SEASONAL MOVEMENTS OF BLACK-TAILED DEER

ON NORTHERN VANCOUVER ISLAND

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

in

FACULTY OF GRADUATE STUDIES

(Faculty of Forestry)

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 1979

Abstract

Columbian black-tailed deer (Odocoileus hemionus columbianus Richardson) were radio-tagged in a deep snowfall region on northern Vancouver Island, British Columbia. These deer were monitored to determine seasonal movements and habitat use. Deer exhibited either resident or migratory movement patterns. Resident deer made seasonal shifts in their home range centres but their seasonal home ranges overlapped. In migratory deer, summer home ranges were separated from both spring and winter home ranges, although their spring and winter home ranges overlapped. Altitudinal migrations occurred by deer moving between high and low elevation habitats. Horizontal migrations occurred by deer moving between a small tributary valley and the main valley.

Seasonal movements of black-tailed deer result from habitat selection by deer seasonally moving to more favourable habitats as determined by more available energy and nutrients, and lower risk of predation. The causal differences between vertical and horizontal migrations as well as seasonal shifts in home range centres can be resolved by a model of habitat selection based on these factors.

The densities of available digestible dry matter in Amabilis Fir - Twisted Stalk, and Mountain Hemlock - Copperbush associations are comparable with those in the shrub and conifer seral stages. This abundance of deer food in high elevation habitats suggests that forest harvesting in high elevations will not affect deer populations, if their other habitat requirements are met. In areas where forested summer ranges already exist,

low elevation logging of Sword Fern - Western Red Cedar, Deer Fern - Western Hemlock, and Western Hemlock - Plagiothecium associations will provide deer with sources of abundant food closer to their winter ranges than the high elevation summer ranges. Use of these food sources may result in only a redistribution and not an increase in the deer population. Logging of Amabilis Fir - Western Hemlock, Salal - Douglas-fir, and Salal - Western Hemlock associations may be detrimental to deer populations because of their need for these habitats during winter.

Management policies emphasizing preservation of severe winter range could be detrimental to deer populations. Habitat management for black-tailed deer must include provision of mild winter range as well as severe winter range. Because mild winter range provides deer with greater amounts of available energy and nutrients, it may be as important to the over-winter survival of deer as is severe winter range.

The mobility of black-tailed deer and their sensitivity to snow suggest that few deer would be trapped in high elevations by early snowfalls. Corridors joining high and low elevations appear unnecessary to facilitate deer migrations.

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1. Introduction

The Columbian black-tailed deer, Odocoileus hemionus columbianus (Richardson), is a small subspecies of mule deer and henceforth will be referred to as black-tailed deer. It inhabits the coastal region of North America from northern California to about 54°N in British Columbia where it merges with the Sitka deer (O. h. sitkensis Merriam) (Cowan 1956). The abundance and accessibility of black-tailed deer makes it one of the most popular big game species in British Columbia.

Early studies reported that few black-tailed deer inhabited the coastal old-growth forests (Cowan 1945, Einarsen 1946, Brown 1961). These observations were made in the Coastal Douglas-fir forests which have minor amounts of herb and shrub understory and hence, provided little food for deer. Since removal of the forest canopy allowed luxuriant growth of grasses, herbs, and shrubs, forest harvesting was concluded to be highly beneficial to this deer species (Cowan 1945, Einarsen 1946, Leopold 1950, Brown 1961, Gates 1968, Smith 1968). These studies were conducted in areas where snow depths were relatively shallow and snow cover was ephemeral. The authors recognized that deer needed tall vegetation for security cover, and that extensive logging could be detrimental to black-tailed deer populations. However, working in milder climates, they had no reason to expect that mature forests would be required as winter habitat for deer in areas of deep snowfall.

In the Coastal Western Hemlock and the subalpine Mountain Hemlock biogeoclimatic zones (sensu Krajina 1965) on Vancouver Island, Edie and Harestad (1971) and Smith and Davies (1973)

observed that black-tailed deer were abundant in some pristine forests far from logged areas. In these regions of deeper snowfall, forested habitats used as winter range by black-tailed deer were thought to be critical to the deer's survival locally (Robinson 1956, Edwards 1956, Cowan and Guiguet 1965, Smith 1972, Alaska Dept. Fish and Game 1973, Jones 1974 and 1975, Bloom 1978). These winter ranges are frequently old-growth forests of high wood volume and easy accessibility, and thus sought after by the forest industry. Jones (1974, 1975) and Bloom (1978) considered effects of forest harvesting on black-tailed deer populations in areas with deep winter snow cover. Their results indicate that harvesting of forested winter ranges could have a detrimental effect on deer abundance.

The disparities among these studies indicate that effects of forest harvesting on black-tailed deer are not clearly understood. Controversy over effects of forest harvesting on deer abundance and competition for use of old-growth forests has created conflicts between users of timber and deer resources. These conflicts can be partially attributed to a lack of basic knowledge concerning movements, food requirements, habitat use, and population dynamics of black-tailed deer .

1.1. Scope And Objectives

In response to the need for more information about black-tailed deer, a series of projects was initiated by Dr. F. L. Bunnell. Movements of black-tailed deer are described in this thesis while complementary studies are concerned with food habits, nutritive quality of the forage, and the abundance and

distribution of lichens and shrubs.

No published studies have been made on the spatio-temporal distributions of free ranging black-tailed deer in coastal forest ecosystems. Studies of home range and seasonal movements have been conducted on Rocky Mountain mule deer, _O. h. hemionus_ (Rafinesque), but these studies were of deer living in open habitats in constrast to the black-tailed deer which in British Columbia occupies forested habitats. Variation in spatio-temporal distribution, particularly social organization, of ungulates has been demonstrated to be highly dependent upon habitat structure (Estes 1974, Jarman 1974). Understanding of spatio-temporal distributions are important to the understanding of mammalian social organizational systems which have become increasingly focused upon in theoretical considerations of mammalian behaviour (Eisenberg 1966, Crook 1970, Alexander 1974, Geist 1974, Crook _et al._ 1976).

Habitat use by black-tailed deer is of particular interest in British Columbia because of the modifications to the deer's environment made by forestry practises, and because information on the habitat requirements of black-tailed deer is necessary for forest management plans. Although certain aspects of habitat requirements have been studied, some have been assumed by extrapolation from deer populations in southern and snow-free regions. Because of differences in climate and vegetation between British Columbia and these regions, it is necessary to examine the dispersion patterns of black-tailed deer and consider their seasonal movments over the whole year.

Seton (1909) wrote that "no wild animal roams at random over the country; each has a home region, even if it has not an actual home". This phenomenon of localization of an animal's activities is proposed to have adaptive value by providing the animal with familiarity of an area. This familiarity would give the animal knowledge of food sources, protective cover, and refugia, thus increasing its efficiency of finding food and its capability of evading predators and ultimately increasing its fitness (Davis et al. 1948, Blair 1953, Metzgar 1967, Covich 1976, Crook et al. 1976).

Following Burt (1943), I consider home range to be the area traversed by an animal during its normal activities associated with feeding, resting, reproduction, and avoidance of predators. Seasonal movements include both migration and seasonal shifts in the centres of home ranges. Migration is the periodic departure from, and return to, an area. Typically, the migrating animal moves from one seasonal home range to another. The seasonal home ranges of a migratory animal are separated, and zones between them are used mainly for travel. The animal spends little time in the zone between seasonal home ranges relative to the amount of time that it spends in the home ranges at each end. Seasonal shifts in home range differ from migrations in that much of the same home range is used throughout the year. However, the intensity of use of portions of the home range is altered seasonally.

Although localization of activities is beneficial because of the familiarity gained of the home range, not all the animal's requirements can be obtained at the same place. This

will be especially true if there are temporal changes in the availability of resources. Animals are therefore obliged to move over an area to satisfy their requirements. The extent of these movements, and hence the size of home range in vertebrates, is related to their energy requirements with modifications to the relationship occurring because of trophic status and habitat productivity (McNab 1963, Schoener 1968, Turner et al. 1969, Harestad and Bunnell, in press). For mammals, home range size expands with increases in energy requirements, and contracts with increases in habitat productivity (Harestad and Bunnell, in press). Since the size of home range depends on the animal's requirements and the availability of energy, it follows that location of the home range may also be influenced by these factors.

The link between food availability and seasonal movements has been proposed for over 80 years (Morgan 1896, Adams 1919). More recent studies (Mackie 1970, Bergerud 1974, LeResche 1974, Bertram and Rempel 1977) have not progressed beyond the statement of this causal relationship. Other studies have described movements of ungulates with changes in local food sources (Byford 1969, Strandgaard 1972), but no quantification of the food supply was made. Some studies have demonstrated potential nutritional differences between the forages on the seasonal ranges (Dealy 1959, Klein 1965 and 1970, Hebert 1973).

Two main processes concerning the food supply are used to explain seasonal movements. In areas where forage is available throughout the year or during spring and summer when the snowpack has melted, quality of the forage is suggested as the

most important factor inducing migratory behaviour (Dalke et al. 1965, Klein 1965 and 1970, Hebert 1973). These nutritive differences in the forage available on seasonal ranges are due largely to differences in the phenological condition of the forage (Cook 1972, Klein 1965), and can result from differences in topography, temperature, or precipitation. In mountainous regions, phenological differences are related to elevation and are thought to induce altitudinal migration by the animal following the most nutritious state of the forage (Russell 1932, Dixon 1934, Longhurst et al. 1952, Knowlton 1960, Dalke et al. 1965, Klein 1965, Hebert 1973, Stelfox 1976).

The second main process used to explain migration in North American ungulates is the effect of snow on food availability. Snow covers food sources, restricts the foraging animal's mobility, and increases costs of locomotion. Through migration, animals seek out areas of appropriate snow depth and density, where food is available (Leege and Hickey 1977, Telfer 1978).

The currently accepted pattern of seasonal movements by black-tailed deer is that of resident populations in low snowfall regions and migratory populations in deep snowfall regions. The migrations are proposed as progressive movements by the population moving in phase with high quality phenological stages of the forage (Dealy 1959, Klein 1965). This proposed pattern implies a transitional series of short term home ranges during the migratory period and would involve the whole population. Winter and summer home ranges have been observed for a non-migratory population of black-tailed deer (Dasmann and Taber 1956) but no studies have been made of the complete annual

behaviour of a migratory population. Furthermore the actual
migrations have not been described for individual deer but
inferred from changes in population dispersion.

In this study, my objectives were to determine if black-
tailed deer occupying coastal forest ecosystems, modified by
logging practises, do have seasonal home ranges, what pattern of
seasonal home range use exists, and to explore some factors
which promote movements by deer between seasonal home ranges.
Finally these movements are considered with regard to changes
that could be implemented in forestry practises and deer
management policies to enhance deer populations.

2. Materials And Methods

2.1. Study Area

The study area is located on northern Vancouver Island, 20 km east of Woss, British Columbia and is centred at 50°12'N 126°25'W. The area, 187 km² in extent, includes the upper Davie River Valley and the Croman Creek Valley (Fig. 1). The Tsitika River originates in and drains the northern side of the area. Although the Davie River Valley is wider than the Croman Creek Valley, the topography on both sides of the Davie River is similar to that found on the east side of Croman Creek. There is a steep sidehill adjacent to the valley floor that rises to between 600 and 700 m. Above this elevation, the slope is gentle as the land rises to 1000 m before steepening near the peaks of Mount Cain and Maquilla Peak.

Access to the study area is from the Nimpkish Valley through a system of logging roads running the length of Croman Creek and Davie River. Tributary roads lead up the slopes of the mountains to elevations of about 600 m in Croman Creek Valley and as high as 1150 m on Mount Cain. Four topographical sectors are delineated in Figure 1. Most of the tagging, location of tagged deer, and habitat assessments were conducted in the Croman (1) and Mount Cain (2) sectors. The biogeoclimatic zones represented in the study area are the Coastal Western Hemlock Zone in the lower elevations (200 to 900 m), the subalpine Mountain Hemlock Zone in the upper elevations (800 to 1600 m), and the Alpine Zone near the mountain tops (above 1500 m) (sensu Krajina 1965). In Croman Valley where the climate is cooler and

Figure 1. Study area. Shaded areas are logged, unshaded areas are unlogged. Sectors are numbered and their boundaries shown by dashed lines cr waterways : 1. Croman, 2. Mount Cain, 3. Maquilla, 4. Hoomak.
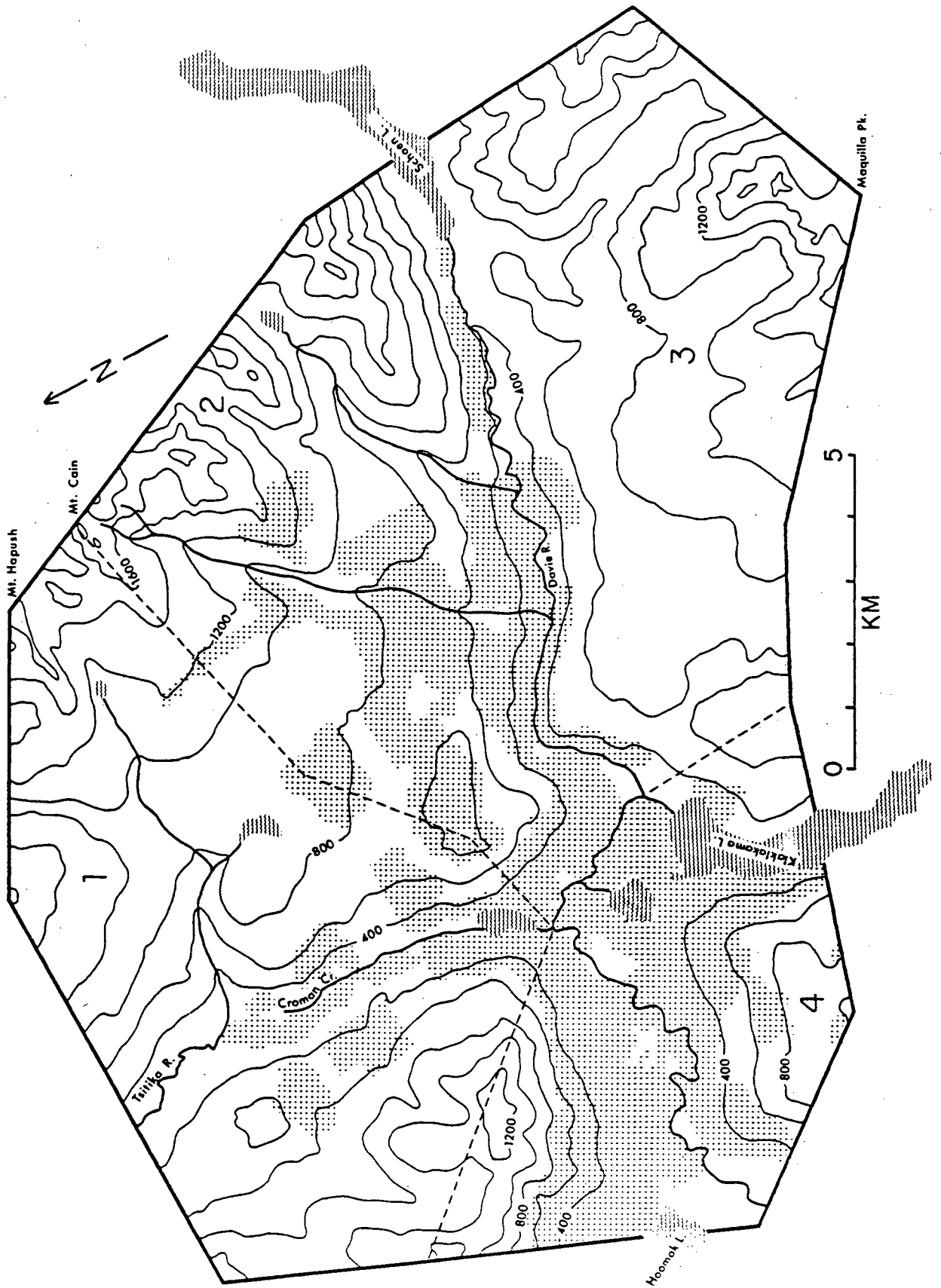
snowfall greater, the subalpine Mountain Hemlock Zone extends closer to the valley bottom than it does in the Mount Cain (2) sector.

