1976

Winter habitat selection by white-tailed deer Odocoileus virginianus in Point Pellee National Park, southwestern Ontario.

Thomas David. Nudds
University of Windsor

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WINTER HABITAT-SELECTION BY WHITE-TAILED DEER

(Odocoileus virginianus)

IN POINT PELEE NATIONAL PARK, SOUTHWESTERN ONTARIO

by

Thomas David Nudds

A Thesis
submitted to the Faculty of Graduate Studies
through the Department of
Biology in Partial Fulfillment
of the requirements for the Degree
of Master of Science at
The University of Windsor

Windsor, Ontario, Canada

1976
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ABSTRACT

WINTER HABITAT SELECTION BY WHITE-TAILED DEER
(Odocoileus virginianus)

IN POINT PELEE NATIONAL PARK, SOUTHWESTERN ONTARIO

by

Thomas David Nudds

A field experiment was designed to test the relative importance of structure-related vs. forage-related characteristics of winter habitats as determinants of habitat selection by white-tailed deer (Odocoileus virginianus) in Point Pelee National Park. Multivariate data analysis revealed that variables related to the vegetative physiognomy of 11 different habitats were superior to forage-related variables as predictors of habitat utilization by deer. Deer select habitats with significantly more dense foliage, exhibiting a form of physiological retreat from cold weather. It is suggested that deer select winter habitats with such specificity for purposes of thermoregulation and energy conservation. The small proportion of this type of habitat available for deer may create stress for female animals trying to meet two different metabolic energy demands: the maintenance of a homeostatic body temperature and the maintenance of a fetus.
Evidence of the interest shown by ecologists in the factors affecting the distributions of organisms, populations, and species in space and time can be found in the earliest natural history accounts of animal species. Until Hutchinson (1958) suggested that the niche could be viewed as an n-dimensional hypervolume enclosing the range of conditions under which the organism could successfully replace itself, the niche concept was only an intuitive idea of the "position" that an animal had in the environment. This intuitive concept, the way the organism lived with respect to its needs for nutrition, reproduction, protection and/or escape from extremes in temperature and predation is extremely important because it may be used to examine the interactions between an organism and the environment from the point of view of the organism (Maguire 1973).

The niche is the genetically determined capacity (range of tolerance) and pattern of biological response of an individual, population, or species to environmental conditions. Environmental conditions include all physical and biological characteristics of the surroundings in which a species, population, or individual lives and interacts. Habitat refers to some particular combination of environmental conditions.

When some measure of the biological response of an organism, population, or species to environmental conditions (e.g., its reproductive success or fitness) is plotted against a single environmental gradient, say, habitat type, a bell-shaped curve usually results. In a situation analogous to this, "tolerance"
curves for more than one environmental factor (variable) can be plotted in n-dimensional space, the addition of each new variable adding more axes and quantitative information about the nature of the habitats. Only a subset of the entire n-dimensional space is optimal for the organism concerned; those regions where its fitness is reduced are suboptimal.

Deer of the North American genus *Odocoileus* have been the subject of intensive field investigations into the nature of the factors affecting habitat selection. Much is known of the influences of many environmental variables on the distribution of deer, although in many cases their effects are reported independent of the effects of other habitat characteristics (e.g., Edwards 1956, Loveless 1964, 1967, Swift 1948). Most studies can be classified into one of two broad categories: those dealing with environmental factors related to physical conditions of the habitats such as snow depth, overstory crown closure, and topography, and those that deal with factors related primarily to forage availability, abundance, and nutritional quality. There is considerable difficulty in assigning relative importance to physical factors vs. diet-related characteristics as they relate to habitat selection by deer because they have not been assessed concurrently and tested satisfactorily (e.g., Anderson et al. 1972).

Deer are diet generalists (Westoby 1974, Freeland and Janzen 1974) and models of energy acquisition (MacArthur and Pianka 1966, Pulliam 1974) suggest that habitat selection by generalist foragers will be on the basis of habitat characteristics other than those related to forage abundance and availability. Other habitat
characteristics that may be influencing deer habitat selection can be designated structure-related variables.

Hirst (1975) has suggested that African ungulates in multi-species communities may select habitats on the basis of structural cues and forage within those patches in avoidance of competition. In accordance with the compression hypothesis (MacArthur and Wilson 1967, Schoener 1974), African ungulates display broad diet overlap and low habitat overlap. Member species of low-diversity ungulate communities in North America, or solitary, allopatric ungulate populations, may show habitat selection on the basis of structural cues for a fundamentally different reason.

During the winter, deer differentially expend energy on the maintenance of a homeostatic body temperature depending on the nature of the thermal regime immediately surrounding the animals (Moen 1967, 1968, 1973, 1976). Selection of habitats which reduce energy requirements for the control of body temperature means that, by the principle of energy allocation (Levins 1968), more energy is made available for other activities such as reproduction. Thus structural features of different habitats such as the density of the vegetation may serve as cues for habitat selection independent of any relationship these factors may have to other habitat components such as food availability and abundance.

The purpose of this study is twofold. I want to identify the habitat characteristics important as determinants of habitat selection by white-tailed deer (Odocoileus virginianus) and test the relative importance of forage-related vs. structure-related variables as predictors of habitat utilization. The hypothesis
being tested is that if deer select habitat on the basis of its shelter value during the winter (i.e., demonstrate a form of physiological retreat), then structure-related variables will be better predictors of habitat utilization than forage-related variables. Secondly, I want to discuss the low reproductive success of the Point Pelee deer herd (Henry 1972, Theberge 1975, Theberge and Oosenbrug 1975) in terms of the winter habitat niche and individual fitness.
STUDY AREA AND HABITATS

Point Pelee National Park, southwestern Ontario (Fig. 1), occupies a 1,554 ha sandspit extending 11.2 km into Lake Erie of which two-thirds is a deep water marsh (Appendix A). Upland areas of the park are characterized by sand dunes which vary in height from 4.5 m to 6.0 m above lake level (Maycock 1970).

The park contains a diverse array of habitat types. Eleven were subjectively chosen for examination on the basis of two criteria: they were as structurally diverse as possible, encompassing the entire seral stage range from recently abandoned farmland to mature forest, and they were known to be inhabited by deer for at least some portion of the year (Henry 1972, 1975, Theberge 1975, Theberge and Oosenbrug 1975). Deer occupy the full range of habitat types in spring, summer, and fall. The proximity to one another of many types of both structurally and floristically diverse habitats (Maycock 1970) and the relatively high deer density of approximately 5-6 animals per 100 ha of upland area (Theberge and Oosenbrug 1975) make the park an ideal "natural experiment" for studies of habitat selection by deer.

