 plots should be sampled per community in order to estimate vegetative parameters with a minimal acceptable accuracy of 60% with 90% confidence (de Vos and Mosby, 1969). Using a species-area curve (de Vos and Mosby, 1969), optimum plot sizes of 0.0008 ha for measures on understory and 0.0065 ha for measures on overstory were obtained. Twenty randomly placed circular plots were sampled in each community except Va and Vb, in which ten for each were sampled because of the greater homogeneity in these alder communities. Understory (less than 4.6 m tall) stems were counted in two height classes (0.9 m to 1.8 m and 1.8 m to 4.6 m tall) in the 0.0008 ha plots. These plots were nested in the 0.0065 ha plots, in which overstory (taller than 4.6 m) stems were counted. Heights of the overstory codominants were measured and averages obtained for each plot. Slash cover to 1.8 m height was visually estimated for each 0.3 m height class by percentage indices (0% = 0, 1 to 25% = 1, 26 to 50% = 2, 51 to 75% = 3, 76 to 100% = 4). Lateral obstruction to 1.8 m was estimated for each 0.3 m height class by percentage indices as for slash cover, using a density board (de Vos and Mosby, 1969). Slash and lateral obstruction indices for height classes were summed to give total indices for each parameter. For example, if in three slash cover height classes the indices were 4, 2, and 1, then the index for slash cover would be 4 + 2 + 1 = 7. Since plots in communities Va and Vb were sampled during winter when foliage was absent, lateral obstruction indices comparable to those for the other communities could not be obtained and were not estimated.

Table 1 indicates that sampling was generally adequate for understory density (0.9 m to 1.8 m), canopy height, and lateral obstruction index, given the previously discussed acceptable accuracy and confidence. Sampling was generally inadequate for understory density (1.8 m to 4.6 m), overstory density, and slash cover index.

Measurement of Hare Utilization

The method used for measuring hare utilization is a modification of the transect methods used by Koskimies (1952) and by Lindlof, Lindstrom and Pehrson (1974) for measuring habitat preference in Scandinavian forest mammals. The 61 ha area was traversed by flagged transect lines running predominately north-south (Figure 1). The transects were 50 m apart, which is the distance specified by Koskimies (1952) to enable optimum detection of utilization. A regularized system of daily routes was developed, each route starting at a point along the southern edge of the area (Figure 1). At least four days were allowed between repeat samplings along the same route, in order to minimize disturbance from the researcher and his trails and to prevent double counting of trails on successive days. Each coordinate along the route was the starting point for a sampling unit (length of transect) that proceeded 50 m in the direction of travel. On days that the route was followed in the opposite direction (*e.g.*, ending at coordinate 1, 4 instead of starting there) the 50-m segment would also proceed in the opposite direction. Thus coordinates were the centers of overlapping 100-m segments, each segment composed of the alternating 50-m sampling units. Data for each 50-m sampling unit were

Table 1. Summary of vegetative estimates by community: Means ± 90% confidence intervals (expressed as percentage of the means).

Community	Understory density (stems/ha) 0.9-1.8 m	Understory density (stems/ha) 1.8-4.6 m	Overstory density (stems/ha)	Canopy height (m)	Lateral obstruction index[a]	Slash cover index[b]
Ia	19938±41%	1625±70%	1939±60%	12.6±17%	11.5±36%	0.9±103%
Ib	22125±42%	2313±87%	2246±71%	10.5±22%	11.2±39%	1.0±100%
Ic	21750±31%	1750±99%	2023±66%	10.6±29%	11.0±40%	1.6±91%
Id	50188±28%	6875±62%	1831±51%	9.8±43%	13.4±38%	1.6±66%
IIa	8938±44%	63±295%	3285±18%	18.3±8%	6.1±66%	1.8±66%
IIb	33188±26%	1875±110%	2415±71%	13.9±13%	9.6±52%	2.0±53%
IIc,d,e	27938±49%	938±128%	1815±67%	13.4±24%	10.0±51%	1.9±56%
III	33438±32%	3500±79%	1792±79%	10.3±21%	12.6±39%	2.1±57%
IVa	90125±16%	6875±39%	8±498%	3.0±22%	16.7±31%	1.6±33%
IVb,e	61625±19%	8250±73%	323±252%	3.8±37%	16.8±31%	2.5±45%
IVc	58125±29%	4875±58%	105±259%	4.0±51%	15.6±36%	2.8±50%
IVd	52625±25%	4375±55%	223±169%	4.4±59%	15.9±35%	2.8±38%
IVf	61250±27%	6125±60%	1092±113%	7.4±31%	16.3±29%	2.1±57%
Va	40625±33%	11250±47%	92±122%	6.4±49%	---	0.2±31%
Vb	39750±49%	15500±91%	492±100%	6.9±51%	---	0.5±270%

[a] Possible range 0-24 (see text).
[b] Possible range 0-12 (see text).

recorded by the coordinate of the starting point (Figure 1). Along each 50-m sampling unit, the following were counted: (1) recent (one-to-two-day-old) trails (designated TL in the analyses), (2) areas with many trails crisscrossed (designated TM), (3) areas covered with indistinguishable trails (designated TH), and (4) recently used (one-to-two-day-old) runways, divided into three subjective categories by intensity of use (designated RL, RM, and RH, for low, medium, and high intensity, respectively). In addition, the first trail or runway encountered in each 50-m sampling unit was followed for 20 m in the hare's direction of travel (if indeterminable, decided by coin flip), counting woody twigs browsed and stems barked by species, noting forms with signs of recent use, and counting any additional trails or runways encountered. These additional trails or runways were included in the count taken on the main part of the transect. Each 50-m sampling unit thus had two major types of information: (1) levels of use, determined by trail and runway counts, and (2) categories of utilization, determined by following trails. The latter type of information was intended to reduce the problem of interpreting transect data that occurs when animals pass through an area on their way to another, possible more preferred, area utilizing the measured area only for travel. Sampling was done on 28 days during January through March, 1976.