Forest harvesting began in the study area in 1948 along the flat valley bottom near Davie River. Much of the lower elevation forests were logged first and then extraction of the sidehill and higher elevation forests began. By 1975, 39% of forests below 800 m in elevation were logged, while only 7% of forests above 800 m were logged. The four sectors of Figure 1 differ in the proportions of the forests that have been cut. Mount Cain (2) is the most extensively logged sector. Here, 64% of the forest below 800 m in elevation is logged. In comparison, the Croman (1) sector has only 27% of the lower elevation forests logged. The pattern of forest harvesting was predominantly clear-cutting, while in more recent years, patch cutting of blocks less than 81 ha has been conducted. Logged areas were usually slashburned. During the study immature seral stages in the study area ranged up to 27 years old.

2.2. Study Period

Field-work began in June 1974 and continued through to May 1977. Technical difficulties with the radio-transmitters subverted attempts at tagging and locating deer in 1974. Reliable radio-transmitters were obtained and attached to deer by the spring and early summer of 1975. The deer were located intensively until the spring of 1976. The intensity of location of the deer was reduced in the summer of 1976 while evaluations of seasonal habitats were made. The deer were located until

December 1976 and the project terminated in May 1977.

2.3. Climatic Data

Five weather stations sponsored by the Resource Analysis Branch (B.C. Ministry of Environment) were maintained in the study area. Monthly minimum and maximum temperatures were taken and a continuous record of temperature was obtained using recording thermographs. During periods with no snow, monthly precipitation was recorded, while during periods with snow monthly snowpack depths were measured.

In addition to the snow depths measured at the weather stations, snow depth and percent of ground covered by snow were estimated every two weeks at stations located every 100 m of elevation from 300 to 1200 m along the Mount Cain road. Snow depths were sometimes measured more often, especially during periods of intense radio monitoring or frequent snowfall.

2.4. Habitat Assessments

The locations for each radio-tagged deer were transferred to aerial photographs. Seasonal home ranges were outlined on the photographs and then stratified according to major mature plant associations and immature seral stages. The mature seral stages will be referred to as <u>forested plant associations</u> or, simply, associations and the immature seral stages referred to as <u>seral stages</u> . Seasonal home ranges were inspected on the ground and, if necessary, the stratification was altered. Typical examples of associations and seral stages were selected within the seasonal home ranges. At these sites, Habitat Assessments were

conducted which included a physiographic description, list of plant species and their percent cover and distribution, and estimates of shrub abundance. Lists of plant species and estimates of percent cover were obtained by the relevé methods used by Orloci (1964) and Brooke et al. (1970).

Plant associations in forests used by radio-tagged deer were determined through comparison of lists of plant species and their percent cover at Habitat Assessment sites to those of the associations defined by Orloci (1964), Brooke et al. (1970), and Bell (1971). Common names of these associations are used and correspond to those of Bell (1971). Cutovers used by deer were classified into five seral stages that are characterized by their percent cover and height of conifers, shrubs, bracken fern (Pteridium aquilinum (L.) Kuhn), and herbs. The criteria used in classification of seral stages were (in ascending hierarchy) : newly logged - recently logged and less than one year old cutover; herb - percent cover of herbs is greater than the percent cover of P. aquilinum ; fern - percent cover of P. aquilinum is greater than the percent cover of herbs ; shrub - percent cover of shrubs is greater than 20% ; conifer - total percent cover of conifers less than 10 m high is greater than 20% .

Forested plant associations used by deer were divided into two groups: those in the Coastal Western Hemlock Zone and those in the subalpine Mountain Hemlock Zone. Within each biogeoclimatic zone, the associations were arranged according to their typical position on the slope and their moisture regime (after Bell 1971). Seral stages were arranged in order of

increasing successional age.

The abundance of lichen, consisting mainly of <u>Alectoria</u> <u>sarmentosa</u> (Ach.) Ach. , was estimated at each Habitat Assessment site by low level, oblique aerial photographs. Colour positives of the forest canopy were projected onto a screen so that the central portion of the image covered an area gridded into 450 one cm squares. The percentage of lichen cover in each square was classed from 0 to 3. The classes corresponded to the following percent cover ranges; 0 = 0-5%, 1 = 6-25%, 2 = 26-75% 3 = 76-100%. The classes were assigned percentage values as the mid-point in the range of the class and an estimate of total percent cover of lichen was obtained for each site. For some sites, a relationship was determined between this percent cover and an independent estimate of lichen biomass obtained by Stevenson (1978). Using this relationship, the percent cover estimate for arboreal lichens at each Habitat Assessment site was converted to biomass (kg ha^{-1}).

Shrub abundance was estimated for <u>Vaccinium</u> <u>parvifolium</u> Smith, <u>V.</u> <u>alaskaense</u> Howell (including other <u>Vaccinium</u> species), and <u>Gaultheria</u> <u>shallon</u> Pursh. by identifying between one and four classes of relative shrub density at the Habitat Assessment site. The proportion of area at the site exhibiting each of these classes of shrub density was then estimated. In a representative area of each class of shrub density, a plot was selected and the height of each stem rooted in the plot was measured. Stems less than 30 cm in height were counted but their heights were not measured. Estimates of the amount of food contributed by these shrubs were made by clipping, drying, and

weighing the annual growth of shoots from stems of various heights. Species-specific regressions of the height:annual growth relationships were then used to estimate the food contributed by all stems measured in the Habitat Assessments.

2.5. Effect Of Snow On The Posture Of Shrubs

The availability of shrubs to deer during periods of snow cover depends on structural reactions of shrub stems to snow accumulation and melt. I was not able to measure the effect of newly fallen snow on the depression of shrub stems. The winter when these effects were to be investigated, 1976-1977, was very mild and little snow fell except during late winter in the higher elevations. Some insight into the depression and subsequent ascent of shrubs was obtained in the spring of 1976 by marking stems buried beneath the snow and then measuring the change in height of the marker after the snow had melted. On June 6, 1976, an area was chosen that had an abundance of shrubs and a shallow snowpack (30 cm) remaining from winter. The area was in an Amabilis Fir - Twisted Stalk association in the forest 250 m southeast of the 900 m Mount Cain weather station. A small hole was dug in the snow until a shrub stem was encountered. A numbered piece of flagging tape was attached to the stem and a second marker was securely placed on the ground directly below the marked stem. The vertical distance between the two markers was measured. Some stems were marked above the first major bifurcation, while other stems were marked in the crown of the shrub. On July 2, 1976, after the snow had completely melted and the stems regained their snow-free postures, heights between the

markers were remeasured. Most of the shrubs marked were _Vaccinium_ _alaskaense_ , although several _Menziesia_ _ferruginea_ Smith were also marked.

2.6. Tagging

Deer were tagged from different parts of the study area to ensure that movements under different environmental conditions were represented. Most of these deer were free-ranging when tagged and were immobilized using a muscle relaxant, succinylcholine chloride, administered in liquid form by Capture Darts (Palmer Chemical Co.) or in powdered form by Pneu Darts (Pneu Dart Inc). The remaining deer that were tagged, were captured in single gate Clover traps (Clover 1956).

Radio-transmitters (Wildlife Materials Inc.) were attached to selected adults and yearlings. The radio-tagged deer were eartagged with a plastic flap on which a reflective number was attached, and with numbered Rototags (Nasco Co.) or metal clip tags.

2.7. Locating Tagged Deer

Radio-tagged deer were located on various schedules depending upon accessibility of the deer and type and value of the information obtained from the locations. Radio-tagged deer were located at least weekly when I was in the study area. During certain periods, locations were made more frequently with selected deer being located every 12 hours. During a ten day session in August 1975, a radio-tagged deer was relocated every two hours in order to determine the optimum schedule for

monitoring movements.

Radio-tagged deer were located using a whip antenna and a hand held, three element Yagi antenna. The whip antenna was used for preliminary search and location of radio-tagged deer from a moving vehicle. The Yagi antenna was used to determine the direction of the radio-tagged deer from known locations. When radio-tagged deer were located, I recorded the tag number, date, time, my location, bearing of the radio signal, and comments. When tagged deer were sighted, I recorded the tag number, date, time, location, and comments.

Bearings of the radio signal direction were quickly obtained at three to five different locations. The radio-tagged deers' locations were estimated by triangulation. Bearings distinctly different from the other bearings were not included in the final estimate of a location. Aberrant bearings frequently resulted from signal bounces and were easily detected after I became familiar with the study area. The location estimate was judged as being "accurate", "rough", or "very rough" depending upon the degree of intersection of the bearings. This accuracy index was based on whether at least two of the vertices of the intersection triangle were within a circle of a radius of less than 100 m (accurate), 100 to 250 m (rough), and greater than 250 m (very rough). Most of the estimates fell within the accurate class. During the spring and summer of 1975, reliability of the telemetry system was tested by taking signals from deer in the field and immediately triangulating their locations. The estimated locations were visited and confirmed by observation of the target deer. After

many locations were confirmed, I was satisfied that the triangulation methods were giving good estimates of a deer's locations.

In the field, a map (3.16 cm to 1.0 km) with rectangular coordinates was used to locate tagged deer and locations from which bearings were taken. Bearing positions were then located on a 2.08 cm to 100 m forest cover map and triangulations performed. Estimated locations of radio-tagged deer and locations of tagged deer were recorded as polar coordinates using a series of origins. Origins were placed so that each was near a concentration of locations, thus minimizing error. These "local" origins were standardized to a single common origin and the polar coordinates converted to rectangular coordinates for use in plotting and analysis of location data.

2.8. Spatial Analysis

Home ranges are an integrated expression of an animal's locations and movements over a specific time interval. Thus, there can be daily, seasonal, and lifetime home ranges. Home ranges can be considered as a proportion of the known locations for an animal within a particular time period. The absolute or 100% home range includes all the known locations of an individual. Other expressions of home ranges include only the closest 90% or 50% of the individual's known locations. Consideration of only a portion of the observed locations is useful in identifying cores of intense use, and for eliminating unusual movements whose inclusion would create erroneous estimates of home range parameters.

Locations and movements of animals are usually considered as home ranges and can be presented in a number of ways. The statistical methods (see Van Winkle (1975) for review), although elegant, do not always provide easily interpreted spatial information. On the other hand, the traditional minimum home range method (Dalke and Sime 1938) does provide a simple spatial description. I have used both the statistical and the minimum home range methods to describe deer movements. The minimum home range method was modified to identify central cores of home range where deer were most often located. Geographical techniques developed by Neft (1966) were adapted for analysis of deer locations. Using these techniques, the locations of a deer can be treated like any other variable, and a mean location and the variability about that mean location can be calculated. Thus, in the analysis of my home range data, I provide a level of descriptive statistics comparable to that commonly available for univariate data.

2.9. Track Counts

During winter and early spring, night counts were not always possible in high elevations. In order to detect when deer were in these areas, track counts were made. Mount Cain Road was travelled and the highest elevation at which a deer track either crossed or followed along the road was recorded. These data can be used to determine when deer first visit high elevations in spring and when deer last leave these elevations in winter.

2.10. Night Counts

Portions of the study area were searched at night using a spotlight shone from a vehicle travelling along predetermined road transects. Three night counts were attempted every two weeks. Because of weather and other commitments, counts were sometimes made less frequently. During certain periods of intense relocation of radio-tagged deer, night counts were conducted each night. The numbers of deer sighted along these fixed road transects provide estimates of relative deer abundance in the cutover areas throughout the year. These night counts are an indirect measure of seasonal movements of the deer population. Radio-transmitters and flap tags were covered with reflective tape and so were readily visible when illuminated at night. Numbers on the tags could usually be read through a window-mounted 20 to 45 power spotting telescope.

2.11. Sample Size

Funding, logistics of capturing and monitoring, and losses of study animals to hunters limited the number of radio-tagged deer. One of the 10 radio-transmitters attached to deer in 1975 failed early in the study. Another transmitter was lost when a yearling male emigrated. This left eight deer with functioning radios in the study area at the opening of hunting season. Deer hunting was not restricted in the study area during 1975 and three of the remaining eight radio-tagged deer were shot.

One of the tagged deer was killed early in September and since I had only a few locations for him I did not include them in the seasonal movements analysis. The two other deer were

killed in early winter and some movements were observed. These deer were included in the analysis even though they were not monitored for a complete seasonal cycle. This study thus consists of the complete seasonal movement patterns of five deer and the partial patterns of two deer.

The movements of the radio-tagged deer are representative of movements that can occur and indicate potential movement patterns of the population. Track counts and night counts give broad trends in the seasonal dispersion of the deer population. Combined, the radio-tagged deer, track counts, and night counts should provide an accurate description of the seasonal movements of black-tailed deer in the study area.