Four forest plots were chosen—one in each of four study grids (Appendix A). The study grids are named for prominent landmarks in their vicinity. Mature forests contained hackberry (Celtis occidentalis), red cedar (Juniperus virginianus), and red and black oaks (Quercus rubra and Q. velutina) which occur in patchy distributions. Other prominent tree species include white pine (Pinus strobus), black walnut (Juglans nigra), sugar maple (Acer saccharum), chokecherry
Figure 1. Map of Essex County, southwestern Ontario, showing the location of Point Pelee National Park.
(Prunus virginiana), and hop hornbeam (Ostrya virginiana). Common lower level woody species included chokecherry, gooseberry (Ribes sp.), and intermittently spaced saplings of most tree species. The forb and herb vegetation layer was composed of sweet cicely (Osmorhiza claytonii), herb robert (Geranium robertianum), false Solomon's seal (Smilicina racemosa), grasses (Graminae, mostly Poa sp.), and white avens (Geum canadense). Mature forests occur along the west side of the sandspit and occupy 46 percent of the upland area of the park.

Field study grids were areas that had been cleared for agricultural practices and since abandoned (Appendix A). Two of the field sites (CC and SH) are designated old fields and were replanted to white pine, red cedar, and honey locust (Gleditsia triacanthus) nine years previous to this study (Henry 1972). Naturally occurring woody species in the old fields were staghorn sumac (Rhus typhina), red cedar, and dogwood (Cornus sp.). Apple (Pyrus malus) remains in abandoned orchards. The most recently abandoned field site (CE) contained few trees, but young red cedar, white pine, hackberry, and staghorn sumac are encountered near ecotones. Grasses predominate in all of the field communities; the most commonly observed were members of the genera Bromus, Poa, and Agropyron. The CE field was composed chiefly of Agropyron repens and contained a greater proportion of grasses than the old fields, but a lower diversity of grass species. Herbaceous plant species are similar among the field sites and included goldenrods (Solidago sp.), mullein (Verbascum thapsus), milkweed (Asclepias sp.), poison ivy (Rhus radicans), asparagus (Asparagus asparagus), white
sweet clover (*Melilotus alba*), and thistles (*Cirsium sp.*). Abandoned farmland constitutes about 18 percent of the park upland.

The rush scrub (Appendix A) contained a characteristic ground cover of scouring rush (*Equisetum-hyemale*). The low canopy is composed almost exclusively of sumac and dogwood. Similar habitats are found in most low-lying, moist areas of the park. Although this particular site was dry throughout the winter, it was seasonally inundated. Areas of the park supporting dense rush growth occupy about 2 percent of the upland. One representative site was included in this study.

The sumac stand (Appendix A) is an abandoned field in an advanced seral stage. Woody species present were staghorn sumac, dogwood, and willows (*Salix sp.*), which occurred on the eastern border of the grid. The ground layers of vegetation are composed of plant forms with a short growth characteristic. Grasses predominated but herbaceous species present included tick-trefoils (*Desmodium sp.*) and goldenrods. Riverbank grape (*Vitis riparia*) was the common vine.

The eastern edge of the CC field adjacent to the marsh proper was subject to seasonal flooding and contained plant species typical of the marsh community. These were mainly cattails (*Typha sp.*), blue joint grass (*Calamagrostis canadensis*), and sedges (*Carex sp.*). Goldenrod, milkweed, and poison ivy were the dominant herbaceous species in the field-marsh ecotone.

Cedar habitats occupy a total of 16 percent of the upland area. The cedar savannas of east and west beaches are structurally similar; both are composed of red cedar or red cedar-common juniper (*Juniperus communis*) on flat, grassy sand beaches. The cedar forest
chosen for study (Appendix A) is an old orchard in an advanced stage of succession. Red cedar occurs in high densities, as do staghorn sumac, dogwood, and fragrant sumac (*Rhus aromatica*). Numerous openings in the low canopy accommodate a dense growth of herbaceous vegetation comprised of a high proportion of grasses (primarily *Poa sp.*), poison ivy, tick-trefoil, milkweed, goldenrod, and asters (*Aster sp.*). Common vines are poison ivy, riverbank grape, and Virginia creeper (*Parthenocissus cinquefolia*).

Table 1 lists the areas of each of the habitats within the study grids.
Table 1. Summary of the sampling effort in eleven habitats studied in Point Pelee National Park, winter, 1975-76. For study grid names, refer to Appendix A.

<table>
<thead>
<tr>
<th>STUDY GRID</th>
<th>HABITAT</th>
<th>AREA OF STUDY GRID (ha)</th>
<th>NUMBER OF TRANSECTS</th>
<th>LENGTH OF TRANSECTS (m)</th>
<th>NUMBER OF STUDY PLOTS</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC</td>
<td>Forest</td>
<td>37.5</td>
<td>5</td>
<td>725</td>
<td>28</td>
</tr>
<tr>
<td>CC</td>
<td>Field</td>
<td>43.8</td>
<td>3</td>
<td>725</td>
<td>28</td>
</tr>
<tr>
<td>CC</td>
<td>Marsh</td>
<td>15.0</td>
<td>3</td>
<td>325</td>
<td>13</td>
</tr>
<tr>
<td>SH</td>
<td>Forest</td>
<td>10.0</td>
<td>2</td>
<td>375</td>
<td>15</td>
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<td>6.3</td>
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<tr>
<td>CE</td>
<td>Field</td>
<td>18.8</td>
<td>4</td>
<td>925</td>
<td>37</td>
</tr>
<tr>
<td>CE</td>
<td>Rush Scrub</td>
<td>11.3</td>
<td>3</td>
<td>300</td>
<td>12</td>
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<tr>
<td>CE</td>
<td>Sumac Stand</td>
<td>12.5</td>
<td>2</td>
<td>450</td>
<td>19</td>
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<td>00</td>
<td>Forest</td>
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<td>875</td>
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<tr>
<td>00</td>
<td>Cedar Forest</td>
<td>37.5</td>
<td>5</td>
<td>825</td>
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<tr>
<td>TOTAL</td>
<td></td>
<td>274.0</td>
<td>39</td>
<td>6375</td>
<td>256</td>
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METHODS

All habitat measurements were taken on transects set out to traverse as many structurally diverse habitats as possible. Three groups of 5 east-west transects and one group of 2 east-west transects, running from the west beach to the marsh or the wet forest, were established as statistical replicates (Appendix A). Within each grid, transects were spaced 50 m apart. Study plots were established at 25-m intervals along each transect and marked with a wooden stake. The entire field study sampled 274 ha of upland area with 6,375 m of transects and 256 study plots. Table 1 summarizes the sampling effort in each of the eleven habitats investigated.