Browse Selection

Browsings were classified by species of plants browsed and major community groups in which browsing occurred (Table 5). Only those browsed species for which 5% or more selection occurred were included in Table 5; a complete listing of species browsed is provided in Table A-1. Mean browsing index per community was computed by dividing the total browse index (twigs browsed plus stems barked) by the number of observation points taken in that community over the study period. Numbers of stems available per community can distort browsing comparisons, by artificially inflating intensity in areas with few stems and deflating intensity in areas with many stems. Therefore, mean browsing index was adjusted for numbers of stems available by multiplying by the number of stems available, and dividied all figures by 10^6.

Other Variables

Several variables were determined from each coordinate on the community map (Figure 1). These were (1) habitat interspersion (numbers of communities within 100 m), (2) distance from lowland conifer communities, (3) distance from alder swamps, (4) distance from upland hardwood-coniferous communities, and (5) distance from clearcut communities. Distances were measured from the coordinate to the closest edge of any community of the appropriate designation.

Although not of primary interest in this study, it is known that weather fluctuations can greatly affect the activity patterns of hares (Bider, 1961). Furthermore, snow conditions may affect the use of runways (O'Farrell, 1965). In order to minimize unexplained variation in any model describing utilization over time, windchill, cloud cover, barometric pressure, precipitation, and snow conditions were measured and included in the analyses. A windchill meter (Verme, 1968) was set up approximately 1.2 km from the study area to record daily windchill index. Cloud cover, precipitation, and barometric pressure were taken from the daily records of the U. S. Weather Bureau at Houghton Lake. Snow depth was measured with a meter stick, and snow compaction was measured with a 9 kg cm^2 compaction gauge (Verme, 1968). Snow conditions were sampled at regular intervals along the transects to provide at least 6 readings per day for each community group; variation was generally slight within these groups. Daily averages were obtained from these samples for each community group, and these averages were used in the analyses. Since the moon was visible on relatively few nights during the study, moon phase was not considered to be an important factor.

Data Analyses

The two analytical approaches used were multiple regression and discriminant analysis. The multiple regression (Draper and Smith, 1966) attempted to describe the types of utilization as functions of the independent variables: habitat structure and weather conditions. Three different models were developed, using the measured independent variables (Table 2) and three dependent variables: track index, browsing index (twigs browsed plus stems barked), and number of forms used, at each coordinate. The track index was computed by weighting the observations in each trail and runway category by arbitrary coefficients: specifically, Track index=TL + 2TM + 3TH + 2RL + 3RM + 4RH.

Table 2. Correlation matrix of untransformed utilization, weather, and habitat variables.

	BR	FR	SND	SNC	WCH	CCL	BAR	DU1	DU2	DO	AH	DB	SC	HI	DII	DV	DI	DIV	PPT
TR	.37	.31	.02	-.06	.05	-.14	.02	-.17	-.11	.17	.16	-.14	-.03	.07	-.04	.02	.00	.15	-.13
BR		.24	.02	.02	.04	-.01	-.01	-.06	-.02	.04	.03	-.04	.07	.05	-.07	.02	.11	.01	-.06
FR			.15	.05	.04	.00	-.06	-.03	.00	.01	.01	-.01	.02	.01	-.01	.02	.00	.02	-.06
SND				.37	-.05	-.06	-.19	.29	.32	-.33	-.34	.35	.18	-.05	.04	.04	.01	-.17	-.07
SNC					.50	.15	.16	.09	.10	-.10	-.11	.11	.04	-.02	.03	.01	-.01	-.04	.19
WCH						-.30	.26	-.03	.00	.02	.01	-.01	-.01	-.04	.04	.02	-.01	.02	-.04
CCL							-.09	.03	.01	-.03	-.01	.01	-.01	.06	-.04	-.03	.00	-.01	.22
BAR								-.01	-.01	.02	.01	-.02	.19	.00	-.04	-.05	.02	-.01	.19
DU1									.87	-.89	-.89	.88	.46	-.04	-.19	-.23	.09	-.61	.02
DU2										-.85	-.90	.92	.51	-.13	.00	.04	.05	-.55	-.02
DO											.96	-.94	-.53	.12	.03	.05	-.21	.57	-.01
AH												-.97	-.53	.12	-.01	-.01	-.12	.56	.01
DB													.46	-.16	.09	.05	.06	-.50	-.01
SC														.02	-.56	-.29	.61	-.63	.04
HI															-.37	-.34	.01	-.23	.03
DII																.71	-.57	.43	-.09
DV																	-.34	.35	-.07
DI																		-.32	.04
DIV																			-.03
PPT																			