3. Results

3.1. Snowpack In The Study Area

Elevations below 1200 m were snow-free from July until late October 1975 (Fig. 2). The first snowfalls below 1200 m occurred late in October and were restricted to high elevations (above 900 m). Subsequent snowfalls progressively extended to lower elevations (below 700 m) and reached the valley bottoms at elevations of 300 m by mid-November. The snow deposited on the ground during the first few snowfalls lasted for only a few days before melting. After the first few snowfalls and snow melts, snow deposited at elevations above 900 m began to accumulate. This accumulation of snow continued until late March when a maximum snow depth of 289 cm occurred at 1200 m. In April, the snowpack began to decrease and was completely melted by early July in most areas below 1200 m. Figure 2 shows a substantial increase in the snowpack above 1000 m. This difference in depth is partly a result of a change in aspect of the Mount Cain Road and the snow depth stations. The stations were on aspects between south and southwest below 1000 m and between southwest and west above 1000 m.

Mid-elevations (700 to 900 m) received their first snow slightly later than did high elevations. They have a pattern of snow accumulation similar to high elevations, except that during mild weather, the rate of snowmelt is greater than the rate of snowfall and the depth of the snowpack decreases for brief periods. The snowpack in mid-elevations did not completely melt at any time between early December and early May. Snow did not

Figure 2. Perspective plot of date, elevation and snowpack depth along Mount Cain road. Most winter ranges were below 700 m where snow depths were shallow and snow cover was intermittent. Summer ranges above 700 m had deep accumulating snowpacks and continuous snow cover over winter.
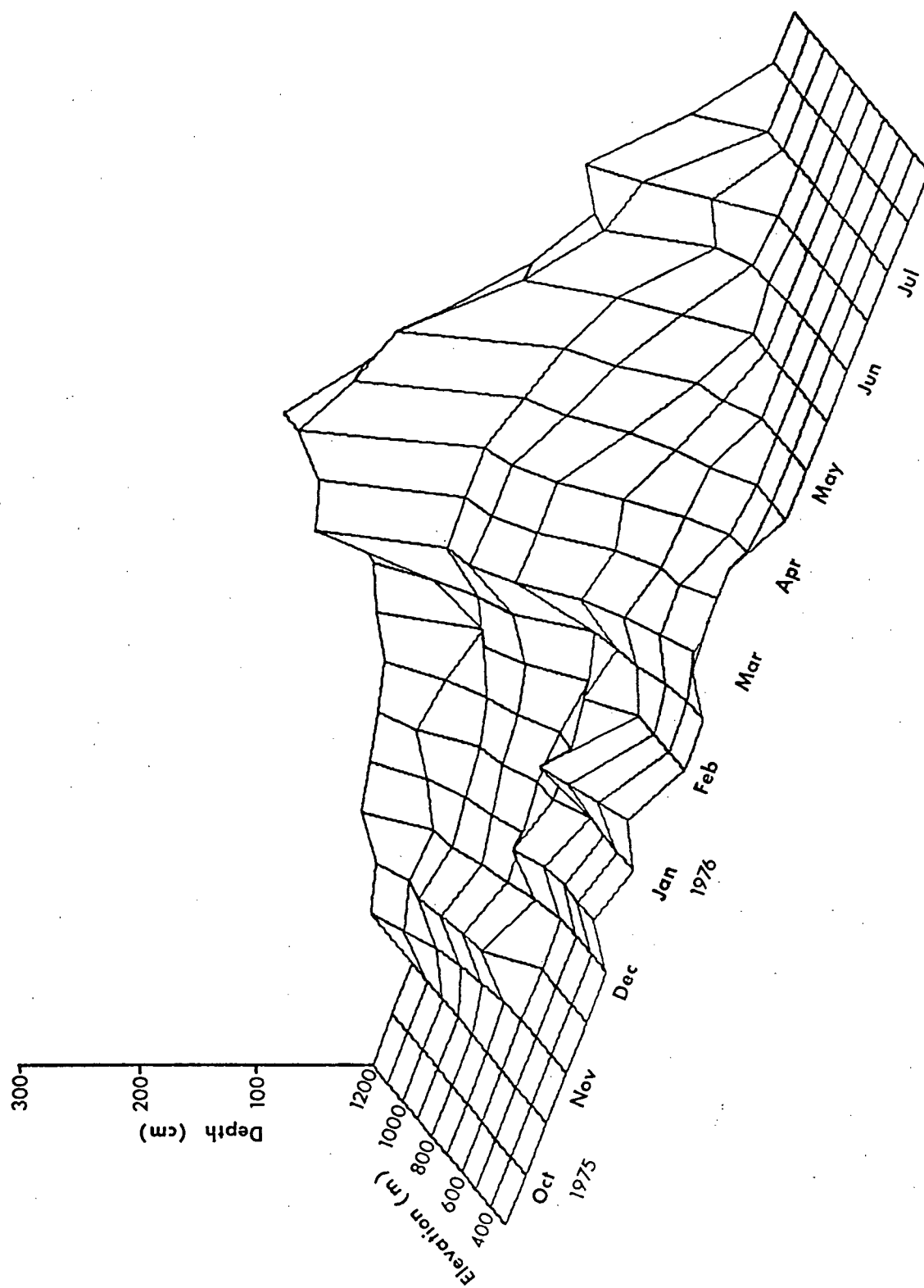
accumulate in low elevations (300 m to 700 m) for as long a period or to as great a depth, as it did in high and mid-elevations. Several times in winter, low elevations were snow-free. They were snow-free after late April 1976, much sooner than were high elevations (Fig. 2).

On Mount Cain, depth of the snowpack increased with increasing elevation except for on the valley floor along the Davie River. The valley floor frequently had deeper and more persistent snow cover than the adjacent south-facing sidehill. Part of the difference in snowpack between the valley floor and the sidehill is a result of their differences in slope and aspect. Snow depths in Croman Valley were not monitored as intensively as they were on Mount Cain. However, snow was deeper, more frequent, and persisted longer in upstream parts of the valley than near the mouth.

3.2. Abundance Of Deer Food

Important food plants of black-tailed deer in the study area are <u>Alectoria sarmentosa</u> , <u>Gaultheria shallon</u> , <u>Vaccinium</u> species, <u>Rubus</u> species, <u>Cornus canadensis</u> L., <u>Linnaea borealis</u> L., <u>Epilobium angustifolium</u> L., <u>Blechnum spicant</u> (L.) Roth., <u>Pseudotsuga menziesii</u> (Mirb.) Franco, <u>Thuja plicata</u> Donn, and <u>Tsuga heterophylla</u> (Raf.) Sarg. (Jones 1975, Rochelle <u>in prep.</u>). Besides these species many other plants are eaten by black-tailed deer (Cowan 1945, Brown 1961, Gates 1968). The diversity in the diet of black-tailed deer and the predominance of palatable species allowed estimates to be made of the amount of food available at each habitat assessment site and a composite

summary of food resources available in each plant association
and seral stage was therefore calculated. Food resources of
these habitats consisted of four major components; lichens,
shrubs, herbs, and conifers. The relative contribution of each
component was estimated using differing techniques as explained
below.

Lichen

The percent cover of lichen, mainly <u>Alectoria sarmentosa</u>,
in the forest canopy of seasonal habitats used by radio-tagged
deer is shown in Table I. On some sites where percent cover of
lichen was measured, biomass estimates were independently
obtained by Stevenson (1978). Both the percent cover and biomass
estimates were transformed to $\log_{10}$ and a linear regression
performed to obtain an empirical relationship between the two
variables (Fig. 3). Although the coefficient of determination is
low (r^2 = 0.41), the slope of the regression line is
statistically different from zero ($p \leq .06$).

The proportion of the standing crop of lichen that falls to
the ground over the winter and thus is available as deer food,
is about 12% (Stevenson 1978). For the purpose of this analysis,
it was assumed that similar litter-fall occurs over the summer.
This assumption likely overestimates the contribution of lichen
to the total amount of food available during summer. However,
since the contribution of lichen to the available food in summer
is small, this overestimate has only a slight effect on the
total amount of available food. Krumlik's (1979) measures of
annual lichen litter-fall in high elevation forest-types on

Table I. Percent cover and estimated food available in summer on forested plant associations and immature seral stages used by radio-tagged deer during the year. Mean and standard error of total weight of food available in each habitat type are indicated. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush. Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

Association or Seral Stage	Plot No.	Herb % cover	Herb kg ha^{-1}	Shrub kg ha^{-1}	Conifer % cover	Conifer kg ha^{-1}	Lichen % cover	Lichen kg ha^{-1}	Total kg ha^{-1}
VS	7	9.2	40.9	1005.7	26.0	79.6	17.8	11.0	1137.2
VS	20	20.9	93.0	700.7	26.0	79.6	28.4	76.4	949.7
VS	41	58.4	259.9	156.8	9.5	29.1	15.1	5.6	451.4
								n=3	846.1 $\pm$ 354.4
SC	13	2.1	9.3	10.5	8.0	24.5	25.6	49.7	94.0
								n=1	94.0
DW	19	2.6	11.6	18.0	22.0	67.3	17.6	10.5	107.4
								n=1	107.4
WP	3	.4	1.8	.1	5.0	15.3	21.4	23.6	40.8
WP	39	1.3	5.8	1.4	5.0	15.3	21.3	23.2	45.7
								n=2	43.2 $\pm$ 3.5
AW	10	1.5	6.7	6.4	28.0	85.7	21.3	23.2	122.0
AW	18	1.0	4.4	5.3	30.0	91.8	17.1	9.3	110.8
AW	44	.9	4.0	269.7	7.0	21.4	32.6	135.6	430.7
AW	45	1.6	7.1	159.8	12.5	38.2	22.0	26.5	231.6
								n=4	223.8 $\pm$ 148.3

Table I (cont.)

Association or Seral Stage	Plot No.	Herb % cover	Herb kg ha^{-1}	Shrub kg ha^{-1}	Conifer % cover	Conifer kg ha^{-1}	Lichen % cover	Lichen kg ha^{-1}	Total kg ha^{-1}
SD	2	.6	2.7	359.4	5.0	15.3	22.6	29.6	407.0
SD	5	.9	4.0	643.9	.0	.0	23.2	33.0	680.9
								n=2	504.4 ± 137.7
SW	4	.7	3.1	218.0	23.0	70.4	35.9	201.9	493.4
SW	6	1.1	4.9	218.1	10.0	30.6	23.9	37.4	291.0
SW	8	1.4	6.2	253.6	8.0	24.5	20.9	21.4	305.7
SW	17	.7	3.1	21.4	28.5	87.2	17.7	10.7	122.4
SW	46	1.0	4.4	164.4	5.0	15.3	28.5	77.5	261.6
								n=5	294.8 ± 132.7
AT	1	2.4	10.7	323.5	12.0	36.7	31.8	122.1	493.0
AT	28	1.4	6.2	1018.0	26.0	79.6	32.0	125.3	1229.1
AT	29	1.4	6.2	279.4	16.0	49.0	24.9	44.3	378.9
								n=3	700.3 ± 461.5
MC	32	.7	3.1	406.5	6.0	18.4	13.1	3.1	431.1
MC	33	12.5	55.6	531.0	1.0	3.1	18.2	12.1	601.8
								n=2	516.4 ± 120.7

Table I (cont.)

Association or Seral Stage	Plot No.	Herb % cover	Herb kg ha^{-1}	Shrub kg ha^{-1}	Conifer % cover	Conifer kg ha^{-1}	Lichen % cover	Lichen kg ha^{-1}	Total kg ha^{-1}
N	38	1.2	5.3	5.4	33.5	102.5	.0	.0	113.2
								n=1	113.2
H	9	41.0	182.9	5.7	.5	1.5	.0	.0	190.1
H	11	36.8	163.8	.3	.0	.0	.0	.0	164.1
H	14	61.3	272.8	.3	2.5	7.6	.0	.0	280.7
H	15	42.1	187.3	.5	1.0	3.1	.0	.0	190.9
H	16	13.1	58.3	.0	3.0	9.2	.0	.0	67.5
H	21	56.5	251.4	20.1	10.0	30.6	.0	.0	302.1
H	23	36.2	161.1	83.8	6.5	19.9	.0	.0	264.8
H	24	91.2	405.8	12.1	4.0	12.2	.0	.0	430.1
H	30	11.5	51.2	55.5	1.0	3.1	.0	.0	109.8
H	31	32.2	143.3	3.4	1.5	4.6	.0	.0	151.3
								n=10	215.1 $\pm$ 106.1
F	12	43.9	194.5	.0	8.5	26.0	.0	.0	220.5
								n=1	220.5

Table I (cont.)