Measurement and Significance of Habitat Variables

Twenty-one variables were measured, or derived from measures, of habitat characteristics chosen according to the criteria outlined by Green (1971). Most importantly, all measured characteristics in the analyses have been shown in the literature as having an effect on deer, or have a reasonable theoretical possibility of effect. As well, in order to describe the winter habitat niche of deer in terms of the n-dimensional model of Hutchinson, as many variables as are relevant to the ecology of deer, and as are possible to measure, should be included, and all should be independent of one another (Pianka 1974: 192).

The factors chosen for measurement can account for deer preference or avoidance of habitats by virtue of their relationship to specific vital functions such as feeding or thermoregulation.
The 21 variables can thus be divided into two groups: those related to structural attributes of the habitat (14) and those related to forage characteristics (7). Although these groups of variables may not necessarily be mutually exclusive, I employed this distinction in order to attempt to assess the relative importance of cover vs. food availability as determinants of habitat selection.

Structure-related variables can be categorized as to those dealing with understory vegetation density and physiognomy and those measuring the overstory crown cover. Moen (1967, 1973, 1976) has demonstrated the effects of shelter requirements on the thermoregulating capacity of white-tailed deer. Heat loss is greater in open, exposed habitats. Stevens and Moen (1970) have suggested that the rate of heat loss from an animal will vary with wind velocity and the position of the animal with respect to the density of the vegetation. The winter "yarding" areas of northern Michigan deer herds are generally in areas of dense foliage cover such as white cedar (Thuja occidentalis) swamps (Verme 1965, Ozoga 1968, Ozoga and Gysel 1972). Selection of dense patches of vegetation in the winter when deep snow prohibits easy movement may also be an evolutionary behavioural response to predation pressure. Foliage density and how it is apportioned to different heights above the ground may thus be important determinants of habitat selection by white-tailed deer.

The structural configuration of the understory vegetation was quantified using an adaptation of the profile board technique (MacArthur and MacArthur 1961). The board is illustrated in Figure 2. Measurements were taken starting well after leaf fall
Figure 2.  A. The vegetation profile board showing construction.
B. The profile board in the rush scrub habitat, Point Pelee National Park.
in late autumn and continued into late January, 1976. The board was read in a randomly chosen compass direction from the centre of each study plot at a standard distance of 15 m. "Calibration" of the board showed this to be the optimum distance for discrimination among habitat types. At distances less than 15 m, the board was almost always completely visible; at distances greater than 15 m, the board was almost always completely obscured by vegetation, allowing no discrimination among habitat types. The proportion of the board surface covered by vegetation at each of 4, 0.5-m intervals was recorded as a single digit corresponding to a range of quintiles. These layers paralleled the natural layers of vegetation in each of the habitat types examined. The layer from 0.0 to 0.5 m approximates the height of the flattened grasses of open field and marsh habitats, the forb layer constitutes the height range from 0.5 to 1.0 m, the low canopy of sumac and dogwood-dominated habitats extends from 1.0 to 1.5 m, and the vegetation associated with saplings and the lower branches of older trees generally occurred from 1.5 to 2.0 m. The variables measured at each plot were as follows:

$L_i$ - The density of the vegetation in the $i$th layer, where $i = 1, 2, 3, 4$.

$\sum_{i=1}^{4} L_i$ - The total amount of vegetation present. Integrating across the face of the board produces data analogous to the "cover" estimates obtained by earlier workers using the density board (DeVos and Mosby 1971: 142).

$\text{VEGHGT}$ - The maximum height of the vegetation at the plot centre was measured from the face of the board to
the nearest 0.25 m. Values ranged from 0.25 m to 2.0 m for early to mid-successional stages. Plots in older-aged stands and mature forests with high canopies were recorded as 3.0 m.

FHD - The understory foliage height diversity, a measure of the complexity of the foliage structure, was calculated by substituting the proportion, $p_i$, of vegetation in each layer into $\frac{1}{\sum p_i^2}$ (Levins 1968).

The arboreal component of cover in deer habitats may be important as a cue for habitat selection for several reasons. Forage production and its nutritional quality have been shown to be influenced by overstory crown closure (Bailey 1967, Behrend and Patric 1969, Halls and Alcaniz 1968, Halls and Epps 1969) and canopy type, i.e., coniferous or deciduous (Halls 1974). Moen (1968) demonstrated that the thermal regimes beneath different canopy types will vary, conceivably influencing thermoregulation by deer. Canopy types also differ in their abilities to intercept snow and prevent its accumulation on the ground (Moen 1973: 72) where it could otherwise impede travel or make potential food resources unavailable. Deer yards in northern Michigan are characterized by a high proportion of coniferous crown cover (Ozoga 1968, Ozoga and Gysel 1972).

The physical structure of the arboreal portions of deer habitats, and related characteristics of the habitats, were measured from early February to mid-March, 1976. The following variables were quantified:
TREES - The total number of trees of all species measuring over 5.0 cm in circumference at breast height within an area described by a circle with radius 5.0 m and having centre located at the study plot centre.

BASAREA - The basal area of all the trees on the plot was found by measuring the circumference of each tree at breast height, converting this measure to basal area, and summing these values.

CONIFBA - The total basal area contributed by coniferous tree species.

DECIDBA - The total basal area contributed by deciduous tree species.

RATIO C/D - The ratio of coniferous to deciduous basal area.

CANOPY - The percentage of the total sky obscured by vegetation. Replicate vertical pictures of the canopy were taken at each station from a height of 1.0 m above the ground. The prints were examined using a transparent plastic overlay marked in 100 equal-area rectangles. The number of rectangles having greater than 50 percent of the sky obscured by vegetation were counted and expressed as a percentage of the total number of rectangles.

SNOW - Snow depth was measured on three occasions from late January to mid-February, 1976, when snow depths were subjectively judged to be greatest and have potentially more effect on deer. Five measurements were taken on every occasion at all stations.
Except for SNOW, all of the above variables were measured by stratified random sampling within habitat types. Time limitations and costs prohibited the measurement of all factors at all 256 plots. A minimum of 2 plots per transect and a minimum of 10 plots per habitat were selected and measured for each variable.

