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ESTIMATING CARRYING CAPACITY OF A WHITE-TAILED DEER WINTERING AREA IN QUÉBEC

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Abstract: The carrying capacity of a white-tailed deer (*Odocoileus virginianus*) wintering area was determined based on food availability and biological characteristics of the animals. The basic information used was measurement of the surface area used by deer, a description of the cover types, an estimate of the accessibility of the browse (integrating biomass available, snow depth, and energy cost of walking), and an assessment of the nutritive requirements of deer based on published results. A model developed to simulate the effect of changes in the original values showed that the estimated carrying capacity could vary between 0 and 18 deer/km^2 depending on sinking depth of deer in a severe winter. Because of the variability of winter conditions, mainly snow depth and length of confinement period, the deer manager should refer to a "desirable stocking rate" for average climatic conditions. Based on this principle, the desirable population in the area studied should be maintained between 15 and 28 deer/km^2. The sensitivity of the model to variations in the original values was tested and the possible strategies for deer and the deer manager are discussed.

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Carrying capacity, defined as "the number of animals that a habitat can maintain in a healthy and vigorous condition" (Dasmann 1964:181), is a basic concept in big game management. However, controversies about deer management policies have arisen when this apparently simple idea was confronted with programs such as artificial feeding or implementation of the buck law (Doman and Rasmussen 1944, Swift 1961, Dasmann 1971). The literature contains few examples where serious attempts were made to estimate the carrying capacity of a given range, but describes many situations where it was exceeded.

A current technique for relating a deer population to its carrying capacity relies on examination of animal characteristics (Severinghaus et al. 1950). Antler development and reproductive parameters are the most widely used characters. Unfortunately, this technique may be useful only after the habitat has seriously deteriorated. The approach involves different confounding factors: (1) the carrying capacity itself and (2) the status of the population related to the carrying capacity. Does a low reproductive rate in an area indicate a low-quality habitat with a population below the carrying capacity or chronic overpopulation and damaged habitat with reduced potential? Due to the low recruitment in the 1st case, a minimum harvest would be the right management decision. In the 2nd case, a higher harvest should be allowed to decrease the population. Moreover, if, as suggested by Klein (1968) for northern regions, the summer component of the range may affect the physical stature of the animal whereas the winter component may be more directly involved in limiting the size of the population, the carrying capacity can be reached on the winter range before any effect is apparent on the fall condition of the animals.

Carrying capacity has been evaluated by different methods. In Michigan, Davenport et al. (1953) used enclosures placed

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in different forest types and estimated from deer performance that the coniferous type could sustain 2–3 times more deer than the deciduous type. Telfer (1971) concluded that carrying capacity for deer in Nova Scotia had declined between 1910 and 1956 based on acreage in open forest and brushland. In northern New York, Jackson (1974) suggested applying a density of 8 deer/km^2 to coniferous forest to obtain long-term carrying capacity. Available browse biomass was used to evaluate carrying capacity for deer by Westell (1954) and for moose (*Alces alces*) by DesMeules (1965). Recent approaches compare food quantity and quality with nutritive requirements of deer, especially the need for energy (Short 1972, Moen 1973, Robbins 1973, Parker 1975, Towry 1975, Whelan 1975, Blair et al. 1977, Wallmo et al. 1977).

Our objective was to assess the applicability of the carrying capacity concept to deer management under climatic conditions in Québec. It involved (1) an attempt to determine the carrying capacity of a well-defined traditional deer yard and (2) an assessment of the relative importance of the main environmental and biological parameters and their variability on the estimated carrying capacity.

We considered that, under our conditions, food and most probably energy would be the limiting factors. Predation is not important in the area and, as suggested by Klein (1969), white-tailed deer do not seem to have behavioral mechanisms contributing to population stability. We used the carrying capacity definition of Edwards and Foyle (1955) as given by Eabry (1970:5): "The maximum number of animals . . . which can be sustained in a given ecosystem through the least favorable environmental conditions that occur within a stated interval of time . . . without deterioration of the ecosystem and without impairing the quality of the animals. Generally, the most appropriate time interval is one year."

The following aspects were considered and incorporated into the carrying capacity model: (1) the estimation of the availability of browse production according to vegetation surveys, (2) an assessment of the effect of snow conditions on the availability of browse, and (3) an assessment of the energetic aspects of the first 2 points based on chemical analyses of browse and published information on deer energetic requirements.

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STUDY AREA

We investigated the Hill Head wintering area near Lachute (45°30′N, 74°19′W), 50 km north of Montréal. The population at the time was estimated at 325 ± 50 deer (90% CI) by the pellet-group count technique. The corresponding average density was 17 ± 3 deer/km^2 in a 19-km^2 wintering area (maximum extent).