Association or Seral Stage	Plot No.	Herb % cover	Herb kg ha⁻¹	Shrub kg ha⁻¹	Conifer % cover	Conifer kg ha⁻¹	Lichen % cover	Lichen kg ha⁻¹	Total kg ha⁻¹
S	27	1.9	8.4	234.0	21.0	64.3	.0	.0	306.7
S	34	12.3	54.7	39.6	4.0	12.2	.0	.0	106.5
S	36	31.6	140.6	.2	2.5	7.6	.0	.0	148.4
S	37	38.9	173.1	7.5	8.5	26.0	.0	.0	206.6
S	40	84.6	376.5	3.0	23.0	70.4	.0	.0	449.9
S	43	42.5	189.1	290.0	6.5	19.9	.0	.0	499.0
								n=6	286.2 ± 161.3
C	22	26.7	118.8	12.7	60.0	183.6	.0	.0	315.1
C	25	6.7	29.8	469.4	28.0	85.7	.0	.0	584.9
C	26	1.9	8.4	461.2	80.0	244.8	.0	.0	714.4
C	35	1.3	5.8	515.8	59.5	182.1	.0	.0	703.7
C	42	6.0	26.7	141.3	115.5	353.4	.0	.0	521.4
								n=5	567.9 ± 163.0

Figure 3. Linear regression of percent cover of lichen on lichen biomass transformed by $\log_{10}$. $r^2 = .41$, $p \leq .06$. $L = .0006 \, P^{4.15}$, where L is lichen biomass and P is percent lichen cover. Lichen biomass increases exponentially with increases in percent cover of lichen.
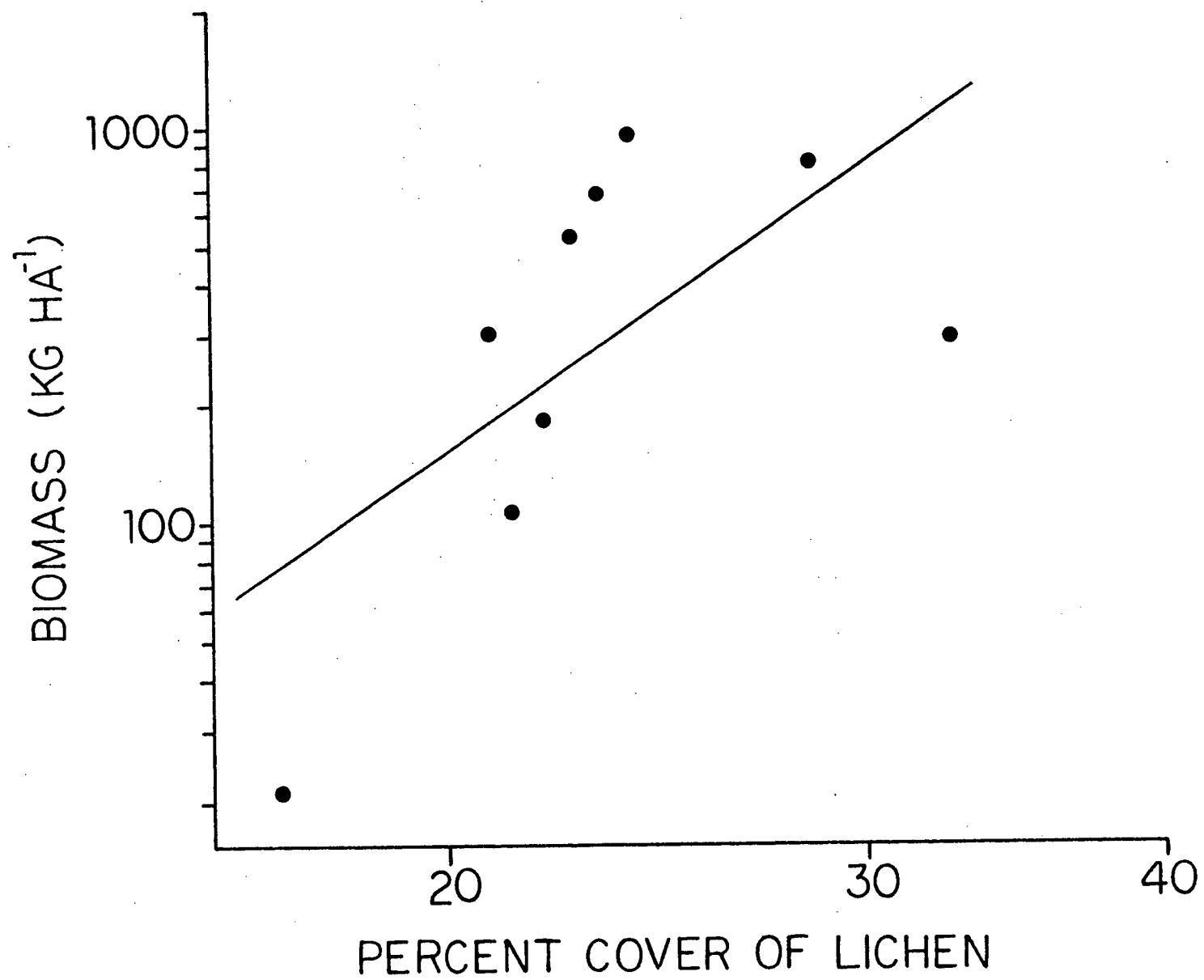
coastal British Columbia ranged between 71 and 426 kg ha⁻¹. In this study high elevation forest plant associations (Amabilis Fir - Twisted Stalk and Mountain Hemlock - Copperbush associations) were estimated to have between 9 and 376 kg ha⁻¹ of annual lichen litter-fall. The similarity between Krumlik's (1979) measures and my estimates led me to accept the values for my study area.

Shrubs

Almost all shrubs at the Habitat Assessment sites were Vaccinium parvifolium , V. alaskaense , or Gaultheria shallon . The contribution by shrubs to the food available to deer was estimated as the annual shoot growth of these species. In all three species, the current year's annual growth increased with increasing stem height (Fig. 4). In both Vaccinium species, variation in the stem height accounts for 72% or more of the variation in annual growth. In Gaultheria shallon , the coefficient of determination is lower with only 49% of the variation in annual growth being explained by variation in stem heights. This low coefficient of determination is likely the result of the more prostrate growth form of G. shallon compared to the vertical growth forms of the Vaccinium species. Hence, height from ground to crown top may not be the best predictor of annual growth in Gaultheria shallon . In both Vaccinium species, the rate of increase in annual growth increases with increasing stem height. In Gaultheria shallon , the rate of increase in annual growth is not significantly different from one (p>.05).

Figure 4. Weight of shoot annual growth per stem and stem height in shrubs important as deer forage. A = annual growth (g), H = height from the ground to the top of the shrub crown (cm).

Vaccinium parvifolium : A = .00056 $H^{1.88 \pm .40}$, p≤.00, r^2=.85

Vaccinium alaskaense : A = .0093 $H^{1.32 \pm .30}$, p≤.00, r^2=.72

Gaultheria shallon : A = .019 $H^{1.17 \pm .46}$, p≤.00, r^2=.49
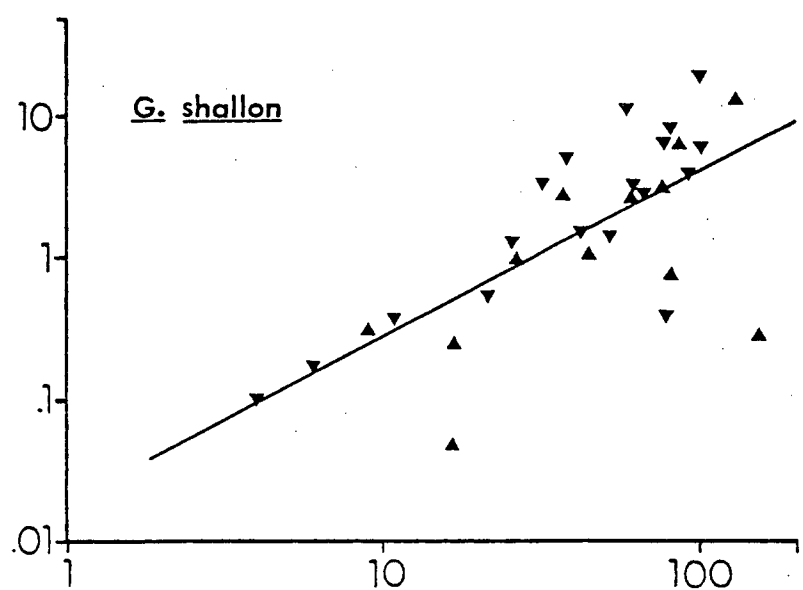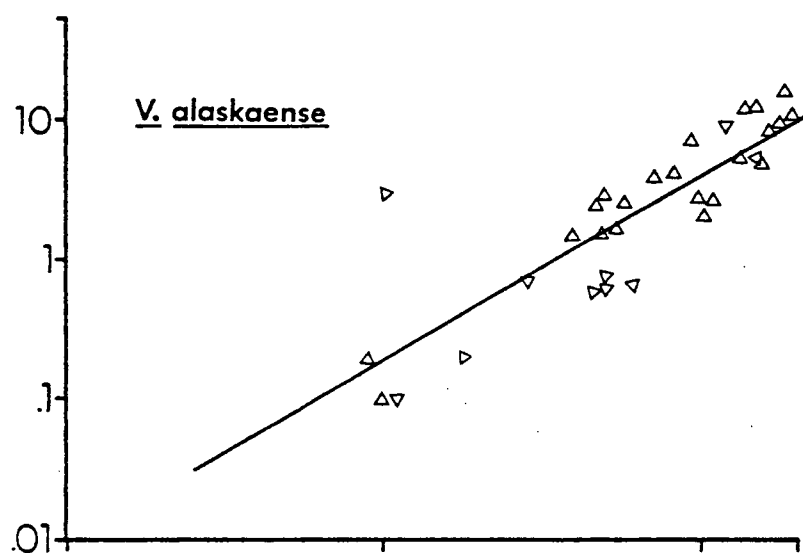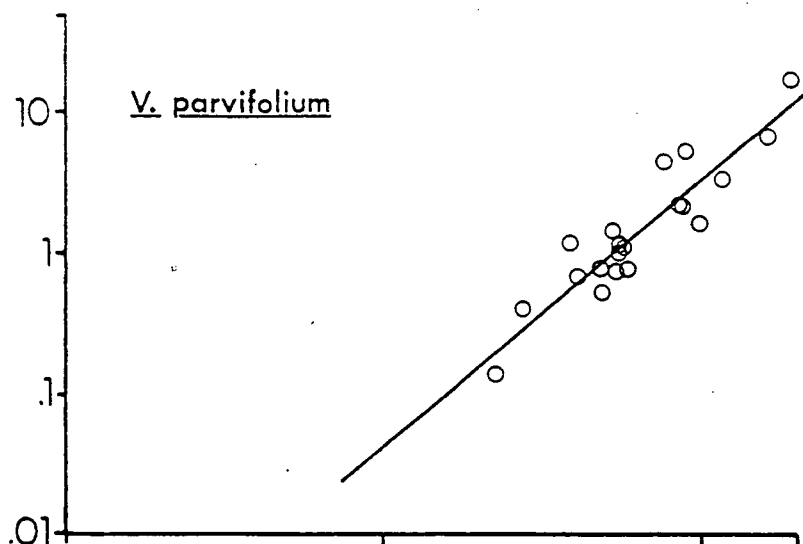
The number and heights of stems were determined for the three shrub species on plots within the Habitat Assessment sites. Using the height-annual growth relationships (Fig. 4) and assuming they were the same for all habitat types, annual growth produced by shrubs at each site was estimated. In these calculations, Vaccinium species other than V. parvifolium were considered to have the same height-annual growth relationship as V. alaskaense . Shrub stems less than 30 cm high were very numerous but at most sites contributed little to the total amount of food available from shrubs. To increase efficiency of the Habitat Assessment these stems were counted but not measured. Stems less than 30 cm high were assigned a height of 10 cm in calculation of the annual growth of shrubs produced at the Habitat Assessment sites. This assigned height was chosen because I felt it best represented the average annual growth of stems less than 30 cm high. For comparison, the total annual growth of shrubs was also calculated with stems less than 30 cm being assigned heights of 0 cm and 30 cm (Appendix 1). At most sites, contribution to total annual growth by stems less than 30 cm was small and use of either assigned height makes little difference to the estimate of annual growth. In some sites, there were substantial differences in the total annual growth estimate depending upon the assigned height chosen for stems less than 30 cm. These sites were mainly in habitats where there are high densities of short stems of Gaultheria shallon . Overall the assigned height of 10 cm for stems less than 30 cm was thought to be most representative and so was used in all calculations of food contributed by shrubs (Table I).

Herbs

The contribution of herbs and ferns to the deer food available at the Habitat Assessment sites was estimated by converting percent cover of herbs and ferns to biomass (kg ha^{-1}). The total percent cover of herbs and ferns, except Pteridium aquilinum , is given in Table I. The total percent cover is the sum of percent covers of all herb and fern species (excluding P. aquilinum) and was obtained from the floristic list at each Habitat Assessment site. Species with less than 5% cover were assigned a percent cover of 0.1. The total percent cover was converted to biomass by a factor calculated from Gates (1968). In Gates (1968 : 49), four sites were given at which percent cover and wet weight of annual herb production biomass were measured. Dry weight of this biomass was estimated as 35% of its wet weight. The dry weights of herbs were then divided by their respective percent covers and a mean dry weight of forage per percent cover was obtained. This calculation gave 4.45 kg ha^{-1} of forage for 1% ground cover of the herb layer. The conversion factor depends upon the heights of the herbs comprising the percent cover estimate (Traczyk and Traczyk 1977). However, in most of the habitat assessments where herbs made a substantial contribution to the total food source, Epilobium angustifolium was the species with the greatest percent cover. This predominance of E. angustifolium would mitigate the problem of differing biomass : cover relationships between species. The contribution of herbs to the total amount of food is given in Table I, acknowledging potential errors involved in estimation of herbaceous forage using the above

method.

Conifers

The contribution by conifers to the available deer food at the Habitat Assessment sites was estimated in a manner similar to that used for herbs. Percent cover of conifers was estimated differently in logged and unlogged sites due to differences in the availability of conifers as food for deer. In the logged areas, the total percent cover of conifers below 10 m high was used in Table I. In forested areas, the percent cover of conifers less than 2 m high was used. The two approaches were employed because, in logged areas, conifers below 10 m high had branches reaching to the ground. In unlogged areas, conifers 2 to 10 m high did not have low reaching branches. A factor used to convert percent cover of conifers to biomass of deer food was calculated from Gates (1968). The dry weights were expressed as 42% of the wet weights using data for Pseudotsuga menziesii given by Gates (1968). Four sites were given in Gates (1968 : 49) at which he measured both the percent cover of conifers and their biomass available as deer forage. At one of these sites, conifer biomass was much higher than the trend from the other three sites. This value appeared to be a result of a misplaced decimal point and so was not used in calculation of the conversion factor. Using the remaining three sites, the conversion factor used in Table I was, 1% of conifer cover equalled 3.06 kg ha^{-1} of conifer forage.

3.2.1. Abundance Of Food During Summer

Total amounts of food available to deer during summer are given in Table I. Estimates made by Gates (1968) of food biomass available to deer in summer are within the 95% confidence intervals of my estimates. Although Gates (1968) worked in the Coastal Douglas-Fir Biogeoclimatic Zone, agreement of our data supports assumptions that I made to estimate shrub productivity. Average food abundance for each association and seral stage is presented in Figure 5. Four of the nine associations (Vaccinium-Skunk Cabbage, Salal-Douglas-fir, Amabilis Fir-Twisted Stalk, and Mountain Hemlock-Copperbush) had much greater food abundance than the other five associations. In these four associations most of the available food was contributed by shrubs.

Two associations, Amabilis Fir-Western Hemlock and Salal-Western Hemlock, had moderate amounts of forage; shrubs were again the main component. The remaining three associations, Sword Fern-Western Red Cedar, Deer Fern-Western Hemlock, and Western Hemlock-Plagiothecium, had small amounts of food. Food in these associations was comprised mainly of conifers. In all plant associations, except the Vaccinium-Skunk Cabbage association, herbs were a small portion of total available food. In the Vaccinium-Skunk Cabbage association, herbs were a minor component compared to total food abundance (15%), but were greater in abundance than in any of the other associations and about two-thirds as abundant as herbs in young seral stages.