Utilization Variables

TR	Track index
BR	Browse index
FR	Forms

Weather Variables

SND	Snow depth
SNC	Snow compaction
WCH	Windchill index
CCL	Cloud cover
BAR	Barometric pressure
PPT	Precipitation

Habitat Variables

DU1	Understory density (0.9-1.8 m)
DU2	Understory density (1.8-4.6 m)
DO	Overstory density
AH	Canopy height
SC	Slash cover
DB	Lateral obstruction
HI	Habitat interspersion
DII	Distance from cedar-fir
DV	Distance from alder
DI	Distance from oak-pine
DIV	Distance from clearcut

The correlation matrix of all variables showed high correlations among 5 of the independent variables: density of understory (in both height classes), density of overstory, canopy height, and lateral obstruction (Table 2). In order to reduce problems in analysing and interpreting such intercorrelated variables (Green, 1971), only density of overstory was used in the regression analyses instead of all five intercorrelated variables. This variable was selected over the others because: (1) It succinctly expresses the structural changes occurring along the light gradient from densely canopied to open areas; the other variables are partly redundant. (2) It is most correlated with the track index. (3) In a future study, it would be one of the easiest variables to measure.

Prior to the regression analyses, the dependent variables were transformed according to the formula $TRANS(Y) = \sqrt{Y + 0.5}$ in an attempt to meet assumptions of normality (Sokal and Rohla, 1969); however, the transformed variables still failed to meet assumptions of normality (Kolgomorov-Smirnov test significant, $p < .05$). In this situation, estimation of parameters (means, regression coefficients) is still valid, but hypothesis testing is not (Searle, 1971); this was acceptable for my study since the primary interest was in description (estimation) and not in hypothesis testing. Since the transformation did make the distributions of the dependent variables more closely resemble the normal distribution, the transformed variables were used in the regression analyses.

Browse index and forms were measured cumulatively because browsings and forms counted on one day could be recounted on successive days. Since fluctuations over time were not relevant to such cumulatively measured variables, these variables were not regressed on the weather independent variables, but only on habitat variables. Treating the browse index and form measurements as cumulative variables could conceivably affect the analyses, if particular browsings and forms were multiply counted, due to artificial magnification of among-community differences. However, I feel that cumulating these variables were justified for two reasons: (1) Browsings and forms were located at points along hare trails followed away from transect lines, and the probability of recounting them was low (I estimate less than 10%). (2) Any minor effects on browse index and forms measurements due to recounting should have enhanced the analyses, since these variables were less likely to be sampled than trails and provided fewer data for comparisons between locations.

The best regression equation for each dependent variable was selected by means of a stepwise procedure (Draper and Smith, 1966). Entry criteria of F = 3.00 for track index and browse index and F = 1.00 for forms were selected by trial and error to yield the best equations (Draper and Smith, 1966; Nie *et al.*, 1975).

The regression equations were poor predictors of utilization, accounting for only 9%, 3%, and 0.3% of the total variation in track index, browse index, and forms, respectively (Table 3). These models were probably inadequate partly because of reasons pointed out by Green (1971): particularly violations of the assumptions of additivity and linearity among the parameters.

In discriminant analysis, groups (any logical units of animal distribution, activity, behavior, etc. defined by an ecologist) are separated in *k*-dimensional space (where *k* is equal to the number of

Table 3. Regression coefficients and proportion of variance explained by multiple regression models. Coefficients are for best equations as selected by a stepwise procedure (see text).

Dependent Variables					
$\sqrt{\text{Track index} + 0.5}$		$\sqrt{\text{Browsing index} + 0.5}$		$\sqrt{\text{Forms} + 0.5}$	
Independent Variable	Standardized* Coefficient	Independent Variable	Standardized* Coefficient	Independent Variable	Standardized* Coefficient
Habitat interspersion	.1455	Distance from oak-pine	.1680	Habitat interspersion	.0395
Distance from clearcut	.2236	Habitat interspersion	.1196	Distance from clearcut	.0593
Distance from cedar-pine	-.1077	Distance from clearcut	.0584	Slash cover	.0260
				Overstory density	-.0300
Precipitation	-.1270	Distance from alder	.0587	Distance from oak-pine	-.0244
Cloud cover	-.1136				
Snow depth	.0469			Distance from cedar-fir	-.0334
				Distance from alder	.0247

Proportion of Variation Explained by Regressions

$\sqrt{\text{Track index} + 0.5}$	$\sqrt{\text{Browsing index} + 0.5}$	$\sqrt{\text{Forms} + 0.5}$
$R^2 = .089$	$R^2 = .03$	$R^2 = .003$

*Mean of 0, standard deviation of 1.

groups defined, minus one) by functions of the environmental variables that the ecologist has chosen to measure. This approach to analysing utilization removes two of the problems inherent in the regression approach used above by (1) eliminating the need to assume linear additive relationships between environmental factors and utilization, and (2) simplifying interpretations by reducing the model from m dimensions to k discriminant functions, where m is the number of environmental parameters considered (in this study, 17 habitat and weather variables) (Green, 1971).

Four utilization groups to be analysed by discriminant methods were defined as follows: Group 1 (Non-utilized) consisted of all observations (each sampling unit on each day sampled) in which there were no signs of hare activity. Group 2 (Travel) consisted of observations in which trails or runways were recorded, but no browsings or forms. Group 3 (Feeding) consisted of observations in which both trails and forms in use were counted; this category also included non-feeding observations, but in most feeding also occurred. The analysis maximized the distances among groups along each of three discriminant function axes (Cooley and Lohnes, 1971).