The exposure is southern, which is typical of northern deer wintering areas. The topography is rolling and the elevation ranges from 70 to 130 m. The forest belongs to the Upper St. Lawrence section (L.2) of the Great Lakes–St. Lawrence region (Rowe 1972). In this section, the dominant cover type is composed of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) associated with other deciduous species. On shallow, acidic, or eroding materials a representation of conifers is usual, particularly Canada hemlock (*Tsuga canadensis*), white pine (*Pinus strobus*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). Northern white cedar (*Thuja occidentalis*) is found on wet sites and also on dry, rocky, or stony sites. Extensive settlement and clearing has taken place over much of the region.

Hill Head belongs to the Outaouais-Laurentides deer region, which has the most favorable climatic conditions within the province (Potvin 1977; R. Joly, unpubl. rep.). Total snowfall is 250 cm and snow depth usually exceeds 50 cm for less than 50 days.

METHODS

Our approach to the estimation of the carrying capacity of the wintering area was based on a comparison between the availability of the resources and the requirements of the animals for a given period of time. The variables considered in the analysis were divided into 7 categories (Fig. 1).

Extent of the Wintering Area

Three aerial surveys were used to map the extent of the area used by deer at different periods of the winter (Potvin 1973). The 1st was conducted when deer were beginning to concentrate (6 cm of snow), the 2nd in midwinter (44 cm of snow), and the last when they were confined (75 cm of snow).

Cover-type Description

Cover types were identified and mapped using 1:10,000 black-and-white aerial photographs taken in winter. Photo interpretation was done with a mirror stereoscope equipped with 3× lenses. Minimal area delimited was 0.5 ha. Seven cover types were classified (Table 1).

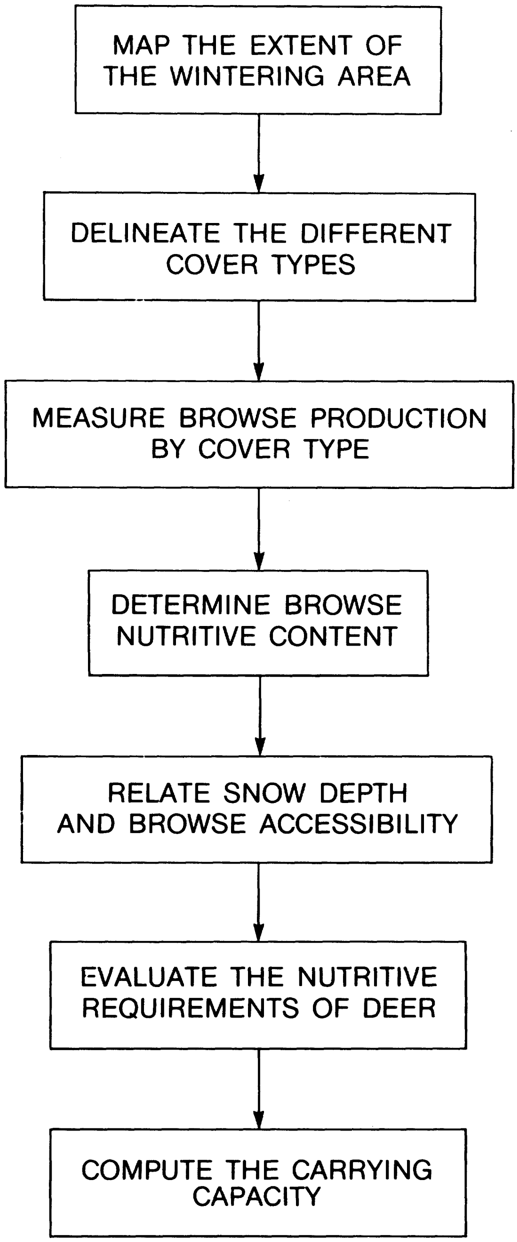

Fig. 1. Procedures needed to evaluate the carrying capacity of the Hill Head white-tailed deer wintering area, Québec.

Browse Production

Browse production was measured by a biomass technique (Potvin 1978). Unbrowsed twigs longer than 4 cm and twigs

Table 1. Cover types, composition, and canopy closure of the Hill Head white-tailed deer wintering area, Québec.

Cover type	Coniferous crown closure (%)	Composition
Hemlock	61–100	Coniferous stands dominated by hemlock
Cedar	61–100	Coniferous stands dominated by cedar
Balsam fir-spruce-pine	61–100	Other coniferous stands
Mixed	21–60	Mixed stands of coniferous and deciduous species, mostly shade tolerant
Deciduous	0–20	Deciduous stands, mostly sugar maple
Cutover and abandoned land		Clear-cut stands and abandoned agricultural land
Nonforested and swamp		Agricultural land, associations of *Alnus rugosa* and bogs

browsed the previous winter were counted in spring inside 1 × 10-m plots ($N = 352$). Twigs were stratified according to their height from the ground into 4 classes: 0–25, 26–50, 51–75, and 76–200 cm. The average weight of a twig was determined for the 5 most abundant species. A sample of 100 annual shoots for each species (except sugar maple) was clipped during winter, oven-dried, and weighed. Two samples of 100 annual shoots each were taken for sugar maple, 1 for the 0–25-cm height class and 1 for the 3 other classes because twigs in the 1st class were abundant and much smaller. Browse production by species was computed by multiplying the number of twigs by the corresponding average weight of an annual shoot.