Conifers provided most of the available food in the newly logged seral stage. Data for this seral stage were based on only one site (a Salal-Western Hemlock association before it was

Figure 5. Abundance of food available to deer during summer in habitats used by radio-tagged deer over the year. Number of assessment sites are indicated above the histograms. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush . Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

FOOD (KG HA^{-1})

herb
shrub
conifer
lichen

VS SC DW WP AW SD SW   AT MC   N H F S C

Coastal Western Hemlock Zone   Mountain Hemlock
Zone

Immature Seral Stages

Forested Plant Associations
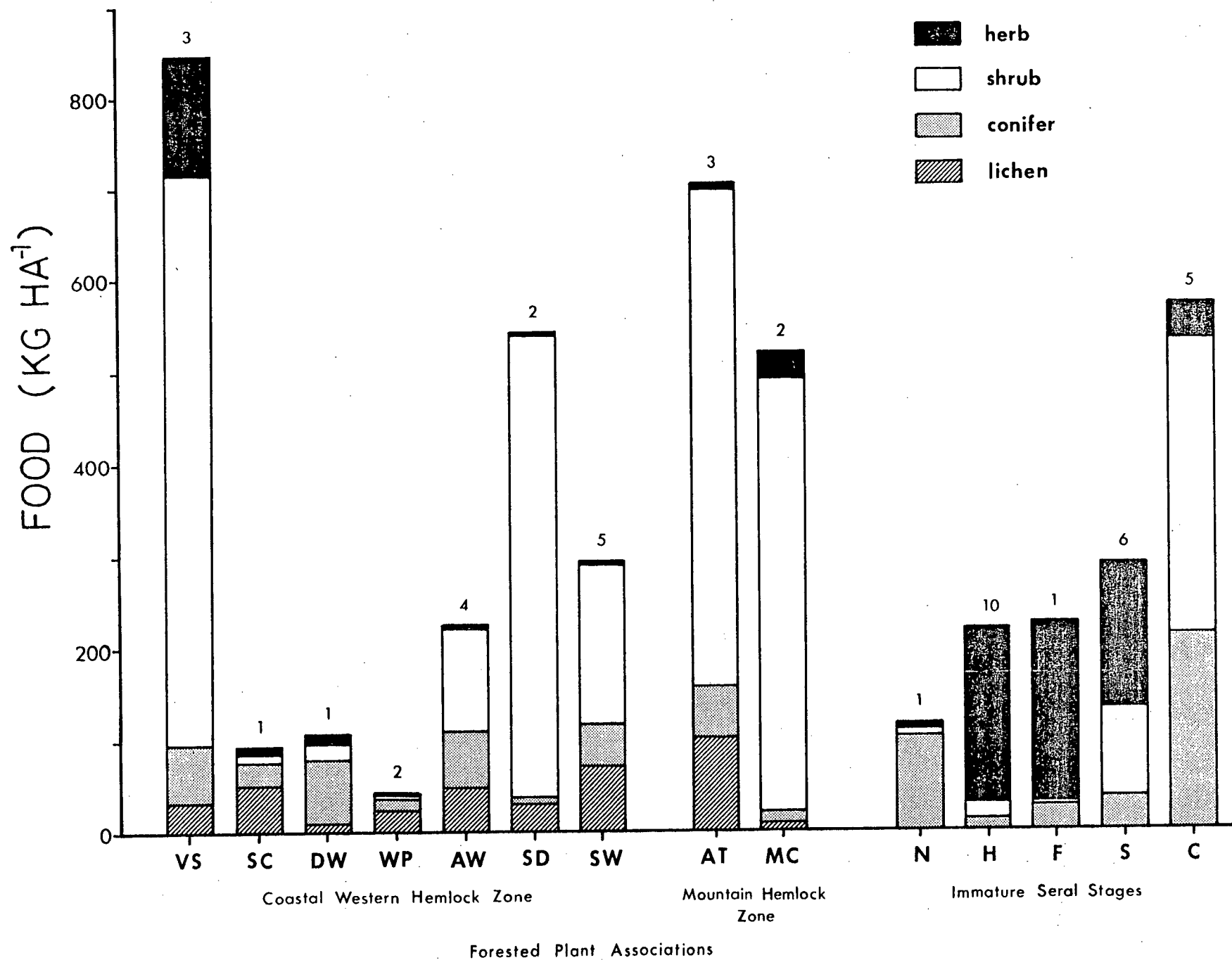
logged). At other sites with different climax plant associations, herbs or shrubs may form the greatest component of available food. In herb, fern, and shrub seral stages, herbs formed the greatest component of available food. The shrub seral stage had less herb food than did the herb and fern seral stages; however, it had a greater total food abundance due to increased amounts of shrubs (Fig. 5). In the oldest seral stage considered, herbs were replaced by shrubs and conifers as the major components of the available food. In this seral stage shrub food was more abundant than conifer food. Total food abundance in the conifer seral stage was greater than in other seral stages.

In contrast to forested plant associations where the main component of the available food was shrubs, food in young seral stages consisted mainly of herbs. Old seral stages were similar to forested plant associations in that shrubs comprised most of the available food. However, older seral stages had much greater amounts of conifer forage than did forested plant associations . In total food abundance, young seral stages had more food available in summer than some forested plant associations ,but much less than the most productive forested plant associations (Fig. 5). The conifer seral stage was comparable in food abundance to some forested plant associations , but food was less abundant in this seral stage than in the Vaccinium-Skunk Cabbage and Amabilis Fir-Twisted Stalk associations.

3.2.2. Abundance Of Food During Winter

During winter, snow accumulation and melt (Fig. 2) affect the amount of food available to deer. Snow can affect food availability in two ways: it can bury food sources or it can restrict deer mobility and thus prevent deer from obtaining exposed food.

The degree to which snow covers and buries food plants can be evaluated by considering the vertical distribution of the shrub component of the food resources. The current year's shoot annual growth of shrubs is contained within the crown and is a major winter food source for deer (Jones 1975, Rochelle in prep.). Crown depths of the three shrub species considered important in the study area were a nearly constant proportion of total stem height (37 to 49%) (Fig. 6). Regression equations (Fig. 6) were used to predict crown depths of shrub stems measured on plots at the Habitat Assessment sites. Noting that the amount of food produced by each stem can be determined from the height-annual growth relationships (Fig. 4), and assuming that the annual growth of each stem is apportioned evenly over crown depth, then the vertical distribution of shrub annual growth within each forested plant association or seral stage can be simulated (Fig. 7). The amount of annual growth occurring above a given height was calculated so that the effect of snow could be evaluated. The effect of snow through depression of shrubs and thus their burial by shallower snow depths, is not accommodated in Figure 7. Such displacement would cause the amounts of food exposed above the snow to be less than those indicated. Under certain snow conditions, downward displacement

Figure 6. Crown depth and stem height in shrubs important as deer forage. The relationship between crown depth and stem height in shrubs allows predictions of the vertical distribution of shoot annual growth. C = crown depth (cm), H = height from ground to top cf crown (cm).

Vaccinium parvifolium : C = -.70 + .49±.09 H , p≤ .00, r²= .79

Vaccinium alaskaense : C = 1.51 + .37±.04 H , p≤ .00, r²= .69

Gaultheria shallon : C = .97 + .49±.06 H , p≤ .00, r²= .88

V. parvifolium

V. alaskaense

G. shallon

CROWN DEPTH (CM)
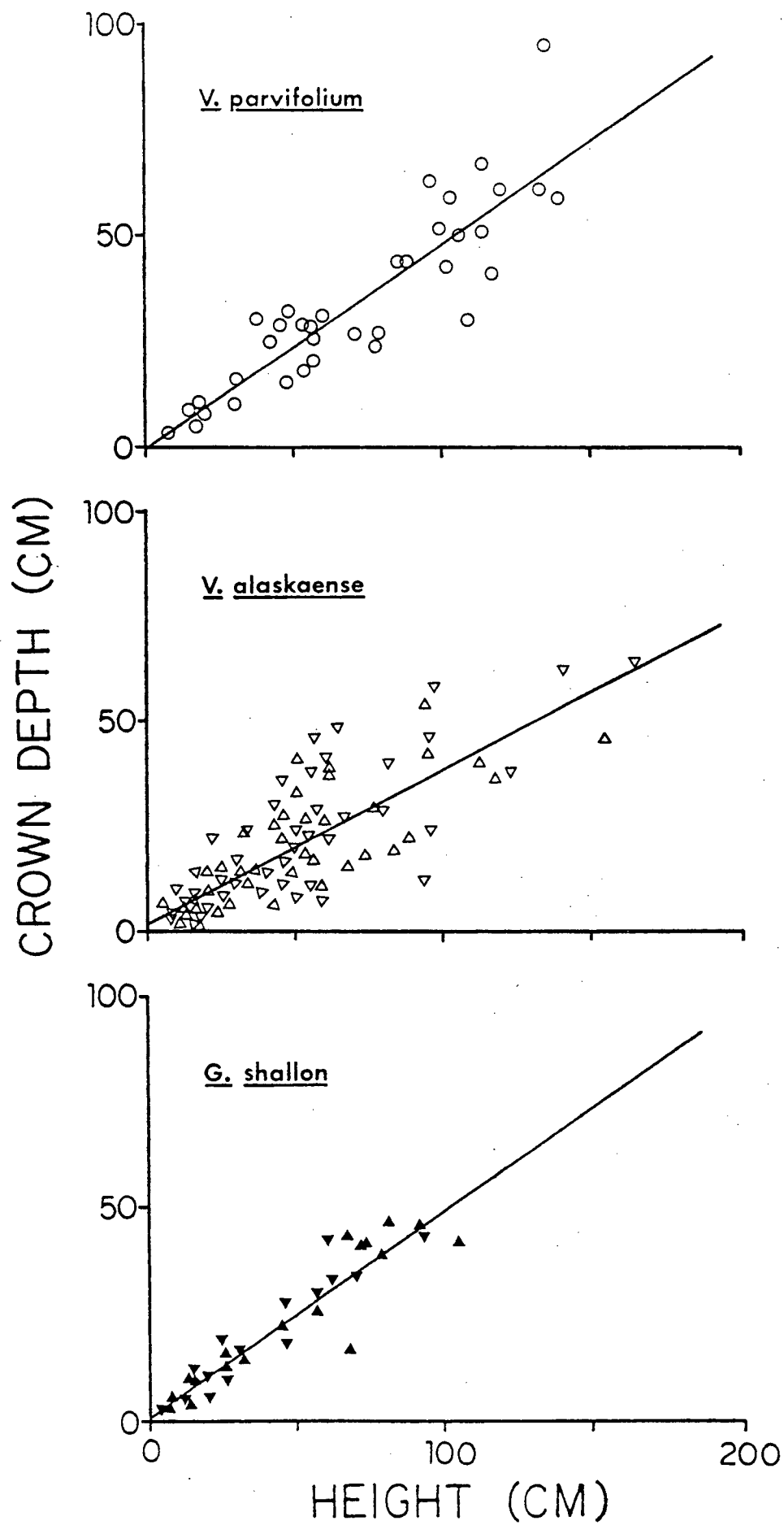
HEIGHT (CM)

Figure 7. Vertical distribution of shrub annual growth in forested plant associations and seral stages. Ordinate is the biomass available above the height from the ground on the abscissa. This biomass is the amount of food that would be available above the snowpack assuming no displacement of shrubs. Estimates of total available annual shoot growth of three main shrub species decrease with increasing height above the ground. When snowdepths are 50 cm, approximately 50% of the shrub food in forested habitats is buried, whereas 80% of the shrub food in immature seral stages is buried. These estimates do not include the effects of shrub displacement by the snowpack. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush . Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.
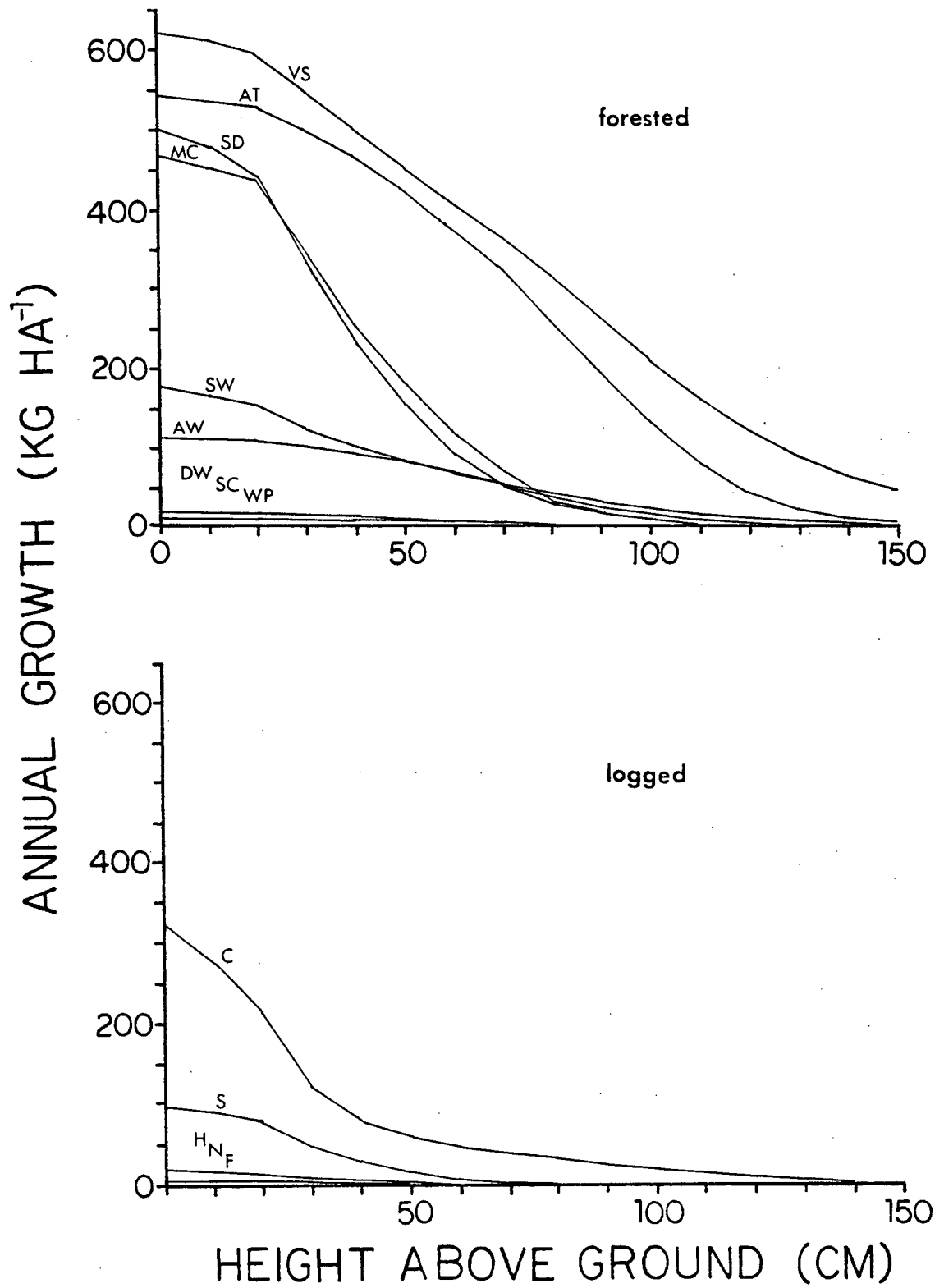
of shrub crowns could permit the complete burial of shrubs by shallow snowpacks.