Computations for all analyses were performed on the Michigan State University CDC 6500 computer, using a packaged statistical program (Nie *et al.*, 1975).

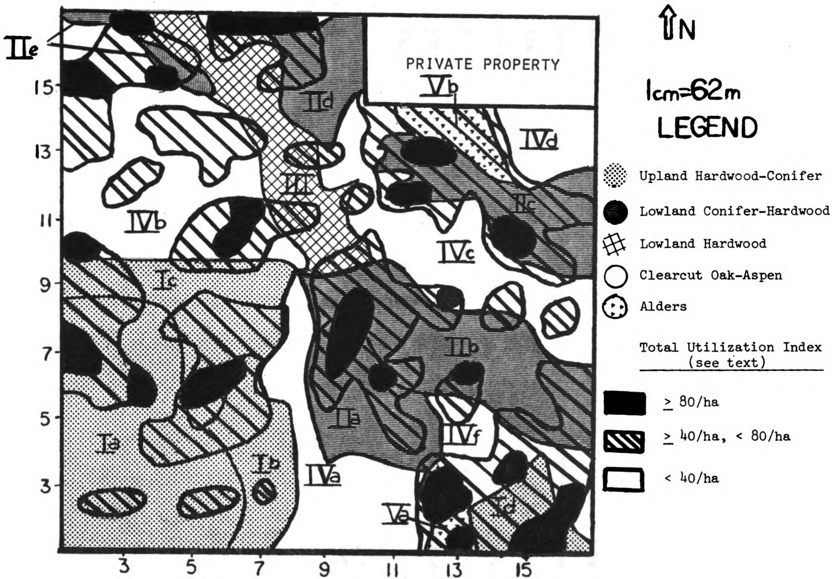
Utilization Map

A descriptive map of utilization was constructed by means of a total utilization index. The index was intended to express total utilization, but to emphasize feeding and form use over travel. This was accomplished by weighting mean track index 1, browsing index 2, and forms 20. Forms were weighted heavily because I felt that 10 instances of browsing were roughly equivalent to 1 instance of form use, in terms of total intensity of utilization. The weighted track, browse, and form indices were summed to give a total utilization index, expressed as utilization per hectare (Figure 2).

Extensive Surveys

In order to broaden the scope of this study, and as a preliminary test of some predictions from the above discriminant model, hare trail surveys were made on two 23 km^2 study areas in March 1976. Both areas had been partially clearcut during 1972 and 1973 and thus had undergone 3 to 4 growing seasons by the time of this study. The areas are predominately mixed upland conifers and hardwoods (oak, jackpine, red pine) 12 m to 15 m tall, with scattered lowland coniferous-hardwood types (cedar, fir, maple, ash). Area I (designated as the M-18 Unit by the Michigan Department of Natural Resources) is located approximately 20 km southwest of the intensive study area, and was 25% clearcut. Area II (designated as the Lanes Lake Unit) encompasses the intensive study area and was 50% clearcut. The areas were sampled by cruising roads and logging trails and counting hare trails and runways to derive a track index as computed by the formula given earlier. Route segments of varying lengths adjacent to mapped cover types were classified by factors determined to be important from the discriminant model (RESULTS section). These were: (1) treatment (uncut *vs* cut), (2) distance from lowland conifer-hardwood canopy cover (level 1: 0 m to 200 m, level 2: 200 m to 400 m, level 3: farther

Figure 2. Density of total hare utilization index by community types. (See text)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Vb
IId
IVd
III
IVb
IIc
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1cm=62m
LEGEND
Upland Hardwood-Conifer
Lowland Conifer-Hardwood
Lowland Hardwood
Clearcut Oak-Aspen
Alders
Total Utilization Index
(see text)
≥ 80/ha
≥ 40/ha, < 80/ha
< 40/ha

than 400 m), and (3) distance from upland hardwood-conifer canopy cover (same levels as above). The track index for each segment was converted to an index per kilometer of the traveled route. Data were also classified by areas (I *vs* II). Weather conditions were used as a blocking factor, grouping the four days on which sampling was done into two groups of two days each, one of mild weather, the other inclement. Before analysis, the data were transformed to $\sqrt{Y + 0.5}$ to correct for non-normality. The distribution of the transformed data was not significantly different from normal ($p > .05$) when tested by the Kolgomorov-Smirnov method (Nie *et al.*, 1975). The null hypotheses of no effect on utilization due to areas, treatments, distance from lowland conifer-hardwood, and distance from upland hardwood-conifer were tested, using weather conditions as a blocking factor, by a five-factor analysis of variance (Nie *et al.*, 1975).

RESULTS

From examination of Figure 2, it is evident that hare utilization was most concentrated in cedar-fir, oak-pine, and alder communities. It is also apparent that utilization tended to be away from the centers of these communities, and toward regions of high habitat interspersion. Clearcut communities were less utilized than canopied communities (except community III), but utilization was heavy around theedges of communities IVb, IVc, IVe, and particularly IVf. Community IVa was very sparsely utilized, and appeared to be acting as a barrier to movement between the oak-pine and cedar-fir communities.