Some evidence suggests that the abundance, availability, and nutritional quality of the understory vegetation may influence deer choice of habitats (Patton 1974, Segelquist and Green 1968, Verme 1965). Often deer habitats are selected on the basis of the abundance of some readily harvested resource relative to resource availability in other habitats. For example, Segelquist and Green (1968) and Harlow et al. (1975) have found differential use of habitats coinciding with oak mast abundance. Habitat switching from hardwoods to those with abundant herbs and evergreen browse may occur when oak mast is scarce.

During the winter, much of the forb and grass resources become covered with snow and are unavailable, or are of lower nutritional quality (Short 1975, Bobek et al. 1973). An evolutionary response to predictable, seasonal fluctuations in food abundance or nutritional quality of food resources may be diet-switching to more energetically efficiently harvested resources. Shifts in the use of major forage classes (i.e., browse, forbs, and grass) that are related to their relative availability in different seasons appears to be the rule in most North American ungulates (Hoefs 1974, Miller 1974, Peek 1974, Smith 1952, Sossaman and Weber 1974).

The diversity of potential food resources may also be a factor influencing deer selection of habitat types. Freeland and
Janzen (1974) suggested that ruminating herbivores are diet generalists and seasonal diet shifts are made with relative ease because selection for strains of rumen bacteria able to digest new plant compounds can occur rapidly. To "condition" the rumen microflora, deer must be sampling a diverse set of potential food resources constantly.

Forage-related variables were measured on randomly selected subsets of study plots within habitats from late November, 1975, to January, 1976. I utilized the line-intercept method of Canfield (1941). A 15-m nylon line marked in decameters was stretched in a randomly selected compass direction from the centre of the study plot and pegged to the ground (Fig. 3). All vegetation present from the ground up to a height of 2.0 m (all forage available and within reach of deer) was tallied by species once for every 1-decameter interval intercepted. The method estimates ground cover by species; it overestimates the abundance or biomass of small, solitary, single-stemmed plants and underestimates the biomass of layered, particularly woody browse, species. Nevertheless, the bias affects readings in all habitats in the same manner and statistical comparisons of the forage-related variables among habitats are warranted.

The diet-related variables included in the analysis are as follows:

FORAGE - The total amount of forage present, calculated by summing the individual plant species abundances.

BROWSE - The abundance of browse, calculated by summing the abundances of individual woody or evergreen browse species.

BSD - The diversity of browse species was calculated by
Figure 3. Schematic representation of the line-intercept technique used to sample understory plant species abundance at Point Pelee National Park.
substituting the proportion, \( p_i \), of the total browse
assigned to the \( i \)th browse species into \( \frac{1}{\sum p_i^2} \) (Levins 1968).

**PBROWSE** - The proportion of the total available forage
contributed by hardwood or evergreen browse species.

**PFORBS** - The proportion of the total available forage
contributed by herbaceous plant species.

**PGRASS** - The proportion of the total available forage
contributed by grass species.

**OAK MAST** - Oak mast was measured in the forest habitats only.
On 10 randomly selected plots within each forest
site, the forest floor litter was gathered and the
ground scraped to a depth of about 5.0 cm inside
a 1-m\(^2\) wooden frame. The weight of the acorn
fragments separated from the leaf litter was
converted to g/ha and used as an indicator of
oak mast productivity among the 4 forest plots.

**Measurement of Habitat Utilization Variables**

Habitat utilization was measured in two ways. Pellet groups
(Neff 1968) lying within 1 m of either side of the transect were
recorded from early December until early March, 1976 during the
course of taking other field measurements. Fresh track counts
(McCaffery 1976) were recorded from first snowfall (about mid-
December, 1975) until snow conditions no longer allowed the
collection of these data (about late February, 1976). Track counts
were also conducted during the execution of other field work,
but several field trips were undertaken for the express purpose
of counting tracks.

As I walked the transects from east to west, all tracks intersecting the transect segment joining two study plots and all pellet groups lying between two plots were recorded as being associated with the next study plot. This convention was adopted due to the paucity of data accumulated within a reasonable radius of individual study plots. Pellet groups were removed or scattered after counting to avoid counting them twice.

The measurement of so many habitat features meant that data had to be collected over the course of the entire winter. It was thus impossible to obtain simultaneous measures of all habitat variables. Neither are measures of habitat utilization coincident with measurements of habitat characteristics. In addition, the sampling schedule could not account accurately for the time of dropping of pellet groups. Pellet groups were certainly covered by snowfalls between sampling periods and not counted until thaw periods. Thus, habitat utilization data (particularly pellet group distributions) reflect habitat use averaged over the entire winter. No attempt is made to distinguish among early, mid-, and late winter use of habitats for these reasons.

Statistical Analysis

All variables were appropriately transformed where such transformations would correct for non-normal distributions of the variates. Variables measured by counting were square root-transformed using $\sqrt{x + 0.5}$ and data expressed as proportions were arcsine-transformed by $\sin^{-1}x$ before subsequent data analysis was performed (Sokal and Rohlf 1969).
Some variables were measured on a subset of plots within habitat types. As a result, complete sets of independent variables for each of the 256 study plots are lacking. In order to obtain sufficient numbers of observations with a complete set of associated variables for anticipated multivariate analyses, I combined data by calculating means for each variable by transects within habitats. The resultant sample sizes, corresponding to the number of transects in each habitat studied, are given in Table 1.

Description of the winter habitat niche of deer on orthogonal axes required that the 21 quantified habitat characteristics be independent of one another. In actual practice, most measurable features of deer microhabitats are highly correlated (Appendix B). In order to satisfy the conditions for description of the habitat niche, and to simplify later analyses, I utilized principal components analysis (PCA). PCA yields orthogonal, linear combinations of the original variables by subjecting the array of points in 21-space to a series of rotations that determine the interrelationships among the original variables and then hierarchically orders the extracted new variables, the principal components (PCs), in terms of their variances (Harris 1975, Pielou 1969, Poole 1974). PC$_1$ is thus the linear combination of the original variables which maximally discriminates among the eleven habitats, given the 21 habitat features measured. PC$_2$ is the second best discriminator, and so forth.

PCs partition the total variance among the original variables into $x$ additive components and each PC "accounts for" a certain proportion of the variation among the original variables. PCA will
extract PCs until all of the variation among the original variables is accounted for. Tests of significance exist to determine how many PCs should be extracted (Harris 1975), i.e., how many PCs are "real" and how many of the remaining PCs explain error variation due to sampling fluctuations. One approach is to examine the cumulative percentage of variation explained by the extracted PCs and delete from further analysis those with the smallest variances (Hirst 1975). This procedure, the one used in this study, is subject to the restriction that each PC retained for subsequent analysis be biologically interpretable.