Browse Nutritive Value

One hundred annual shoots for each of the 3 most important species in the deer diet (Potvin 1979) were systematically collected in winter. They were oven-dried at 70 C for 48 hours, ground in a Wiley mill with a 1-mm-mesh screen, and analyzed for crude protein content. Digestibility of these species was derived from the literature.

Browse Accessibility

Snow is the most important factor affecting browse accessibility. It covers low-growing vegetation, increases energy expenditure of foraging, and confines deer to restricted habitats. Snow depth was measured every 2 weeks throughout winter in 5 different cover types. Stratification of the browse survey enabled us to estimate the amount of browse available (above the snow level) for different snow accumulations. Linear regression was used to relate browse availability to snow depth. The food available is not necessarily accessible because the energetic demand to get it may be higher than its nutritive value. We considered that browse was accessible when there was a positive balance for deer between the energy expenditure required to get the browse and the metabolizable energy (ME) of the food above the snow level. Energy expenditure of walking deer for different snow depths can be approximated by the following equation from Mattfeld (1974): log(kcal/30 m traveled) = 0.0199(sinking depth in cm) + 0.4145. We assumed that deer would browse a 1-m-wide strip while walking and computed the biomass of browse available and its ME in each cover type at specific times in winter.

Nutritive Requirements of Deer

Nutritive requirements of deer were derived from the literature. Different estimations of daily ME requirements of penned deer in winter have been reported: 131 kcal/kg$^{0.75}$ for pregnant does (Ullrey et al. 1970), 125 for fawns (Thompson et al. 1973), 153 for fawns (Holter et al. 1977), and 116–127 for fawns (Holter et al. 1979). We arbitrarily used 130 kcal/kg$^{0.75}$. Although basal metabolism is not static throughout winter (Silver et al. 1969), its variation is minimal compared to the effects of snow depth and activity on total energy expenditures. Catabolism of fat reserves and proteins provides a part of this energy demand. Mautz (1978) suggested that a healthy deer can lose 20–30% of its fall weight and deCalesta et al. (1975) did not detect short-term effects with weight losses less than 30%. We applied a weight loss of 25% and assumed that tissues were catabolized at a constant rate throughout winter. We used a caloric content of 6 kcal/g of body substance loss as did Mautz et al. (1976) based on Moe et al. (1971) and Reid and Robb (1971). Fawns, adult females, and adult males weighing, respectively, 40, 70, and 90 kg at the beginning of winter and 30, 52.5, and 67.5 kg at the end would have average daily ME requirements of 1,870, 2,850, and 3,440 kcal (based on midwinter weight and 130 kcal/kg$^{0.75}$ ME requirements). Assuming a 90-day winter interval, food ingested would have to provide a minimum of 1,200, 1,680, and 1,940 kcal of ME per day.

Carrying-capacity Model

Based on the above information and principles, a model was constructed to estimate the carrying capacity of the Hill Head wintering area and to simulate changes in the original values. The confinement area was identified as the "ecosystem" because it sustained 83% of the deer days and provided 90% of the deer diet during the 1975–76 winter (Potvin 1979). That winter was one of the most severe for the area in the last 25 years (Potvin 1977) and was well documented. Therefore, snow depths during winter 1975–76 were considered to represent "the least favorable environmental conditions" that may occur in this ecosystem. A 90-day time interval was used as a basis for the model, which corresponds to the period when snow depth exceeded 50 cm in the open (1 Jan–31 Mar).

We set 50% of the available biomass of browse as the maximum permissible use rate to prevent shrub damage and potential food reduction. This rate of twig use is generally considered acceptable for browse (Aldous 1952, Robinette et al. 1952, Garrison 1953, Lay 1969, Dasmann 1971: 31, Wallmo et al. 1977), although some species such as mountain maple (*Acer spicatum*) may support a much higher rate (Aldous 1952). Finally, we assumed that the quality of the animals was not impaired if the ecosystem could provide enough energy to maintain the population during the critical 90 days, assuming a 25% weight loss by deer. Daily ME requirements (130 kcal/kg$^{0.75}$) included the energy spent by an animal during its normal activities excluding the energy expenditure of walking to get food. The deer population model assumed equal numbers of fawns, adult females, and adult males as derived from the either-sex harvest structure observed in the province.