The magnitude of differences in shrub abundance between plant associations and seral stages does not permit a direct comparison of the sensitivity of shrub abundance to snow depth in these habitats (Fig. 7). Differences in sensitivity of shrub availability to snow depth is more evident when the vertical distribution of shrub annual growth is considered relative to the total amount of shrubs available during snow-free periods. Generally, food abundance was less affected by snow in forested than in cutover areas. This difference results because shrubs were taller in forests than in cutovers. If only burial by snow is considered and no displacement of stems is accounted for, then, in forested habitats, snow depths of between 50 and 110 cm are needed to cover 75% of the food provided by shrubs; in logged areas snow depths of between 20 and 50 cm achieve the same effect.

Effect Of Snow On Posture Of Shrubs

In the Amabilis Fir - Twisted Stalk association at 900 m, nearly all the shrub stems were prostrate on the ground on June 6, 1976 and covered by up to 30 cm of snow. At this time the mean distance and 95% confidence limit from the ground to the markers on <u>Vaccinium</u> <u>alaskaense</u> stems buried beneath the snow was 8.8 ± 4.2 cm (n = 17); for <u>Menziesia</u> <u>ferruginea</u> stems this distance was 6.2 ± 3.1 cm (n = 3). On July 2 after the snow had melted and the shrubs had returned to their snow-free postures, the mean distance from the ground to the markers was 64.1 ± 14.5

cm for Vaccinium alaskaense and 102.0 ± 36.2 cm for Menziesia ferruginea. Before the snow had completely melted, the shrubs were depressed to less than 14% of their snow-free height.

The markers were located near the crowns of the stems suggesting that deer food provided by shrub crowns was also vertically redistributed by snow. On June 6, most of the Vaccinium alaskaense crowns were within 10 cm of the ground and covered with snow even though the snow was generally less than 30 cm deep. It appears that V. alaskaense stems are buried by the deepening snowpack and become entrapped within it. Because of snow metamorphosis the snow compacts and decreases in depth. The entrapped stems are pulled down with the collapsing snowpack. The shrub stems are eventually released at the bottom of the snowpack when their encasing snow melts. On sloping terrain snowcreep would also contribute to the burial process.

Where shrubs are covered by snow in winter and entrapped in the snowpack, the displacement of crowns would make the shrubs unavailable as deer food until virtually all the snow had melted. When the snowpack melts, the amount of available food contributed by shrubs is increased.

The burial of shrubs by snow is dependent not only on snow depth, but also on duration of snow cover, relative rates of snowpack accumulation and melt, and the shrub's structure. Although not quantified, interception of falling snow by crowns of Vaccinium species was usually insufficient to cause large vertical displacements of the stems. However, Gaultheria shallon intercepts snow readily and consequently is noticeably displaced after a snowfall.

Amount Of Food Available During Winter

The amount of food exposed above the snowpack changed with each snowfall and period of snow melt. To illustrate the effect of snow depth on food abundance, snow depths recorded on March 31, 1976 were applied to the vertical distribution of shrub food for each Habitat Assessment site. Snow depths in Figure 2 were used for logged areas. Snow depths in forested habitats were estimated using the relationship modified from Fitzharris (1975):

C = -26.0 + 0.65 L

C = the amount of snow beneath a canopy, L = snow depth in logged areas. Fitzharris (1975) expressed snow depths in cm of water equivalent but found no consistent trends in snow densities inside and outside of forested areas. Therefore I multiplied the y intercept by 10 to estimate snow depth. The amount of food contributed by shrubs and exposed above the snowpack was calculated on the basis of direct burial by snow and did not include downward displacement of the stems. Herbs were considered unavailable to deer during these snow conditions. Conifers were thought to have the same availability in winter as they had in summer. This assumption would overestimate the abundance of the conifer component in young seral stages where the young trees are short and would be covered with snow. Since there was only a small amount of conifer food available in these areas during snow-free periods (Fig. 5), this assumption would not make substantial differences to annual trends in food abundance. In older seral stages and in forested habitats, the conifer understory was much taller. Snow

would cover some of the lower conifer food sources, and at the same time raise the substrate so that previously unavailable conifer food sources would be within reach of deer. Consequently, the assumption would not introduce major errors in estimation of the conifer component over the range of snow depths encountered. The contribution by lichens was based on the total five month litter-fall and was estimated as 12% of the total lichen biomass present (Stevenson 1978).

These estimates of food exposed above the snow depths recorded on March 31 are illustrated in Figure 8. They consider only burial of shrubs; effects of shrub displacement on these estimates would be substantial for some habitats and minor in others. The vertical distribution of shrubs would be most affected in areas where there were partial reductions in the snowpack while still having a continuous snow cover throughout winter. In these areas, shrubs would be progressively displaced downward with each snowfall and subsequent metamorphosis of the snowpack. On the south-facing slope of Mount Cain where snow depths in Figure 2 were obtained, elevations above 700-800 m had continuous snow cover throughout winter. These elevations would be subjected to the displacement of shrubs by the settling snowpack. On the more northerly facing and less steep slopes, the elevation above which shrub entrapment and displacement occurred would extend lower than 700-800 m.

With one exception all the sites classed as either Amabilis Fir-Twisted Stalk or Mountain Hemlock-Copperbush associations were above 700 m. The exceptional site was at an elevation of 678 m and on a north-northeast-facing slope. All of the sites

Figure 8. Abundance of food available to deer during winter on seasonal home ranges. Number of assessment sites are indicated above the histograms. Arrows indicate that the shrub component would be reduced because of displacement of their crowns by snow. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush . Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

Legend:
- □ shrub
- ▨ conifer
- ▧ lichen

FOOD (KG HA^{-1})

800
600
400
200
0

VS   SC   DW   WP   AW   SD   SW   AT   MC   N   H   F   S   C

Coastal Western Hemlock Zone

Mountain Hemlock Zone

Immature Seral Stages

Forested Plant Associations

54
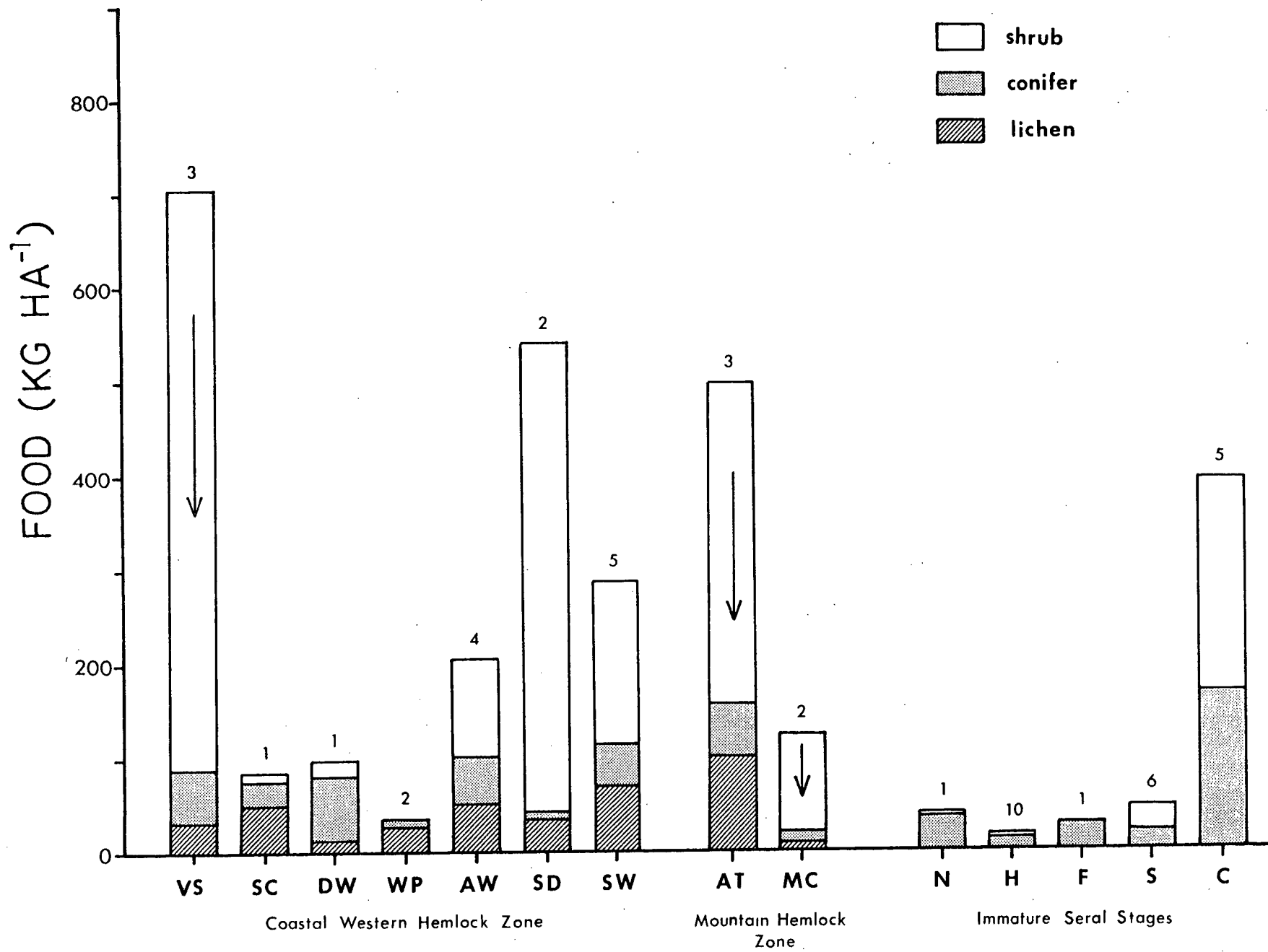
are within the altitudinal zone in which shrub entrapment and displacement would occur. Thus, food abundance in winter is likely overestimated for Amabilis Fir-Twisted Stalk and Mountain Hemlock-Copperbush asscciations.

Another forested plant association for which food abundance is probably overestimated was the Vaccinium-Skunk Cabbage association. Estimates of food abundance in this association were based on three areas in the Croman Valley bottom. Two of these Habitat Assessment sites were located in the middle and upper portions of the valley. These sites had deeper snow and longer lasting snow cover than did similar elevations in the Davie River Valley. Although few snow depths were taken in Croman Valley, the snow regime was similar to that of mid-elevations on the south-facing slope of Mount Cain. Considering the deeper snowpack and shrub displacement, the amount of food exposed in the Vaccinium-Skunk Cabbage association would be less than estimated in Figure 8.

Because of potential over-estimates of food abundance in winter on Amabilis Fir - Twisted Stalk, Mountain Hemlock - Copperbush, and Vaccinium - Skunk Cabbage associations, direct comparison of these associations with others in Figure 8 may be misleading. Estimates for the other plant associations were based on sites located below 700 m and therefore should be comparable and representative of actual amounts of food exposed above the snowpack. Since snow cover in these lower elevations was intermittent over winter, displacement of shrubs through entrapment in the snowpack would be much less than that at the higher elevations.

During winter, low elevation forested plant associations generally had more food exposed above the snowpack than did logged areas. Herb, fern, and shrub seral stages had more food than Amabilis fir - Western Hemlock and Salal - Western Hemlock associations in summer but had much less in winter (Fig. 5 and 8). Newly logged, herb, fern, and shrub seral stages provided even less food than Sword Fern-Western Red Cedar, and Deer Fern-Western Hemlock associations and were similar in food abundance to the Western Hemlock-Plagiothecium association.

Of the six forested plant associations that can be compared, Amabilis Fir-Western Hemlock, Salal-Douglas-fir, and Salal-Western Hemlock associations had greater amounts of food than did other forested associations. These differences were mainly due to differences in shrub abundance. Rochelle (in prep.) measured 96 and 392 kg ha^{-1} of available deer forage in low and mid-elevation forested habitats respectively. These values are similar to my estimates of available deer forage (43 to 504 kg ha^{-1}) at these elevations. The conifer seral stage was the only logged habitat that had substantial amounts of food during winter. This seral stage had more food available than did Amabilis Fir - Western Hemlock and Salal - Western Hemlock associations, but less than that in the Salal - Douglas-fir association. In the conifer seral stage and the three forest associations in which food was most abundant, the shrub component of the total available food was greater than the conifer and lichen components.

The amounts of food available to deer in the different forested plant associations and seral stages were not determined for spring but evaluated qualitatively and presented later.

3.3. Density Of Available Digestible Dry Matter

The densities of food available to deer in the habitats during summer and winter (Fig. 5 and 6) were converted to densities of digestible dry matter (Fig. 9) using factors provided by Rochelle (in prep.) for the major forage components.

During summer the Vaccinium - Skunk Cabbage, Amabilis Fir - Twisted Stalk, and Mountain Hemlock - Copperbush associations had the highest densities of available digestible dry matter of all the forested plant associations (Fig. 9). During winter the density of digestible dry matter available in these associations declined and may be below the densities of digestible dry matter available in the Amabilis Fir - Western Hemlock, Salal - Douglas-fir, and Salal - Western Hemlock associations. The Sword Fern - Western Red Cedar, Deer Fern - Western Hemlock, and Western Hemlock - Plagiothecium associations have low densities of available digestible dry matter in both summer and winter.