The use of PCA simplifies a problem encountered by biologists using multiple linear regression analysis (MRA). Since orthogonal PCs are used as variables in MRA, $R^2$ is partitioned into $x$ uncorrelated sources of predictability and thus analysis using PCs rather than the 21 original variables can be performed with a minimal loss of information.

I performed stepwise multiple linear regression of the habitat utilization variables against the values of the principal components extracted from the original 21 variables. All subsequent data analysis was also carried out using the PCs as independent variables. One-way ANOVAs and Duncan's multiple range test were performed in order to identify the patterns of variation in habitat characteristics and habitat utilization among the various habitat types.

All statistical analysis was performed using the Statistical Analysis System (Barr and Goodnight 1972) on an IBM 360 computer in the Computer Centre of the University of Windsor.
RESULTS

A summary of deer use of habitats based on two measures of utilization are given in Table 2. The basic pattern is essentially the same as that reported by Henry (1975) and Theberge and Qosenbrug (1975). Track counts per 25-m transect segment indicate that deer use six of the eleven habitats in winter. In decreasing order of intensity of use, they are the cedar forest, the sumac stand, the rush scrub, the CE forest, the OO forest, and the CE field (F=47.1, p<0.0001). Duncan's multiple range test indicates that each habitat receives significantly different use. Use of the CE field was not significantly different from no use (p<0.05) and tracks found on transects in this habitat were located near ecotones.

Pellet groups per 25-m transect segment were significantly different among habitats (F=58.3, p<0.0001) indicating differential habitat use, but only three habitats recorded the presence of pellets. Two of these, the sumac stand and the rush scrub, did not receive significantly different use as determined by Duncan's multiple range test. The cedar forest received significantly greater use than the other habitats recording pellet groups present. The two northerly study grids (CC and SH) had no deer sign present at any time throughout the winter.

Seven principal components were extracted from the original data matrix. The first four PCs accounted for 75 percent of the variation among the original variables and were retained for later analysis. Table 3 shows the results of the subsequent principal components analysis which was restricted to extracting only the
Table 2. Summary of habitat utilization by deer in Point Pelee National Park, winter, 1975-76. The values of TRACKS and PELLETS have been square-root transformed (see text).

<table>
<thead>
<tr>
<th>HABITAT</th>
<th>TRACKS (per 25-m)</th>
<th>PELLETS (per 25-m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC Forest</td>
<td>0.71 ± 0.00</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>CC Field</td>
<td>0.71 ± 0.00</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>CC Marsh</td>
<td>0.71 ± 0.00</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>SH Forest</td>
<td>0.71 ± 0.00</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>SH Field</td>
<td>0.71 ± 0.00</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>CE Forest</td>
<td>1.80 ± 0.29</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>CE Field</td>
<td>0.91 ± 0.15</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>CE Rush Scrub</td>
<td>2.13 ± 0.70</td>
<td>1.03 ± 0.30</td>
</tr>
<tr>
<td>CE Sumac Stand</td>
<td>2.67 ± 0.17</td>
<td>1.11 ± 0.37</td>
</tr>
<tr>
<td>OO Forest</td>
<td>1.52 ± 0.29</td>
<td>0.71 ± 0.00</td>
</tr>
<tr>
<td>OO Cedar Forest</td>
<td>3.43 ± 0.23</td>
<td>2.35 ± 0.24</td>
</tr>
</tbody>
</table>
Table 3. Factor structure for the original 21 habitat variables showing the variables contributing to the formation of each principal component. * indicates important variables contributing substantially to the PC; † indicates marginally important variables.

<table>
<thead>
<tr>
<th>HABITAT VARIABLES</th>
<th>PC₁</th>
<th>PC₂</th>
<th>PC₃</th>
<th>PC₄</th>
</tr>
</thead>
<tbody>
<tr>
<td>L₁</td>
<td>-0.16</td>
<td>0.81*</td>
<td>-0.05</td>
<td>-0.44</td>
</tr>
<tr>
<td>L₂</td>
<td>-0.06</td>
<td>0.91*</td>
<td>-0.07</td>
<td>-0.08</td>
</tr>
<tr>
<td>L₃</td>
<td>-0.03</td>
<td>0.92*</td>
<td>0.02</td>
<td>0.27</td>
</tr>
<tr>
<td>L₄</td>
<td>0.03</td>
<td>0.89*</td>
<td>-0.14</td>
<td>0.18</td>
</tr>
<tr>
<td>TOTVEG</td>
<td>-0.06</td>
<td>0.96*</td>
<td>-0.05</td>
<td>-0.03</td>
</tr>
<tr>
<td>FHD</td>
<td>0.08</td>
<td>0.16</td>
<td>0.20</td>
<td>0.79*</td>
</tr>
<tr>
<td>VEGHGT</td>
<td>0.88*</td>
<td>0.26†</td>
<td>-0.22</td>
<td>0.18</td>
</tr>
<tr>
<td>TREES</td>
<td>0.07</td>
<td>0.54†</td>
<td>0.10</td>
<td>0.29</td>
</tr>
<tr>
<td>BASAREA</td>
<td>0.89*</td>
<td>-0.19</td>
<td>-0.20</td>
<td>0.04</td>
</tr>
<tr>
<td>CONIFBA</td>
<td>0.48</td>
<td>0.03</td>
<td>-0.55†</td>
<td>0.18</td>
</tr>
<tr>
<td>DECIDBA</td>
<td>0.82*</td>
<td>-0.23</td>
<td>0.00</td>
<td>-0.02</td>
</tr>
<tr>
<td>CANOPY</td>
<td>0.61*</td>
<td>-0.04</td>
<td>-0.60*</td>
<td>-0.04</td>
</tr>
<tr>
<td>SNOW</td>
<td>-0.58†</td>
<td>0.17</td>
<td>0.15</td>
<td>-0.45</td>
</tr>
<tr>
<td>RATIO C/D</td>
<td>0.03</td>
<td>0.41</td>
<td>-0.68*</td>
<td>-0.11</td>
</tr>
<tr>
<td>BSD</td>
<td>0.68*</td>
<td>0.56†</td>
<td>0.06</td>
<td>0.03</td>
</tr>
<tr>
<td>BROWSE</td>
<td>0.33</td>
<td>0.75*</td>
<td>0.28</td>
<td>-0.29</td>
</tr>
<tr>
<td>OAK MAST</td>
<td>0.22</td>
<td>-0.15</td>
<td>-0.62*</td>
<td>-0.25</td>
</tr>
<tr>
<td>FORAGE</td>
<td>-0.31</td>
<td>0.47</td>
<td>0.46</td>
<td>-0.43</td>
</tr>
<tr>
<td>PBROWSE</td>
<td>-0.69*</td>
<td>-0.52†</td>
<td>0.08</td>
<td>0.07</td>
</tr>
<tr>
<td>PFORBS</td>
<td>0.78*</td>
<td>-0.16</td>
<td>-0.43</td>
<td>0.00</td>
</tr>
<tr>
<td>PGRASS</td>
<td>-0.91*</td>
<td>-0.18</td>
<td>0.24</td>
<td>-0.04</td>
</tr>
</tbody>
</table>
first four PCs (i.e., only four PCs were allowed to partition the total variance among the original 21 variables). The resulting factor structure (Table 3) indicates original variables which are combined to form the new variables.