Precipitation and cloud cover appeared to have depressing effects on utilization (Table 3). Most browsing occurred away from the oak-pine communities. Form use was essentially unpredictable from the variables measured (Table 3). Examination of the residuals from the regression equations plotted over time (Draper and Smith, 1966) revealed no apparent time trends in utilization.

Three discriminant functions were able to classify correctly 39.2% of the observations into utilization groups; the apparent error (Lachenbruch, 1975) of prediction was thus 61.8%. The main habitat factors determining function I were distance from cedar-fir, habitat interspersion, and distance from clearcut communities. The main habitat factor determining function II was distance from oak-pine. Overstory density and distance from oak-pine were both important in determining function III. The three functions accounted for 58.1%, 28.3%, and 13.6% of the among-group variation, respectively (Table 4). These functions are combined in a three-dimensional representation of habitat volume (Figure 3). According to this representation, hare utilization was centered in diverse areas near cedar-fir canopy cover and away from clearcut communities; within these areas, hares fed farther from oak-pine canopy cover, rested and fed closer to oak-pine, and traveled between.

Table 5 indicates that red maple and speckled alder were the most frequently selected woody browse species for the entire study area. Browse selection shifted from pine and maple in the upland hardwood and conifer communities to maple and alder in the lowland communities and aspen, maple, and blackberry in the clearcut communities. Browsing intensity was highest in the clearcut and alder communities, and lowest in the lowland hardwood communities.

Most hare utilization in the extensive study areas occurred close to or in lowland coniferous communities. However, heavy utilization often occurred along lowland coniferous-clearcut edges, especially on the canopied sides. There was no significant ($p > .05$) difference in hare utilization ascribable to areas or distance from upland conifer-hardwood types, while there was a significant ($p < .05$) difference in utilization due to treatments (uncut *vs* cut) and distance from lowland conifers (Table 6). There were significant ($p < .05$) interactions between treatment and distance to lowland conifer-hardwood, and between treatment and distance to upland hardwood-conifer. These tests may be biased because of significant (chi-square = 14.68, $p < .05$) heterogeneity of variance as determined by a Bartlett's (1937) test.

Table 4. Summary of the results of the discriminant analysis, using four utilization groups and three discriminant functions of weather and habitat variables (see text).

	Percent of Among Group Variation Accounted For		
	Function I	Function II	Function III
	58.1	28.3	13.6
	Utilization Group Means in Standardized Discriminant Space (Mean of 0, standard deviation of 1)		
	Function I	Function II	Function III
Non-utilized	.30112	-.01572	-.00720
Travel	-.31506	.20048	-.20258
Feeding	-.34515	-.34168	.07273
Resting-feeding	-.23008	.42295	.39531
	Standardized Discriminant Function Coefficients (Mean of 0, standard deviation of 1)		
Variable	Function I	Function II	Function III
Snow depth	-.35387	.76778	.48167
Snow compaction	.48146	-.19218	.25257
Windchill	-.34835	.08275	.28534
Cloud cover	.13023	.10845	.32748
Barometric pressure	.03628	-.24078	-.05040
Overstory density	-.30427	.23087	-.34401
Slash cover	.13035	.10011	-.00205
Habitat interspersion	-.43779	-.12182	.25652
Distance from cedar-fir	.43967	.10033	-.28304
Distance from clearcut	-.46021	.10857	.15195
Distance from alder	-.23866	-.10818	.16055
Distance from oak-pine	-.28698	-.61225	.34036
Precipitation	.32657	.02800	-.16715

Table 4 (Cont'd):

Classification Results

	Utilization Group				
	Non-utilized	Travel	Feeding	Resting-Feeding	Total
Percent correctly classified	41.0	28.7	43.3	45.1	39.2