An iterative computer program using the APL language was developed to perform analyses with the model (Fig. 2). A given number of deer was chosen by the experimenter and the program would test whether or not that number could be sustained throughout winter given a selected set of conditions. The winter was divided into 4 periods of equal length for computation purposes and a mean snow depth was assigned to each cover type for each period. Ten equations were used in the model (Table 2).

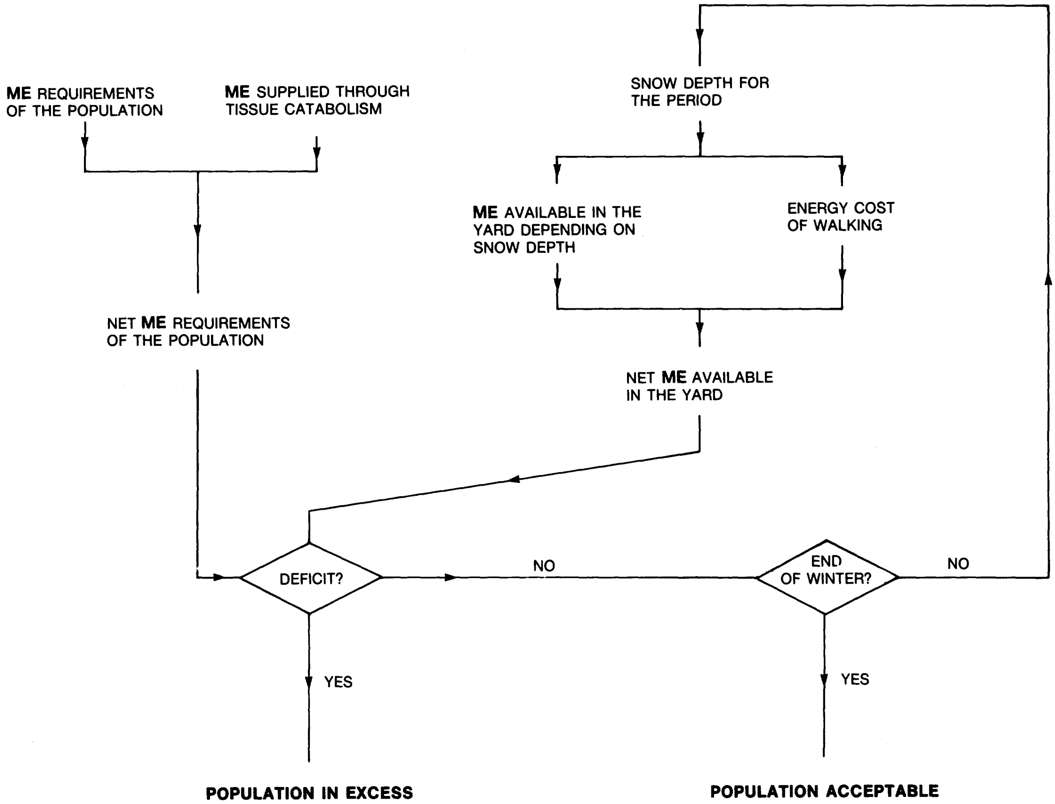

Fig. 2. The carrying-capacity model for the Hill Head white-tailed deer wintering area, Québec.

RESULTS AND DISCUSSION

The maximum extent of the wintering area from the 3 aerial surveys was 19 km^2. We divided it into 2 zones: (1) the confinement zone (10 km^2), which was the area used by deer at the time of the last survey (75 cm of snow), and (2) the peripheral zone (9 km^2). Hill Head yard is characterized by the predominance of coniferous stands (40% of the total area) and the limited area that has been cut over (3%). Agriculture affects 20% of the total wintering area and includes pasture, cultivated, and abandoned lands. Mixed and deciduous stands occupy 24 and 14% of the total area, respectively. The confinement zone (Table 3), as compared to the peripheral zone, is characterized by a greater abundance of hemlock, cedar, nonforested, and abandoned land cover types with less of the balsam fir-spruce-pine, mixed, and hardwood types.

Browse production 50–200 cm above the ground amounted to 37 ± 7 kg/ha, with a higher value for the peripheral zone (45 kg/ha) than for the confinement zone (29 kg/ha). In the latter, cutovers and abandoned land, mixed, and balsam fir-spruce-pine stands were the most productive cover types (Table 3). Balsam fir predominated in the confinement zone (39% of the browse production), followed by sugar maple (13%), cedar (12%), red maple (*Acer rubrum*) (4%), and hemlock (4%).