PC₁ accounts for 36.6 percent of the variation among the original variables (Table 4) and the first principal axis describes a continuum of habitats from short vegetation, low basal area (few trees), deep snow, and relatively less browse and forbs than grass to habitats with few grasses, increased browse and forb abundance, increased basal area, and greater overstory crown closure (Fig. 4). This parallels a succession gradient from open fields to mature forests.

The second principal axis is a measure of vegetation density and browse abundance (Table 3). Habitats are ranked along a gradient from low, open, sparsely vegetated fields and open understory forests with little available browse through several seral stages to the densely packed vegetative layers of the cedar forest habitat which, because the bulk of the vegetation is near the ground, also has a greater amount of browse within reach of deer (Fig. 4). The horizontal density of the vegetation in the understory of the forests is not significantly different from that of open fields during the winter. Mid-seral stages possess the greatest vegetation densities from 0.0 to 2.0 m. This principal component accounts for 38.8 percent of the total variance among the original 21 variables.

The third principal component accounts for 14.3 percent of the variance and describes habitats on an axis of increasing
Table 4. The percentage of the total variance among the original variables accounted for by each of the four principal components.

<table>
<thead>
<tr>
<th>PRINCIPAL COMPONENT</th>
<th>VARIANCE</th>
<th>%</th>
<th>CUMULATIVE %</th>
</tr>
</thead>
<tbody>
<tr>
<td>PC₁</td>
<td>5.82</td>
<td>36.6</td>
<td></td>
</tr>
<tr>
<td>PC₂</td>
<td>6.17</td>
<td>38.8</td>
<td>75.4</td>
</tr>
<tr>
<td>PC₃</td>
<td>2.26</td>
<td>14.3</td>
<td>89.3</td>
</tr>
<tr>
<td>PC₄</td>
<td>1.63</td>
<td>10.3</td>
<td>100.0</td>
</tr>
</tbody>
</table>
Figure 4. A. Histograms showing the ranking of habitats along the first principal axis, a measure of structural changes associated with advances in seral age, in order of increasing seral age. The habitats are coded as follows: A, D, F, J, mature forests; B, E, old fields; C, marsh; G, recently abandoned farmland; H, rush scrub; I, sumac stand; and K, cedar forest. Solid lines below histograms indicate and/or join all habitats used by deer. Habitats recording pellet groups were fewer and are indicated by a dashed line. B. Habitats are arranged along the second principal axis, a measure of horizontal vegetation density, from those with low vegetative cover to those with greater shelter value for deer.
canopy cover, increasing coniferous basal area relative to deciduous basal area, and decreasing oak mast productivity. PC4 accounts for the remaining 10.3 percent of the variation in the original data and is mainly a measure of habitat structural complexity (FHD).

Each principal component is treated in the analysis as a predictor variable of habitat utilization by deer since they are linear combinations of several related habitat characteristics. Table 5 shows the means and standard deviations of the principal components for each of the eleven habitats.

One-way ANOVAs indicate the habitats are significantly different with respect to the values of PC1 (F=30.2, p<0.0001) and PC2 (F=19.4, p<0.0001). Duncan's multiple range test demonstrates that the mature forests and the cedar forest are not significantly structurally different with respect to total basal area, canopy cover, snow depth, and forage class composition. The sumac stand, rush scrub, and old fields are likewise similar, and the abandoned farmland (CE field) and marsh are not significantly different. However, the significant differences among the habitats with respect to horizontal vegetation density are attributed to differences between the cedar forest, sumac stand, and rush scrub, the old and recently-abandoned fields, the CE forest, and the marsh and the remaining three forests.

Horizontal vegetation density was the most important determinant of deer habitat utilization, explaining 40 percent of the variation in track counts among habitats and 51 percent of the variation in pellet group counts among habitats (Table 6). In both MRA models, PC1 (structural changes associated with advancing seral age) was
Table 5. Mean values of the principal components by habitat type.

<table>
<thead>
<tr>
<th>HABITAT</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
</tr>
</thead>
<tbody>
<tr>
<td>CC Forest</td>
<td>0.83 ± 0.58</td>
<td>-0.60 ± 0.34</td>
<td>-0.46 ± 0.73</td>
<td>0.24 ± 0.64</td>
</tr>
<tr>
<td>CC Field</td>
<td>-0.75 ± 0.03</td>
<td>0.20 ± 0.18</td>
<td>-0.10 ± 0.33</td>
<td>-0.24 ± 0.64</td>
</tr>
<tr>
<td>CC Marsh</td>
<td>-1.69 ± 0.10</td>
<td>-0.56 ± 0.35</td>
<td>0.14 ± 0.06</td>
<td>1.23 ± 0.13</td>
</tr>
<tr>
<td>SH Forest</td>
<td>0.84 ± 0.31</td>
<td>-1.08 ± 0.40</td>
<td>-2.52 ± 1.63</td>
<td>0.73 ± 0.09</td>
</tr>
<tr>
<td>SH Field</td>
<td>-0.61 ± 0.47</td>
<td>0.42 ± 0.70</td>
<td>0.23 ± 0.48</td>
<td>0.36 ± 0.20</td>
</tr>
<tr>
<td>CE Forest</td>
<td>0.68 ± 0.28</td>
<td>-1.12 ± 0.57</td>
<td>0.95 ± 0.41</td>
<td>-0.40 ± 1.47</td>
</tr>
<tr>
<td>CE Field</td>
<td>-1.68 ± 0.07</td>
<td>-0.34 ± 0.04</td>
<td>-0.29 ± 0.20</td>
<td>-0.11 ± 0.33</td>
</tr>
<tr>
<td>CE Rush</td>
<td>-0.32 ± 0.65</td>
<td>1.43 ± 0.84</td>
<td>-0.50 ± 1.00</td>
<td>-1.59 ± 0.94</td>
</tr>
<tr>
<td>CE Scrub Stand</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CE Sumac</td>
<td>-0.05 ± 0.30</td>
<td>0.91 ± 0.39</td>
<td>1.73 ± 0.06</td>
<td>1.27 ± 0.92</td>
</tr>
<tr>
<td>OO Forest</td>
<td>0.74 ± 0.21</td>
<td>-0.35 ± 0.31</td>
<td>0.70 ± 0.29</td>
<td>-0.55 ± 0.95</td>
</tr>
<tr>
<td>OO Cedar Forest</td>
<td>0.68 ± 0.16</td>
<td>1.59 ± 0.17</td>
<td>-0.46 ± 0.35</td>
<td>0.52 ± 0.43</td>
</tr>
</tbody>
</table>
Table 6. Regression models produced by stepwise multiple linear regression.