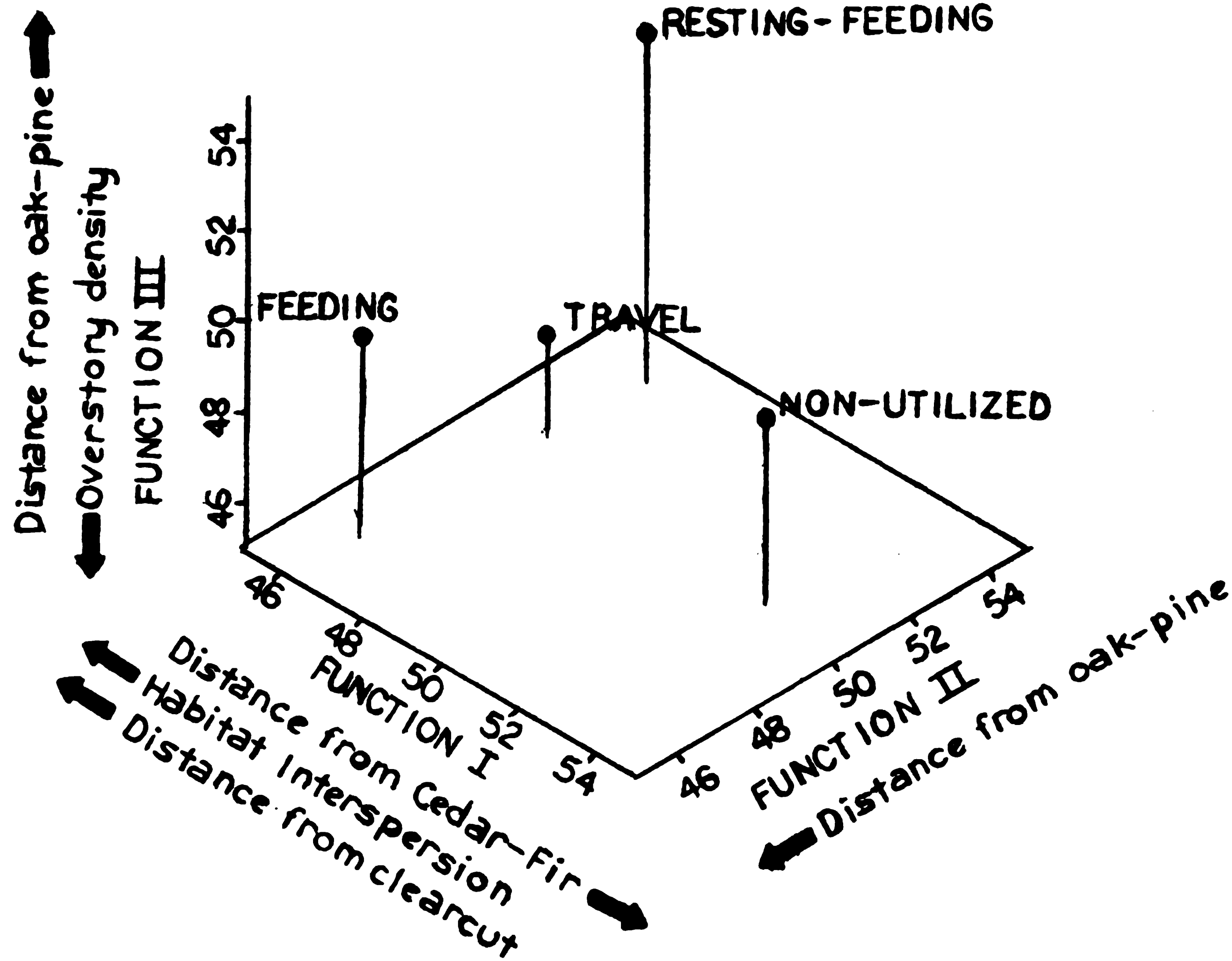

Figure 3. Utilization group means in standardized (Mean = 50, standard deviation = 10) discriminant space. Arrows indicate direction of increase in major discriminating variables.

Table 5. Percentage of total number of twigs browsed and stems barked for each community, grouped by species. ( ) = numbers browsed.

Browse Species	Community I Oak-pine	II Cedar-fir	III Ash-elm	IV Clearcut	V Alder	All Areas
Red maple	22.6(70)	38.0(186)	30.4(38)	23.0(137)	13.2(14)	27.3(445)
Speckled alder	0	20.4(100)	33.6(42)	10.1(60)	34.9(37)	14.7(239)
Aspen (*Populus* spp.)	*	6.1(30)	11.2(14)	29.0(173)	0	14.1(230)
Blackberry (*Rubus* spp.)	*	*	*	14.4(86)	*	8.4(117)
Pine (*Pinus* spp.)	33.9	*	*	*	*	7.5(122)
Other (less than 5% each)[a]	14.5(45)	21.1(103)	15.2(19)	17.3(103)	14.2(15)	29.1(474)
Total	100(310)	100(489)	100(125)	100(597)	100(106)	100(1627)
# stems available[b]	537,897	364,699	184,690	1,629,550	64,275	2,781,111
Browsing intensity[c]	0.13	3.3	5.5	0.5	19.6	0.45

[a] Listed in Appendix Table 1.

[b] # stems/ha (Table 1) X # ha in community.

[c] Total browsing ÷ # observation points in community X # stems available ÷ 10^6.

Table 6. Analysis of extensive track survey data. Dependent variable is $\sqrt{\text{track index/km} + 0.5}$.

Source of Variation	Sum of Squares	df	Mean Square	F
Blocks (weather conditions)	604.632	1	604.632	
Main Effects				
Areas	.167	1	.167	.016
Treatments (uncut, cut)	63.847	1	63.847	6.063*
Distance from cedar-fir	161.844	2	80.922	7.685*
Distance from oak-pine	5.867	2	2.934	.279
Two-way Interactions				
Treatments X Distance from cedar-fir	67.648	2	33.823	3.212*
Treatments X Distance from oak-pine	67.493	2	33.824	3.205*
Other two-way	127.490	13	9.806	.931
Residual (pooled error and higher interactions)	493.930	47	10.530	

*Significant, $p < .05$.

Therefore, selected contrasts among cell means were made, using a Scheffe (1953) test. These indicate that increasing distance from lowland conifers has a significant ($p < .05$) depressing effect on hare utilization in uncut communities. The response is parallel but non-significant ($p > .05$) for clearcut communities. The only significant ($p < .05$) difference between cut and uncut response occurred during inclement weather and farther than 400 m from lowland conifers (Figure 4). Clearcut communities, regardless of their location, had less utilization as entities than did canopied areas; however, clearcuttings near lowland coniferous cover had significantly higher utilization than those away, and did not differ significantly from canopied areas.