In cutover areas during summer the densities of available digestible dry matter in all seral stages except the newly logged seral stage were similar to those available in the Vaccinium -Skunk Cabbage, Amabilis Fir - Western Hemlock, Salal - Douglas-fir, Salal - Western Hemlock, Amabilis Fir - Twisted Stalk, and Mountain Hemlock - Copperbush associations (Fig. 9). During winter all seral stages, except the conifer seral stage

Figure 9. Density of digestible dry matter during winter and summer in habitats used by radio-tagged deer. Number of assessment sites are indicated above the histograms. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush . Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

Figure showing DIGESTIBLE DRY MATTER (KG HA⁻¹) on the y-axis for Forested Plant Associations. Bars grouped by Coastal Western Hemlock Zone (VS, SC, DW, WP, AW, SD, SW), Mountain Hemlock Zone (AT, MC), and Immature Seral Stages (N, H, F, S, C), with summer (filled) and winter (open) categories.
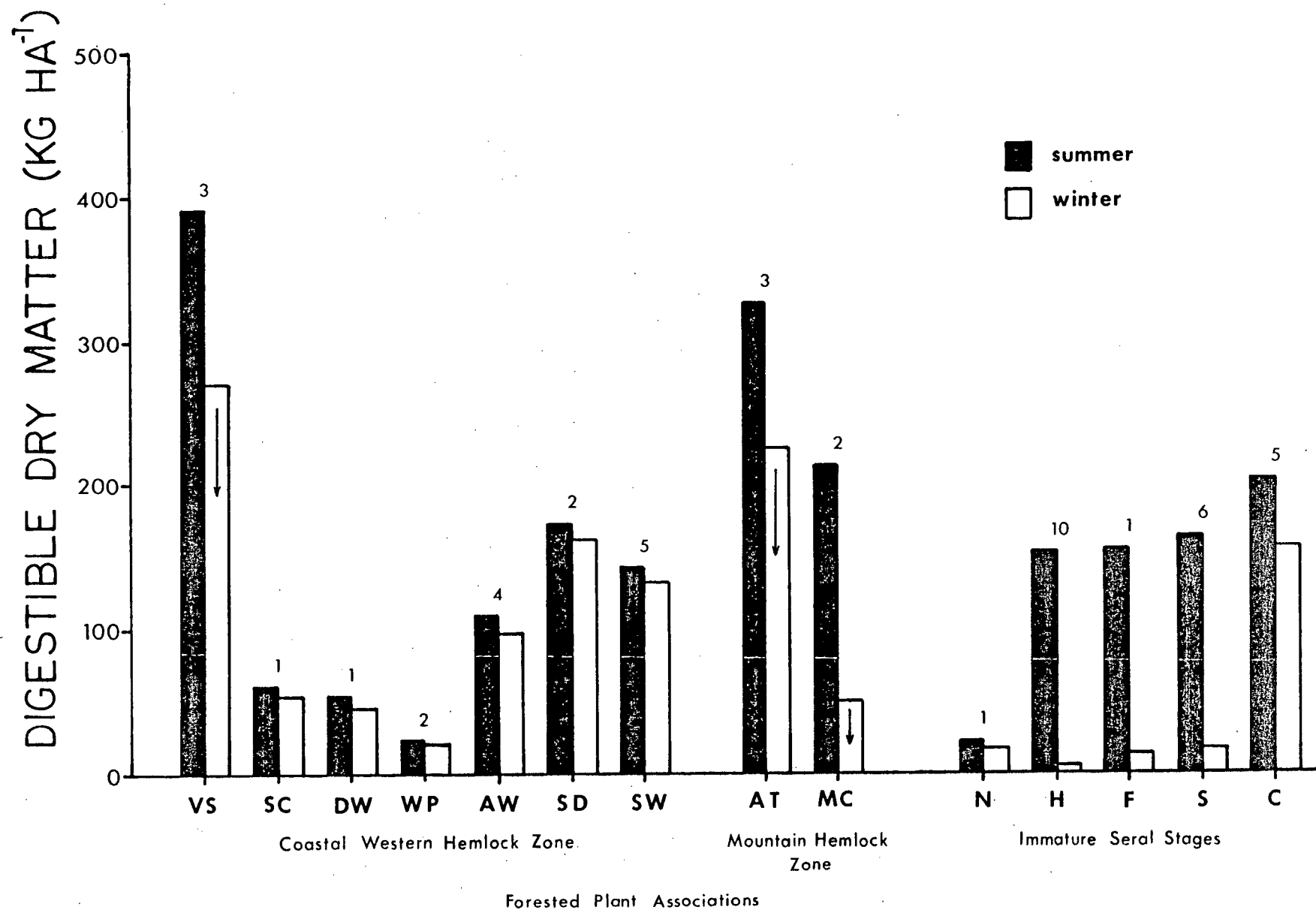
had low densities of available digestible dry matter. These differences in the density of available digestible dry matter between summer and winter were primarily a result of the lack of herbs and burial of shrubs by snow during the winter.

The density of digestible dry matter available to deer during the spring on the forested plant associations and seral stages could not be adequately estimated and so are not included in this section. This season will be compared qualitatively to the other seasons when the movements and habitat use of the deer have been presented.

The implications of the relative densities of available digestible dry matter to the seasonal movements of black-tailed deer will be discussed later. First seasonal movements and habitat use of black-tailed deer are described. These movements are then evaluated with regard to the densities of available digestible dry matter and other factors.

3.4. Seasonal Movements Of Radio-tagged Deer

Sufficient data were collected from seven radio-tagged deer (Table II) to consider their patterns of seasonal movements. The locations of these deer over the year suggested that generally three seasonal home ranges were used, corresponding to spring, summer, and winter. For five deer, seasonal home ranges of each deer were separated. For two deer the seasonal home ranges of each deer overlapped extensively. In both of these latter deer, seasonal home ranges were defined by different areal distributions of locations obtained between certain dates. The dates were based on shifts in locations of the deer together

Table II. List of radio-tagged deer and seasons for which home range data were obtained. All radio-tagged deer were adults.

	Deer	Sex	Sector	Spring	Summer	Winter	Comments, Observation Period, (Number Of Locations)
MIGRATORY	OFL61	male	Croman	X	X	X	May 1975 to September 1976. (106)
	OFL68	female	Mount Cain	-	X	X	no locations obtained for spring; killed at beginning of winter, 1975; accompanied by one fawn. July to November 1975. (36)
	OFL67	female	Maquilla	X	X	X	June 1975 to June 1976. (98)
	OFL60	female	Croman	X	X	X	accompanied by one fawn in 1976. May 1975 to April 1976. (64)
	OFL71 *	female	Croman-Hoomak	X	X	X	accompanied by two fawns in 1976. July 1975 to September 1976. (212)
RESIDENT	OFL58	female	Mount Cain	X	X	X	few locations obtained for spring; killed at beginning of winter, 1975. April to November 1975. (47)
	OFL62	male	Croman	X	X	X	May 1975 to June 1976. (165)

* horizontal migrator

with the occurrence of seasonal movements by the five migratory
deer and night count observations. Spring home ranges were
occupied between March and June; summer home ranges between June
and November; and winter home ranges between November and March.
These periods of seasonal home range occupancy differed between
deer and are discussed more fully in Section 3.4.4.

3.4.1. Statistical Parameters Of Home Ranges

Statistical evaluation of seasonal changes in the position
of home range centres can be made if the locations approximate a
bivariate normal distribution. The locations of each deer were
grouped by season and the dispersion parameters of these groups
were estimated. Arithmetic mean centres (after Neft 1966) were
calculated for the seasonal distributions of radio-tagged deer.
The deer's locations in each seasonal home range were
hypothesized to be distributed about the arithmetic mean centre
according to a bivariate normal distribution. Comparisons of
seasonal distributions to bivariate normality were tested using
the "ring" test (Kowalski 1970). The "ring" test compares the
frequency distribution of distances between locations and the
arithmetic mean centre, to the frequency distribution of these
distances in a bivariate normal distribution. The Kolmogorov-
Smirnov one-sample test (Siegel 1956 : 47) was then used to test
the significance of differences between the two distributions.

Sixteen of the 21 seasonal home ranges were not
significantly different (p > .05) from a bivariate normal
distribution (Table III). Five home ranges differed
significantly (p ≤ .05) from a bivariate normal distribution in

Table III. Statistical characteristics of seasonal home ranges. Areal distributions that are significantly different (p≤.05) from a bivariate normal distribution are underlined. The "ring test", incorporating the Kolmogorov-Smirnov test, was used to compare the seasonal areal distributions with the bivariate normal distribution.

	Standard Distance Deviation (m) [+]			Skewness / Kurtosis		
	spring	summer	winter	spring	summer	winter
OFL61	376.6 (34)	1001.6 (39)	534.7 (33)	.18 / .38	.87 / -.10	.28 / .34
OFL68	-	395.1 (26)	649.9 (10)	-	.44 / .30	.34 / .71
OFL67	250.3 (50)	495.7 (10)	491.0 (38)	.12 / .50	.25 / .51	.26 / .42
OFL60	311.6 (15)	679.2 (20)	-	.44 / .05	1.08 / -.46	-
"	------------------ winter range		398.2 (12)	------------------------------		.24 / -.07
"	--------- auxiliary winter range		412.1 (17)	------------------------------		.17 / .29
OFL71*	157.4 (19)	490.5 (167)	262.2 (26)	.73 / -.19	.20 / .82	.12 / .57
OFL58	171.6 (3)	924.5 (29)	370.6 (15)	1.36 / -.50	.24 / .81	.47 / -.25
OFL62	484.2 (50)	508.1 (46)	455.2 (69)	.19 / .71	.31 / .03	.19 / -.26

MIGRATORY (rows OFL61–OFL71*)

RESIDENT (rows OFL58, OFL62)

+ number of locations are enclosed in brackets

* horizontal migrator

that they were all leptokurtic (more locations near the mean centre and at the tails than in a normal distribution) and slightly skewed (slightly asymmetrical). In one instance, that of the summer home range of OFL67, the difference between the observed distribution and the hypothesized bivariate normal distribution, was likely caused by inaccuracies in location. The summer home range of OFL67 was located in a remote area and, because of poor radio reception, I was able to get accurate locations on only a few occasions. The location of OFL67, when precise location was not possible, was estimated on the basis of several days's observations. This estimation resulted in several locations occurring at the same position and, when coupled with a small sample size, gave the appearance of a leptokurtic distribution.

Of the remaining four home ranges that differed significantly (p ≤ .05) from bivariate normality two home ranges, OFL58 summer and OFL62 spring, were not different at a probability level of 0.01. In all four home ranges, the differences from the bivariate normal distribution although significant, were not substantial with kurtosis reaching a maximum of 0.82 and skewness a maximum of 0.26.

3.4.2. Home Range Size

Home range size was calculated using modified versions of the minimum home range method first proposed by Dalke and Sime (1938) (Table IV). The 100% home range is the area enclosed by a convex polygon surrounding the outermost locations of the deer during a particular season. This is the most commonly used

Table IV. Size of seasonal home ranges. The 90% home ranges eliminate inflated home range sizes caused by extreme locations. The 50% home range is the area of intense deer use.

Size of Home Range (ha)

	Number of locations			100 %			90 %			50 %		
	SP	SM	WT	SP	SM	WT	SP	SM	WT	SP	SM	WT
MIGRATORY												
OFL61	34	39	33	89.3	406.6	186.7	38.6	274.1	84.7	4.2	30.7	10.6
OFL68	-	26	10	-	66.9	49.7	-	34.0	13.3	-	9.0	.6
OFL67	50	10	38	66.8	63.2	79.3	21.3	16.8	65.3	4.4	-	5.5
OFL60	15	20		27.0	138.1		14.9	88.4		4.6	28.3	
" ----- winter range			12			49.5			20.3			2.6
" aux. winter range			17			59.5			33.9			8.2
OFL71*	19	167	26	6.7	185.6	36.6	5.5	36.4	12.5	.5	13.5	2.4
RESIDENT												
OFL58	3	29	15	.3	152.0	16.0	-	20.0	12.0	-	4.1	2.7
OFL62	50	46	69	146.1	147.5	104.5	52.6	88.9	83.0	6.8	29.1	26.5
mean				56.0	165.7	72.7	26.6	79.8	40.6	4.1	19.1	7.4

* horizontal migrator

estimate of home range size. The size of the 100% home range is sensitive to extreme or abnormal locations of the animal. In order to circumvent this sensitivity, I calculated the 90% home range . This estimate of home range is the area enclosed by a polygon surrounding the closest 90% of the locations and eliminates the inflation in area caused by extreme locations when the 100% method is used. A third expression of size of home range is the 50% home range . This estimate is the area of a polygon enclosing the closest 50% of the locations and is useful in identifying the core of deer use within the 100 or 90% home ranges.

The 90% home ranges (Table IV) are shown in Figures 10 to 16. The 50 and 100% home ranges are not delineated, although locations of the deer are indicated. Size of home range is an areal expression of variability in a deer's average position. Since the area of a circle is proportional to the square of its radius then home range size should be proportional to the square of the standard distance deviation. Since the standard distance deviation (after Neft 1966) includes all locations, the 100% home range area was used as the dependent variable (Fig. 17). The r^2 of the regression was 0.61 and the slope of the regression line was significantly different from zero ($p \leq .05$). The exponent of the regression equation, 2.52 ± 0.97, included the hypothesized value of 2 in its 95% confidence limits.

Since 100% home range size was a function of standard distance deviation, a test for homogeneity of variance was used to determine if there were seasonal differences in the size of 100% home ranges (Tables IV and V). Aside from three exceptions,

Figure 10. Seasonal 90% home ranges of altitudinal migrator OFL61. Shaded areas are logged, unshaded areas are unlogged.

▦ 90% spring home range	○	spring location
▤ 90% summer home range	■	summer location
▧ 90% winter home range	●	winter location

OFL 61

0   1   2

KM

Croman Cr.

Tsitika R.