Vertical browse distribution followed

Table 2. Equations used in the carrying-capacity model of the Hill Head white-tailed deer wintering area, Québec.[a]

Component	Equation[b]	
Mid-weight of fawns, adult females and adult males in winter, kg	$POIM = \frac{POI + [POI - (POI \times PPOI)]}{2}$	(1)
Daily ME requirements of fawns, adult females, and adult males, kcal	$TBE = MER \times POIM^{0.75}$	(2)
Energy supplied daily through tissue catabolism for fawns, adult females, and adult males, kcal	$TAE = \frac{(POI \times PPOI) \times 1{,}000 \times EPPOI}{JCON}$	(3)
Net ME requirements of the deer herd for each period, kcal	$TBEN = \frac{TBE - TAE}{3} \times NCV \times \frac{JCON}{4}$	(4)
Biomass of browse above snow level by cover type, kg/ha	$BIO = MBIO \times ENN$	(5)
ME of browse above snow level by cover type, kcal/m^2	$EBIO = \frac{BIO \times LB \times BME \times TU}{10}$	(6)
Energy cost of walking by cover type, kcal/m	$EDEP = DEP \times ENF$	(7)
Net ME available to deer by cover type, kcal/m^2	$ENET = EBIO - EDEP$	(8)
Total net ME available to deer by cover type, kcal	$TENET = \frac{ENET \times SR \times 10{,}000}{LB}$	(9)
Area of each cover type not previously browsed during the current winter,[c] ha	$SR = SR - \left[\left(\frac{TBEN \times TENET}{\Sigma\, TENET}\right) \times \frac{TU}{ENET \times 10{,}000}\right]$	(10)

[a] The winter is divided into 4 periods of equal length for computation purposes. Equations (1) to (4) are performed 1 time at the beginning of a simulation whereas equations (5) to (10) are applied successively for each period.

[b] BME = ME content of browse (2.00 kcal/g).
DEP = coefficients of the prediction equation for the energy cost of walking (Table 6).
ENF = deer sinking depth (25 cm).
ENN = average snow depth (cm) by cover type for each period (Fig. 4).
EPPOI = energy provided by tissue catabolized (6 kcal/g).
JCON = number of confinement days (90).
LB = width of the browsed strip (1 m).
MBIO = coefficients of the prediction equation between the biomass of browse above snow level and snow depth for each cover type (Table 4).
MER = daily ME requirements of deer (130 kcal/kg$^{0.75}$).
NCV = number of deer tested (fawns, adult females, and adult males each comprise an equal segment of the herd).
POI = weight of fawns (40 kg), adult females (70 kg), and adult males (90 kg).
PPOI = weight loss throughout winter (25%).
TU = browse use rate (50%).

[c] The model assumes that an area browsed by deer cannot be used again during the current winter. Allocation of TBEN is proportional by cover type on an energy basis. For the initial period, SR is equivalent to the total area of each type (Table 3).

the same pattern in most cover types (Fig. 3). About half of the biomass was within 50 cm of the ground except in the mixed, nonforested, and swamp types, where the 76–200-cm height class provided 50% or more of the biomass. Prediction equations between the biomass above the snow level and the snow depth were highly significant for each cover type (Table 4).

There were important differences for the nutritive content of annual shoots among species (Table 5). Balsam fir and hemlock contained more crude protein than cedar but were less digestible and provided less metabolizable energy. The protein content of a composite diet (9.2%, ME = 2.00 kcal/g) was above the maintenance requirements generally reported.

There were similar patterns in snow depth trends during winter among the dif-

Table 3. Proportion of total area, browse production, and carrying capacity of each cover type in the confinement zone of the Hill Head white-tailed deer wintering area, Québec, winter 1975–76.

Cover type	Total area (%)	Browse production[a] (kg/ha)	Carrying capacity[b] (deer/km^2)
Hemlock	14	18	13
Cedar	9	9	6
Balsam fir-spruce-pine	19	35	24
Mixed	19	43	32
Deciduous	12	13	2
Cutover and abandoned land	12	45	17
Nonforested and swamp	14	18	19
Entire area		29	18

[a] 51–200 cm from the ground.
[b] Assuming a severe winter (Fig. 4) and a 25-cm sinking depth.

Table 4. Coefficients of the prediction equation between biomass of browse above snow level and below 200 cm from ground, and snow depth, by cover type in the Hill Head white-tailed deer wintering area, Québec, winter 1975–76.

Cover type	Coefficients[a]		
	a	*b*	r^2
Hemlock	39.0	−0.360	0.990
Cedar	28.9	−0.304	0.986
Balsam fir-spruce-pine	76.2	−0.772	0.993
Mixed	69.9	−0.484	0.991
Deciduous	34.8	−0.388	0.983
Cutover and abandoned land	75.9	−0.644	0.989
Nonforested and swamp	39.4	−0.184	0.989

[a] Coefficients of the regression

$$Y = a + bX$$

where:
Y = biomass of browse above snow level (kg/ha), and
X = snow depth (cm).

Each regression is based on 4 height classes (0–200, 25–200, 50–200, 75–200 cm). The linear model is most adequate for the 0–75-cm range, but a different model should be used for predictions above this value.

ferent cover types, with maximum depth occurring in mid-March (Fig. 4). Snow depth increased from the hemlock and cedar types to the mixed, deciduous, and cutover types.