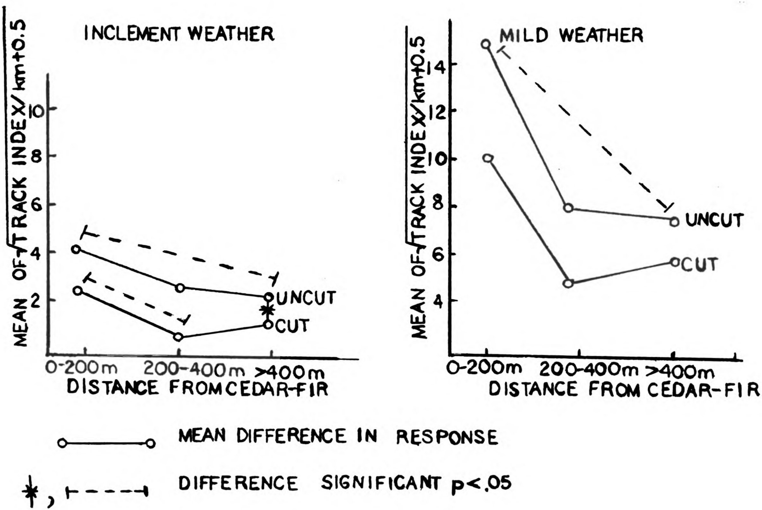

Figure 4. Mean differences in transformed track index by treatments (cut *vs* uncut) and distance from cedar-fir for extensive track surveys.

DISCUSSION

The results of the discriminant analysis and utilization map strongly suggest that proximity to coniferous cover, especially cedar-fir, and habitat interspersion are the two most important factors determining hare utilization. Utilization centers around cedar-fir and oak-pine communities that have a number of other communities nearby. In looking at the utilization map (Figure 2), the indication from the discriminant analysis (Figure 3) that increasing distance from clearcut communities positively affects utilization appears contradictory. However, clearcut communities are very scattered throughout the study area, and most points in the area are closer than 100 m from a cutting edge; this factor is thus relatively invariant. Since most activity in clearcuttings occurs around the edges, where vegetative diversity is great, habitat interspersion (numbers of communities within 100 m) may be a more biologically meaningful variable than distance from clearcuttings; it is also more variant.

Increased habitat interspersion appears to have an important effect on the diversity of food available to and utilized by hares; this was indicated by the increased intensity of browsing and shift to include more aspen in the diet in clearcut areas. Maple and alder, although possibly of low nutritive value for hares (Bookhout, 1965) appeared to be the mainstays of their winter woody diet in the lowland communities. Trembling aspen (*Populus tremuloides*), red pine, and jackpine are more palatable and nutritious for hares than either alder or maple (Bookhout, 1965). In communities where pine or aspen were available in abundance, browse selection shifted to these species. This was especially true in the clearcut communities, where aspen is the dominant understory species.

The highly interspersed areas also tend to have relatively denser low cover than the uniformly canopied areas, although this was not always reflected by the data. These areas have the benefit of both heavy low cover and canopy cover overhead or nearby. The heavy utilization found in these areas is consistent with Adam's (1959) findings on the optimum density of woody vegetation for hares.

Brocke (1975) concluded that coniferous cover 2.5 m to 4.5 m tall with dense coniferous understory acts as "base cover," where hares spend the day resting in forms. Prior to clearcutting my intensive study area was fairly continuously canopied; in this respect it was similar to Brocke's area. Observations on other similarly typed but uncut areas, made while I was conducting the extensive track surveys, indicate that hare utilization is generally quite concentrated around lowland types (cedar-fir and alder). This was probably the case on my intensive study area prior to cutting. Hares were most likely concentrated in areas near the edges of the cedar-fir and oak-pine communities; the lowland-hardwood and alder communities would have provided the only major breaks in the canopy, and utilization was probably high in areas where these communities were adjacent to cedar-fir and oak-pine. By creating many new edges, clearcutting apparently has begun to disperse activity away from these old centers; this has occurred to the greatest extent in community IVf, possibly because that cutting has been in existence longer than the others.

Based on the analysis of the intensive study area using the utilization map, and discriminant model, I made predictions regarding utilization of similar areas by hares: (1) Utilization would be highest in cedar-fir communities and in canopied communities adjacent to them. (2) Utilization would be low in young clearcuttings far from cedar-fir canopy cover, but much higher when they are close, due to the increased habitat interspersion. (3) Predictions regarding the oak-pine communities were less clear. Based on Function I of the discriminant model, it was expected that utilization would not occur in the oak-pine communities unless cedar-fir was nearby. However, distance to oak-pine was important in accounting for a large portion (30%) of the among-groups variation. The utilization map also indicates that important centers of utilization were located in these communities. Nevertheless, I predicted that utilization would not be concentrated in oak-pine communities unless these were close to cedar-fir types. These predictions applied only to communities in successional stages similar to those on the intensive area; this was the case on the two extensively surveyed areas.

The results of the track surveys in the extensive study areas tend to support these predictions. Utilization was generally higher along the clearcut-lowland conifer edges than in the centers of the canopied communities; however, this could not be shown by the data, since edges were not classified separately. The lack of significant difference between the 25% clearcut area (I) and the 50% clearcut area (II) and the significant interactions between treatment (uncut *vs* cut) and distance from canopy cover appears to indicate that the proportion of forest clearcut is not as important in determining hare utilization as is habitat interspersion; habitat interspersion is greatest in the region adjacent canopy cover.