<table>
<thead>
<tr>
<th>DEPENDENT VARIABLE</th>
<th>INDEPENDENT VARIABLES ENTERED IN MODEL</th>
<th>IMPROVEMENT IN $R^2$</th>
<th>F-value</th>
<th>SIGNIFICANCE LEVEL</th>
</tr>
</thead>
<tbody>
<tr>
<td>TRACKS</td>
<td>$PC_2$</td>
<td>0.40</td>
<td>18.58</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>$PC_1$</td>
<td>0.51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PELLETS</td>
<td>$PC_2$</td>
<td>0.51</td>
<td>24.11</td>
<td>0.0001</td>
</tr>
<tr>
<td></td>
<td>$PC_1$</td>
<td>0.57</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
the next best predictor of habitat use, increasing $R^2$ by 11 percent in the TRACKS model and increasing $R^2$ in the PELLETS model by 6 percent. Both 2-variable models are highly significant (TRACKS, $F=18.6$, $p<0.0001$; PELLETS, $F=24.1$, $p<0.0001$) and both variables are significant in each model ($0.0001<p<0.03$).

The linear relationships between TRACKS and $PC_1$ and $PC_2$ are shown in Figure 5. TRACKS and $PC_1$ (Fig. 5B) are marginally significantly correlated ($r=0.32$, $p<0.04$) but TRACKS and $PC_2$ (Fig. 5A) are highly correlated ($r=0.63$, $p<0.0001$). In addition, PELLETS is not correlated with $PC_1$, but is significantly related to $PC_2$ ($r=0.72$, $p<0.001$). The remaining PCs are not correlated with either TRACKS or PELLETS and together explain less than 3 percent of the variation in TRACKS among habitats and less than 5 percent of the variation in PELLETS among habitats.
Figure 5. A. The relationship between track density and PC2 for eleven habitats in Point Pelee National Park, winter, 1975-76. The correlation is highly significant ($r=0.63, p<0.0001$). Habitats are coded as in Figure 4. B. The relationship between track density and PC1, which is marginally significant ($r=0.32, p<0.04$).
DISCUSSION

Maguire (1973) modelled niches as hypervolume space with internal structure in addition to boundaries, sizes, shapes, positions, and overlaps. This extension of the niche model considers species response levels inside the tolerance limits of the niche. The tolerance limits of the white-tailed deer winter habitat niche are defined by the outer isopleths of Figures 6A and 7A. Within these niche boundaries, deer display differential responses to various combinations of environmental conditions (i.e., habitats). Since the winter habitat niche of deer is best described on two axes (Fig. 6 and 7), deer response to each of these prime environmental factors is discussed separately.

The most important variable affecting deer choice of habitats is the second principal component which measures vegetation density. Both track counts and pellet group densities are significantly correlated with PC2. Deer do not make use of old fields, recently abandoned farmland, marshes, and open-understory forests at the north end of the park. Heavy use is made of the cedar forest, sumac stands, and wet, rush scrub habitats. The two southerly forest plots (00 and CE) recorded track densities, but these habitats were adjacent to heavily used, densely-structured stands of vegetation. Only the edge of the recently abandoned farmland was visited by deer, and then only infrequently. The few study plots on ecotones did not permit a statistical evaluation of the "edge effect", but examination of the data suggests that they were not used more than homogeneous habitat types. One might predict, on
Figure 6. A. The arrangement of the 6 habitats recording track densities on the first two orthogonal niche axes. Isopleths of track density indicate relative use of habitats within the total winter habitat niche of white-tailed deer. Isopleths are drawn at 0.50-unit intervals (see Table 2). Habitats are coded as in Figure 4.

B. A three-dimensional representation of the total winter habitat niche of deer at Point Pelee National Park as estimated by the distribution of track densities. This figure is implicit in Figure 6A.
Figure 7. A. Similar to Figure 6A, except that the shape of the niche is based on habitat utilization as indicated by pellet group distribution and densities. B. A three-dimensional representation of the figure implicit in Figure 7A.
the basis of the similarity of the vegetation density in the rush
scrub, sumac stand, and old field habitats (Table 5), that the old fields
would be used by deer, but distance to the old fields from the prime
winter habitats precluded their use. Deer use of suboptimal habitat
decreases with distance from habitats providing prime shelter
(Cahill 1965).

Deer exhibit a lower tolerance level for vegetation density
but are insensitive to high levels of vegetation density as determined
by track counts (Fig. 5A). Pellet group densities were also positively
related to vegetation density. Presumably, however, vegetation
density could reach an upper tolerance limit for deer to the
point where they are unable to manoeuvre through it. (Deer skirt
very dense thickets of sumac and dogwood in the cedar forest.)
The isopleths of Figures 6A and 7A are thus drawn to indicate the
possibility of sharp truncation of the habitat niche at extremely
high levels of vegetation density.

The relationship between track densities and pellet group densities
and PC1, a linear combination of variables which collectively
describe structural habitat changes associated with increased seral
age, is marginally significant in the first case and not significant
in the latter. Figures 4A and 5B show that most deer tracks are
found in habitats with low, closed canopies, tall vegetation, many
trees of small diameter, and similar contributions by all forage
classes to total forage abundance. In addition, pellet groups are
only found in mid-aged seral stage habitats. The northerly forest
sites (CC and SH) are at the extreme end of the seral stage continuum;
this fact, combined with their distance from the prime winter habitats,
contribute to their disuse by deer. At the other extreme, open habitats with little vegetation of shelter value for deer (i.e., low values of PC1 indicating little canopy cover, few trees, and an abundance of grass) receive no use. The winter habitat niche of deer has more distinct upper and lower limits for values of PC1, and deer are generally associated with mid-aged seral stages as depicted in Figure 4 (Verme 1965).