Net ME available was computed by cover type for different snow accumulations by considering vertical browse distribution, its nutritive value and permissible use rate, and the energy cost of a deer walking in different snow depths (Table 6). All cover types would provide a positive energy balance up to a 50-cm accumulation of snow. At this snow depth, deer would get more energy from what they ate than they expended through walking. Only the most productive types could maintain this positive balance with 75 cm of snow and none could when snow depth exceeded 100 cm. Thus, foraging strategy of deer should be influenced not only by the biomass of browse available in a given cover type but also by snow depth and the additional energy demand it implies. For example, a hemlock stand with 50 cm of snow would be more advantageous for deer than a cutover area with 75 cm of snow, even though browse production was 100% higher in the latter type (Table 3).

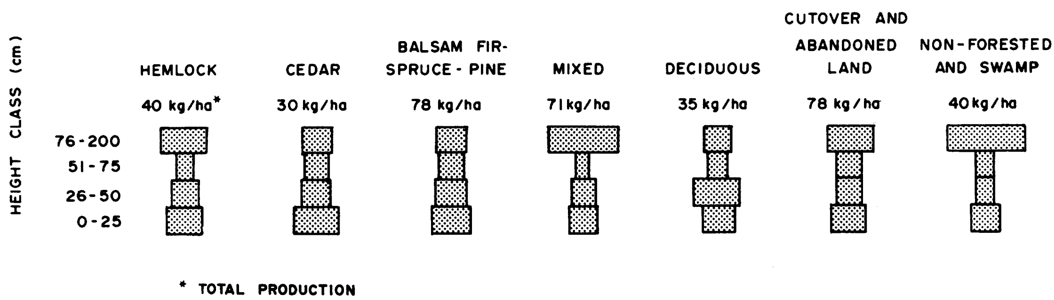

Fig. 3. Vertical browse distribution by cover type in the confinement zone of the Hill Head white-tailed deer wintering area, Québec, winter 1975–76.

Table 5. Nutritive content of the white-tailed deer diet (dry weight basis) in the Hill Head wintering area, Québec, winter 1975–76.

Item	Balsam fir	Cedar	Hemlock	Composite diet[a]
Crude protein, %	9.7	7.0	9.3	9.2
Apparent dry matter digestibility, %	48[b]	60[c]	49[b]	
Gross energy, kcal/g	5.28[b]	5.36[c]	5.13[b]	
Metabolizable energy, kcal/g	1.95[b]	2.47[c]	1.87[b]	2.00

[a] A typical diet of 77% balsam fir, 12% cedar, and 11% hemlock based on Potvin (1979).
[b] Mautz et al. (1976).
[c] Ullrey et al. (1972).

Under the snow conditions recorded in 1975–76 and assuming a maximum sinking depth (depth to ground), the Hill Head wintering area had a carrying capacity of 0 deer/km^2 (Fig. 5). However, deer rarely sink to the bottom of the snow pack. Assuming a 25-cm sinking depth for 90 days, the area should have sustained 18 deer/km^2, with higher densities in the mixed and balsam fir-spruce-pine types (Table 3). In the absence of snow, the carrying capacity would have been 3 times as great. Therefore, from the strict definition, the carrying capacity of Hill Head wintering area was between 0 and 18 deer/km^2. Using normal snow depths for this area (about 30% lower in midwinter) and assuming a 25-cm sinking depth, the density that could be sustained would have been 28 deer/km^2 (Fig. 5).

As suggested by Wallmo et al. (1977), it seems that the concept of a stable carrying capacity is not realistic. In areas where severe winters are frequent, the