CONCLUSIONS

Based on the results of the discriminant analysis, the utilization map, the extensive surveys, and my subjective observations, I conclude that: (1) Communities very distant from canopy cover, especially lowland coniferous types, or in areas of low habitat interspersion, will not be heavily utilized by hares in winter. (2) Since utilization of clearcuttings is highest near the edge where habitat interspersion is great, and use decreases significantly toward the middle, cuttings managed for hares should be small or else shaped so that canopy cover is within 100 m of all parts of the cutting. (3) Although the importance of slash cover is not evident from my analyses, much hare activity did center around slashpiles, especially near the edges of the clearcut and oak-pine communities. Furthermore, clearcut areas in which slash was sparse or poorly distributed, especially community IVa, had light hare utilization. In managing for hares, slash should be left along likely feeding and travel lanes.

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LITERATURE CITED

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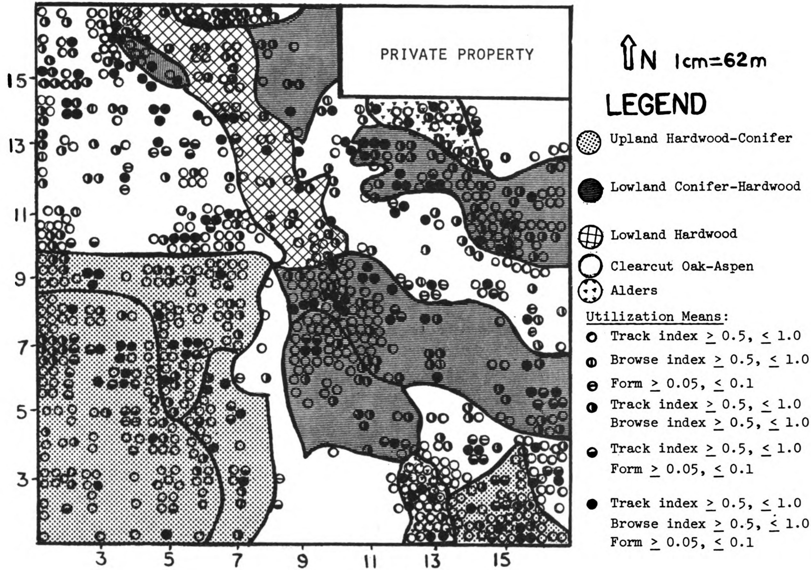
APPENDIX

Table A-1. Percentage of total number of twigs browsed and stems barked in all communities, grouped by species. ( ) = numbers browsed and barked.

Browse Species	Percentage of Total
Balsam fir (*Abies balsamea*)	3.3 (52)
Red maple (*Acer rubrum*)	27.8 (445)
Juneberry (*Amelanchier* sp.)	4.8 (76)
Speckled alder (*Alnus rugosa*)	15.0 (235)
Birch (*Betula* sp.)	0.3 (4)
Alternative leaved dogwood (*Cornus alternifolia*)	0.1 (2)
Gray dogwood (*C. racemosa*)	0.1 (2)
Red-osier dogwood (*C. stolonifera*)	4.0 (64)
Hazelnut (*Corylus* sp.)	0.9 (14)
Hawthorn (*Crataegus* sp.)	0.4 (7)
Black ash (*Fraxinus nigra*)	0.3 (4)
Witch hazel (*Hamamelis virginiana*)	1.4 (22)
Honeysuckle (*Lonicera* spp.)	0.4 (7)
Jackpine (*Pinus banksiana*)	4.4 (71)
Red pine (*P. resinosa*)	1.2 (19)
White pine (*P. strobus*)	1.9 (31)
Pine (*Pinus* sp.)	0.1 (1)
Balsam poplar (*Populus balsamifera*)	0.2 (3)
Aspen (*Populus* spp.)	14.2 (227)
Cherry (*Prunus* spp.)	4.2 (67)
Oak (*Quercus* spp.)	2.6 (41)
Poison ivy (*Rhus radicans*)	0.1 (1)
Gooseberry (*Ribes* spp.)	0.4 (7)
Blackberry (*Rubus allegheniensis*)	6.1 (97)
Raspberry (*Rubus idaeus*)	1.3 (20)
Willow (*Salix* xp.)	0.6 (11)
White cedar	1.5 (24)
American elm (*Ulmus americana*)	1.8 (28)
Blueberry (*Vaccinium* sp.)	0.4 (6)
Viburnum (*Viburnum* spp.)	0.1 (1)
Unidentified woody browse	1.4 (23)
Total	100 (1626)

Figure A-1. Distribution of hare utilization by community types.


PRIVATE PROPERTY
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LEGEND
Upland Hardwood-Conifer
Lowland Conifer-Hardwood
Lowland Hardwood
Clearcut Oak-Aspen
Alders
Utilization Means:
Track index ≥ 0.5, ≤ 1.0
Browse index ≥ 0.5, ≤ 1.0
Form ≥ 0.05, ≤ 0.1
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Browse index ≥ 0.5, ≤ 1.0
Track index ≥ 0.5, ≤ 1.0
Form ≥ 0.05, ≤ 0.1
Track index ≥ 0.5, ≤ 1.0
Browse index ≥ 0.5, ≤ 1.0
Form ≥ 0.05, ≤ 0.1
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