The important predictor variables of habitat use by deer in Point Pelee are those related to structural features of the habitats. This finding supports the hypothesis of habitat selection primarily on the basis of thermal-regulatory considerations, and not due to selection for food resource abundance. Forage-related characteristics, however, are inextricably related to structural features of the habitats (Appendix B) but otherwise are not good predictors of habitat use. For example, BROWSE and TOTVEG are highly correlated (r=0.63, p<0.01), but the measured increase in browse abundance in mid-aged seral stages is a direct result of increased "layering" of browse food resources in dense, uniformly structured habitats.

This conclusion is further supported by some anecdotal evidence based on observations of deer feeding habits in habitats of differing structural attributes. Red cedar is high on the list of "preferred" deer foods at Point Pelee. Its heavy use in the cedar forest I studied has been attributed to depleted range conditions (Henry 1972), yet on open beach cedar savannah habitats, red cedar is not eaten and the habitats are rarely used by deer during the winter (Henry 1972, Theberge and Oosenbrug 1975). If habitat selection were on the basis of forage availability, the red cedar in the beach habitats
should have been utilized during the winter. A more plausible explanation follows. The low, open vegetative physiognomy of the beach savannas is not attractive to deer during the winter because the structure of the vegetation is not sufficient to meet deer needs for maintaining homeostatic body temperatures. Deer at Point Pelee are habitat specialists during the winter but forage within habitats in a fine-grained manner (i.e., take foods in proportion to their relative availability). This is the general pattern of diet selection by generalist herbivores such as deer, although it is not always stated in those explicit terms (e.g., Allen 1968, Murphy and Noble 1972, Sossaman and Weber 1974). The high degree of use of red cedar in the cedar forest may thus be a simple consequence of its greater relative abundance in that habitat.

Point Pelee deer execute a common form of physiological retreat not unlike that demonstrated by more northern populations. Verme (1965), Ozoga (1968), and Ozoga and Gysel (1972) have observed deer use of coniferous cover in northern Michigan during the winter. Deer movements in and out of white cedar swamps is coincident with changes in microclimate and deer forage in surrounding upland hardwoods during milder periods of the winter. Otherwise, animals remain in dense vegetation for days or weeks, often depleting available coniferous browse and forsaking abundant hardwood browse in exposed upland habitat.

Intensive use of the three densely-structured habitats at Point Pelee (those with both track and pellet deer sign present) and less intensive use of the two adjacent hardwood forests (only track sign present) indicates that deer may be making similar foraging
trips into the hardwood stands. Although the winter climate of southwestern Ontario is not comparable to the harshness of the northern Michigan winters, the topography and the geographical situation of the peninsular sandspit (Fig. 1) with respect to the prevailing winds may produce chill factors which would cause deer to seek shelter in the denser cedar habitat.

Maguire (1973) has suggested that the definitions of fundamental and realized niches be extended to include solitary populations. For a population in a non-competitive context, then, the fundamental niche is the niche space represented by the maximum tolerance limits on each of the niche dimensions. Organisms recognize realized niches within this total niche space which vary with environmental conditions. Figure 6B represents the fundamental winter habitat niche of white-tailed deer. The fundamental niche space includes habitats deficient in vegetation required for shelter, but also includes habitats visited during foraging activities. Figure 7B approximates the realized winter habitat niche of deer where presumably all requirements for winter welfare of deer are met. Habitats within the realized niche can further be ranked on the basis of their use by deer. The cedar forest provides the optimum conditions for winter survival—primarily dense, sheltering vegetative structure and, secondarily, food abundance.

The Point Pelee deer herd has a history of extremely low reproductive success (Henry 1972, Theberge 1975, Theberge and Oosenbrug 1975). This has been attributed to a low nutritional plane affecting reproductive success and/or an unbalanced sex ratio (Theberge and Oosenbrug 1975) and behavioural interactions which restrict mating.
This latter suggestion does not seem worthwhile pursuing, since it is difficult to imagine how an unbalanced sex ratio could affect the number of serviced females in a polygamous species. At the same time, Theberge (1975) has discounted any explanation of the low reproductive output of the population due to an inadequacy of food resources.

The effects of the nutritional plane of ungulates during the winter, however, have attracted considerable attention (Verme 1962, 1967, 1969, Ransom 1967, Robinson 1960). Experimental evidence indicates that deer on diets sufficient for maintaining and delivering fetuses will resorb fetuses unless shelter requirements for bedding (e.g., dense coniferous cover) are met. Evolutionarily, the "choice" to produce or resorb a fetus appears to be a function of energy allocation to two different metabolic energy drains--thermoregulation or reproduction. Unless the doe is an extremely old individual, the optimal reproductive strategy to maximize fitness over its entire lifetime may be to resorb a fetus that would otherwise place a costly energy demand for survival through the winter on the parent. Thus, every female could theoretically be serviced every fall, but many of the females may resorb fetuses through the winter due to the small proportion of habitats with dense vegetation that provide shelter from prevailing winds. The older does at Point Pelee, those whose expectation of future offspring (Pianka 1974) has dropped considerably, may be the individuals giving periodic birth to fawns. However, the small size of the herd precludes the collection of life history data. Nevertheless, based on existing experimental evidence, data collected previously at Point Pelee on
food resource availability and abundance (Theberge 1975), and the pattern of habitat selection presented here, the most reasonable explanation for the low reproductive success of the Point Pelee deer herd would appear to lie in the relationship between conflicting energy demands—the production of offspring and the maintenance of body temperature. An increase in the size of the Point Pelee herd should be observed after sufficient time has been allowed for the abandoned farmland to mature to mid-aged seral stage habitats characterized by dense vegetation.
LITERATURE CITED


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Appendix A. Detailed map of Point Pelee National Park showing locations of habitats studied within study grids.
MAP 3 -
TIP SECTION

OLD ORCHARD (00)
TRANSECTS

LAKE ERIE
Appendix B. The correlation matrix of the original 21 habitat variables. Conservative estimates of significant r-values are as follows: $\alpha=0.05$, $r=0.325$; $\alpha=0.01$, $r=0.418$. 