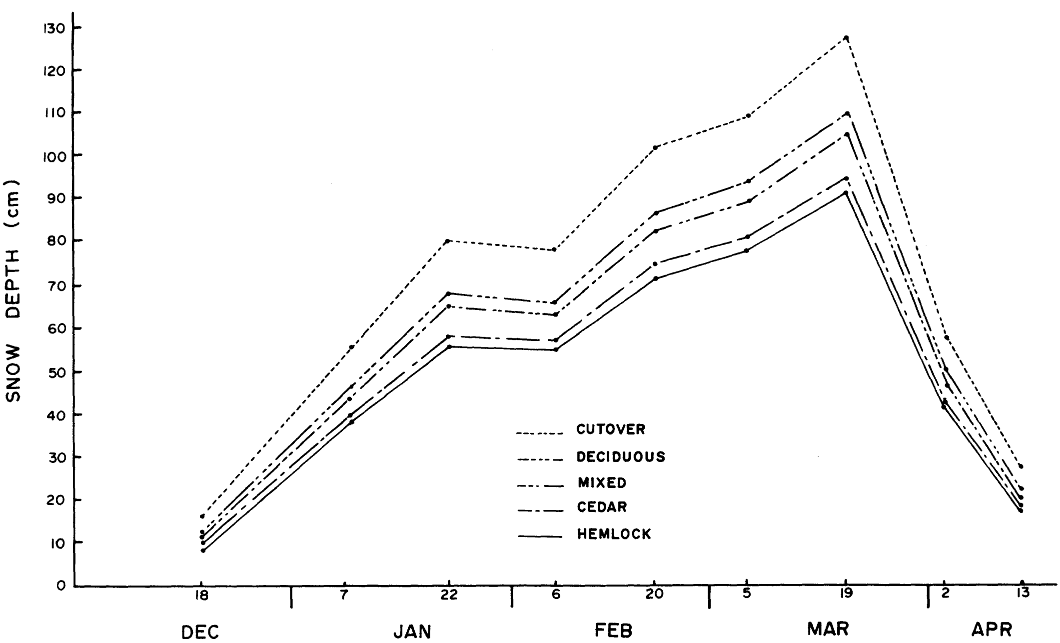

Fig. 4. Snow depth by cover type in the Hill Head white-tailed deer wintering area, Québec, winter 1975–76.

Table 6. Net ME available by cover type for different snow depths assuming a maximum sinking depth, a 50% use rate, and 1-m-wide browsed strip in the Hill Head white-tailed deer wintering area, Québec, winter 1975–76.

Cover type	Net ME available[a] (kcal/m²) for different snow depths (cm)				
	0	25	50	75	100
Hemlock	3.8	2.6	1.4	*[b]	*
Cedar	2.9	1.8	0.8	*	*
Balsam fir-spruce-pine	7.6	5.1	2.9	0.2	*
Mixed	6.8	5.3	3.0	1.8	*
Deciduous	3.4	2.4	0.7	*	*
Cutover and abandoned land	7.6	5.3	3.5	1.1	*
Nonforested and swamp	3.8	3.2	2.1	0.9	*
Energy cost of walking[c]	0.1	0.3	0.9	2.7	8.5

[a] Net ME available = (biomass of browse above snow level × ME content × 50%) − energy cost of walking.
[b] Energy cost of walking is higher than ME available.
[c] Based on Mattfeld (1974): log(kcal/30 m traveled) = 0.0199(sinking depth in cm) + 0.4145.

deer manager should have a goal of a population that can be sustained under average environmental conditions, a "desirable stocking rate." At this density, limited winter mortality would be expected to occur in normal winters but no permanent damage to the range should be apparent.

The sensitivity of the predicted carrying capacity to changes in the original values of the variables was tested to evaluate the most advantageous strategies for deer and the deer manager (Table 7). The most influential variables were daily ME requirements and the number of confinement days. In each case, a 25% reduction of the original value caused a 78% increase in the carrying capacity. Because the number of confinement days can rarely be modified, the best strategy for deer would be to (1) decrease its metabolic rate, (2) choose or create by a trail system areas where snow depth is minimal, (3) lose more weight, and (4) feed where browse is most abundant and nutritive. The deer manager should try to (1) decrease the energy expenditure of deer by minimizing harassment and making browse accessible, (2) provide the best coniferous cover to reduce the energy cost of access to food, and (3) increase food quantity and quality.

The carrying-capacity model discussed is imperfect. One of the main problems arises from the fact that it is based on a concept (carrying capacity) that is not yet sufficiently well defined by wildlife managers to be operationally used. Many of the data are still imprecise, affected by biases, or unavailable for wild ruminants. For instance, the sinking depth varies from day to day and even from hour to hour. Thermal losses, one of the important variables not included in the model, were im-

Table 7. Effect of a 25% increase (+) or decrease (−) of the original values in the carrying-capacity model of the Hill Head white-tailed deer wintering area, Québec.

Value modified	Deer/km²	Change (%)
None[a]	18	
Weight of deer, −	22	+22
Weight loss, +	24	+33
Daily ME requirements,[b] −	32	+78
Energy/g of tissue catabolized, +	22	+22
Number of confinement days, −	32	+78
Area of the confinement zone, +	23	+28
Browse production, +	24	+33
ME/g of browse, +	24	+33
Browse use rate, +	21	+17
Snow depth, −	29	+61
Snow sinking depth, −	19	+6
Energy cost of walking, −	19	+6
Width of the browsed strip, +	21	+17

[a] Assuming a severe winter (Fig. 4) and a 25-cm sinking depth.
[b] Excluding energy cost of walking.

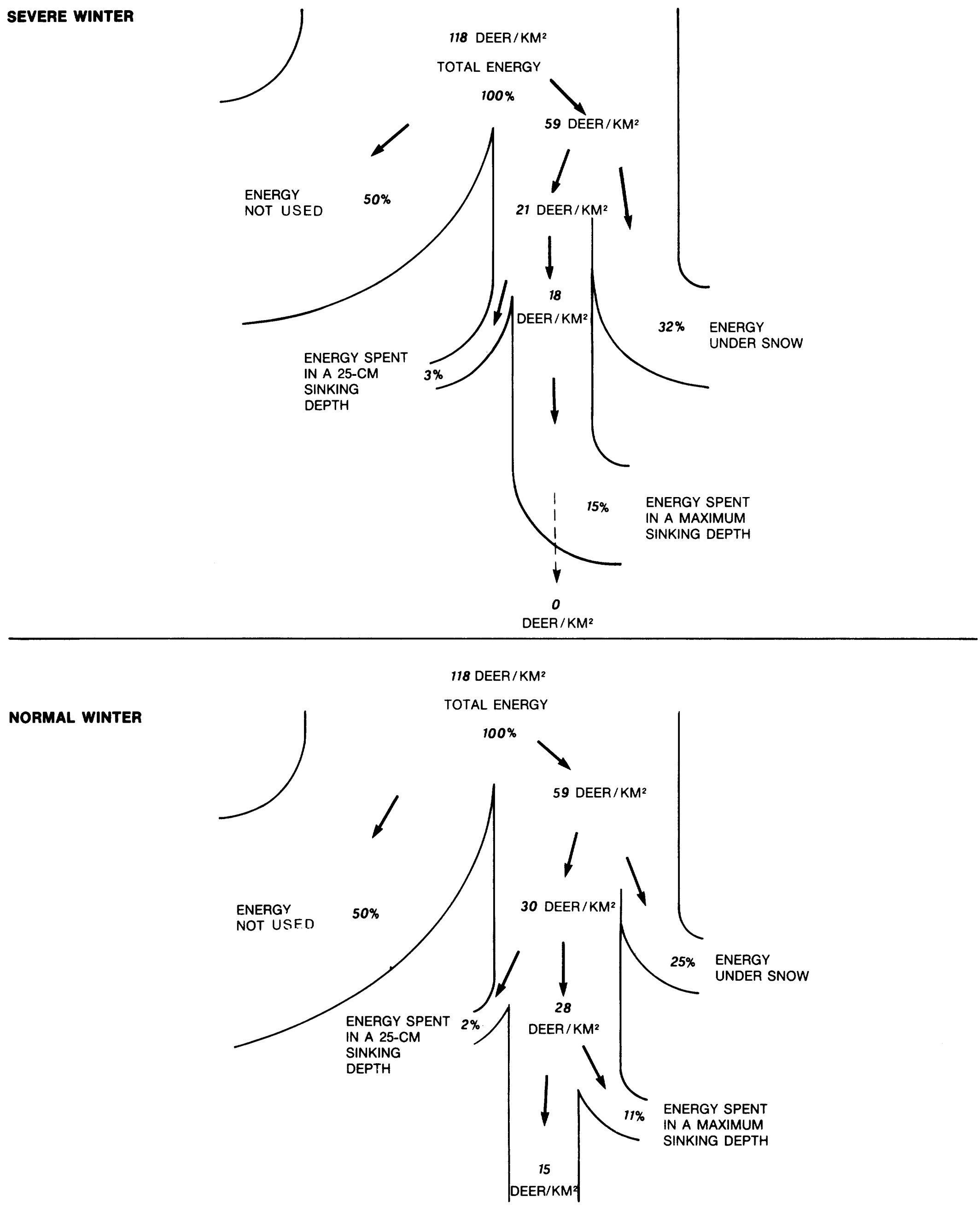

Fig. 5. Energy partitioning and corresponding white-tailed deer densities in the carrying-capacity model for the Hill Head wintering area, Québec.

possible to assess due to temporal and local variability. The other energy requirements of deer are still partly unknown and difficult to estimate in a variable and complex winter environment. The distance from a trail to available browse appears to vary. Trails are probably not randomly distributed but may, for instance, be in areas of higher browse availability, which would improve the energy balance. Moreover, browse distribution is not uniform, which probably affects deer foraging strategies. Sources of food other than browse in the shrub layer are not considered. The model is more a contribution to the understanding of the complex relationship between deer and their winter habitat under Québec conditions than a tool for decision making.

The model gives more insight to the idea previously expressed by Potvin et al. (1977, 1981) that, under Québec conditions, periodic severe winters can act independently of deer density to prevent overuse of the range. Because the density that can be sustained is highly variable, depending on snow conditions, mortality by starvation is expected. As overbrowsing cannot be demonstrated, except for limited areas inside deer yards (along main trails), this mortality is not related to chronic overpopulation and sufficient browse is still present. However, it is biologically inaccessible, because energy expenditure to get it is prohibitive due to extreme snow conditions. Moreover, the range can be protected from chronic overuse by periodic adverse snow conditions.

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