400

800

1200

400
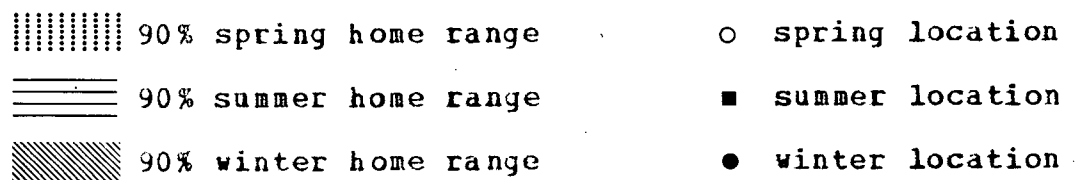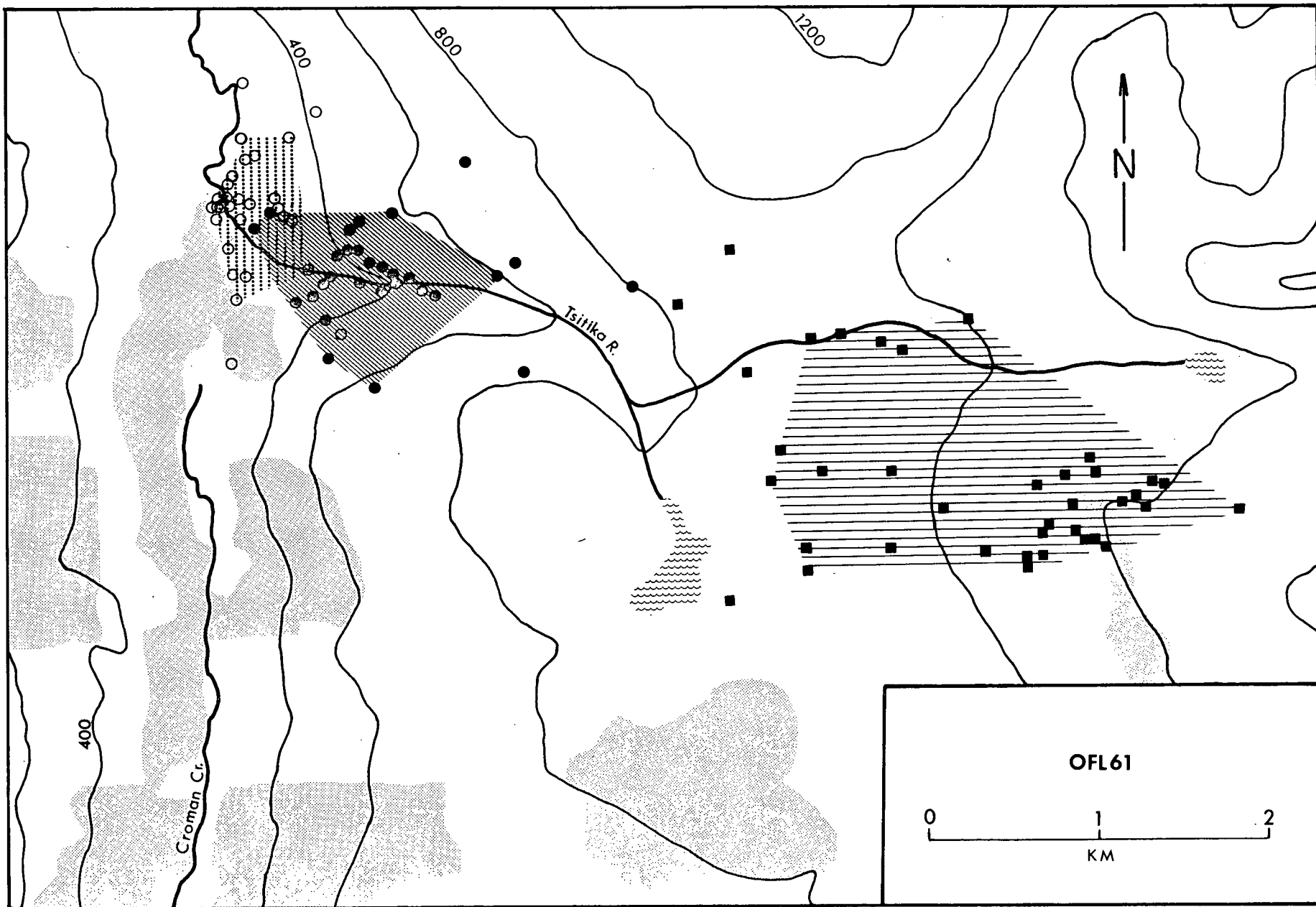
Figure 11. Seasonal 90% home ranges of altitudinal migrator OFL68. Shaded areas are logged, unshaded areas are unlogged.

≡≡≡ 90% summer home range   ■ summer location

▨▨▨ 90% winter home range   ● winter location

OFL 68

0   1   2

KM

Davie R.

Cain Cr.

1200

800

400

400
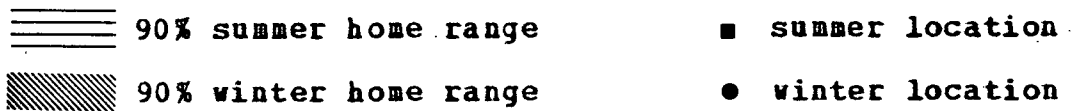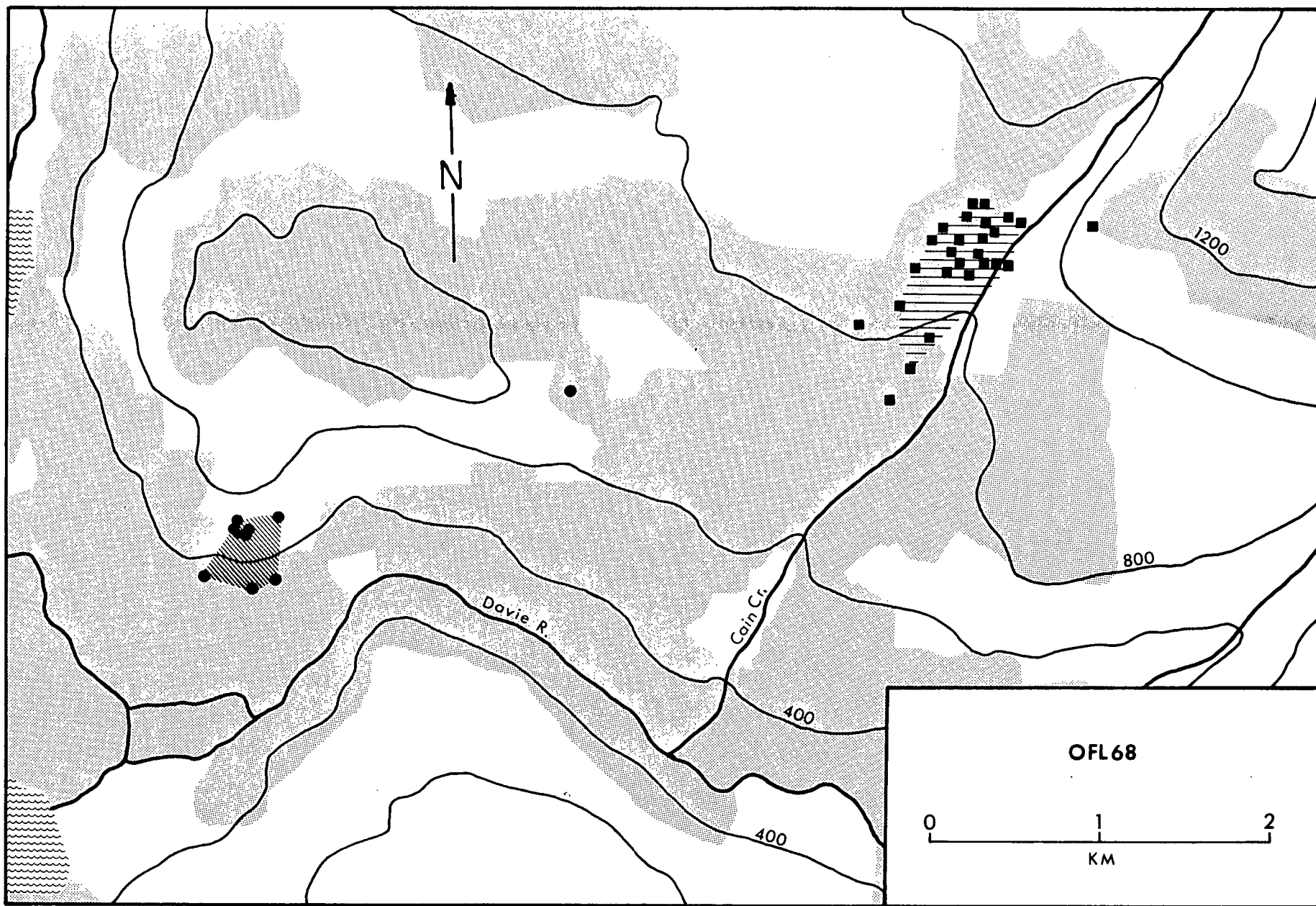
Figure 12. Seasonal 90% home ranges of altitudinal migrator OPL67. Shaded areas are logged, unshaded areas are unlogged.

|||||||||| 90% spring home range   ○ spring location

≡≡≡ 90% summer home range   ■ summer location

▨▨▨ 90% winter home range   ● winter location

OFL67

Able Cr.

Cain Cr.

Dovie R.

800

400

400

800

N

0   1   2
        KM
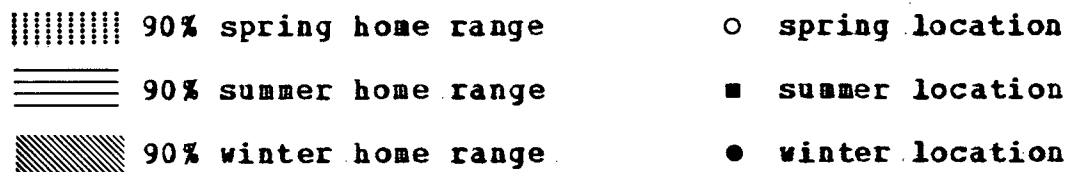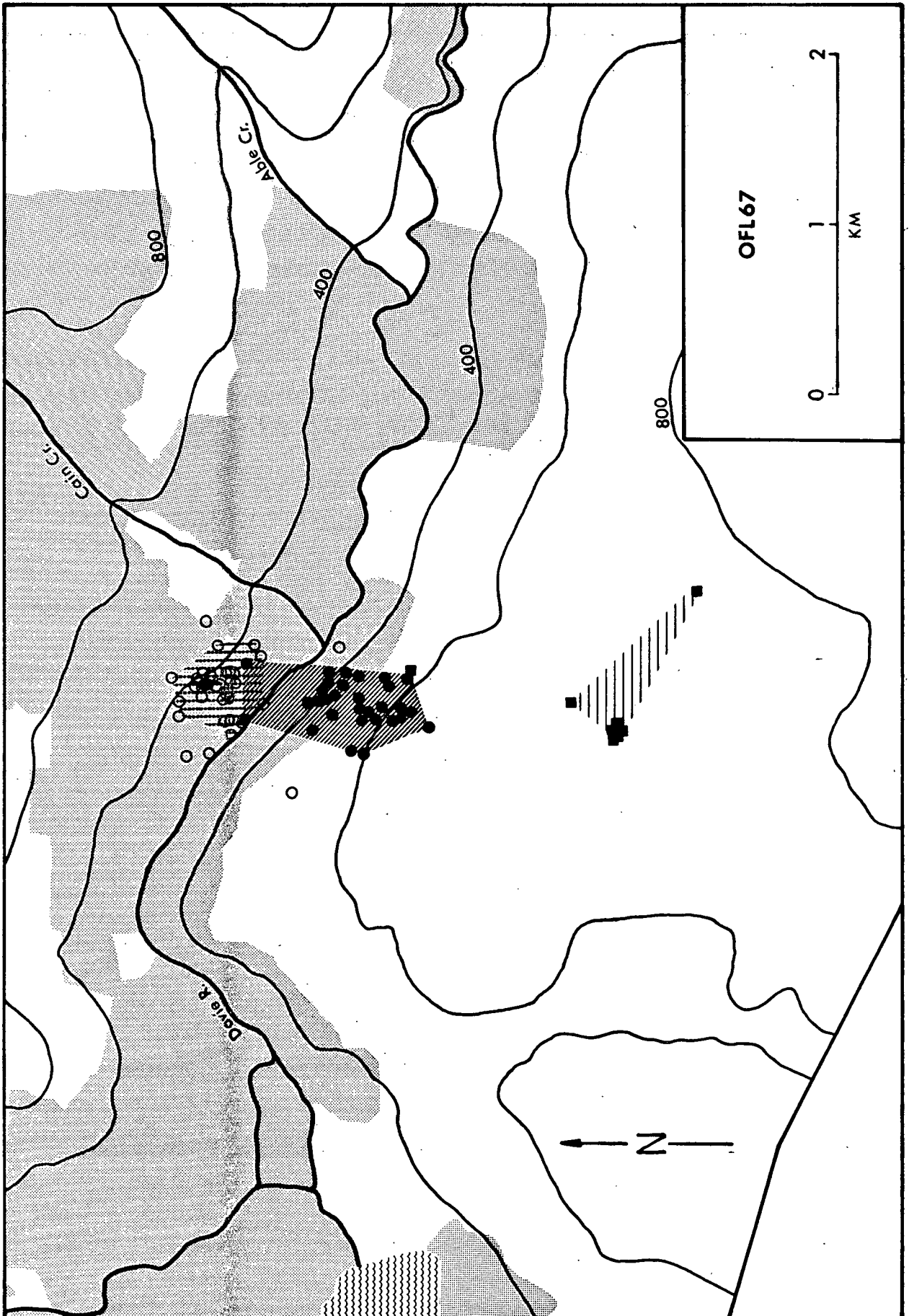
Figure 13. Seasonal 90% home ranges of altitudinal migrator OFL60. Shaded areas are logged, unshaded areas are unlogged.

‖‖‖‖‖	90% spring home range	○ spring location
≡≡≡	90% summer home range	■ summer location
▨▨▨	90% winter home range	● winter location

Croman Cr.

N

OFL60

0   1   2
KM
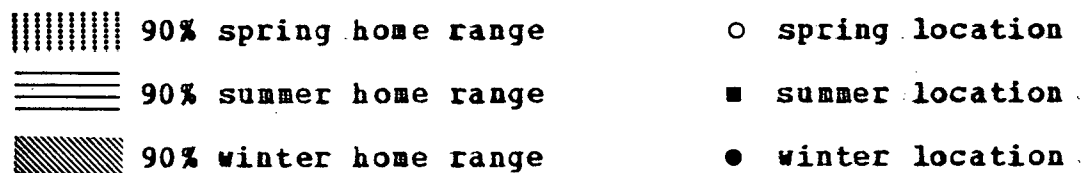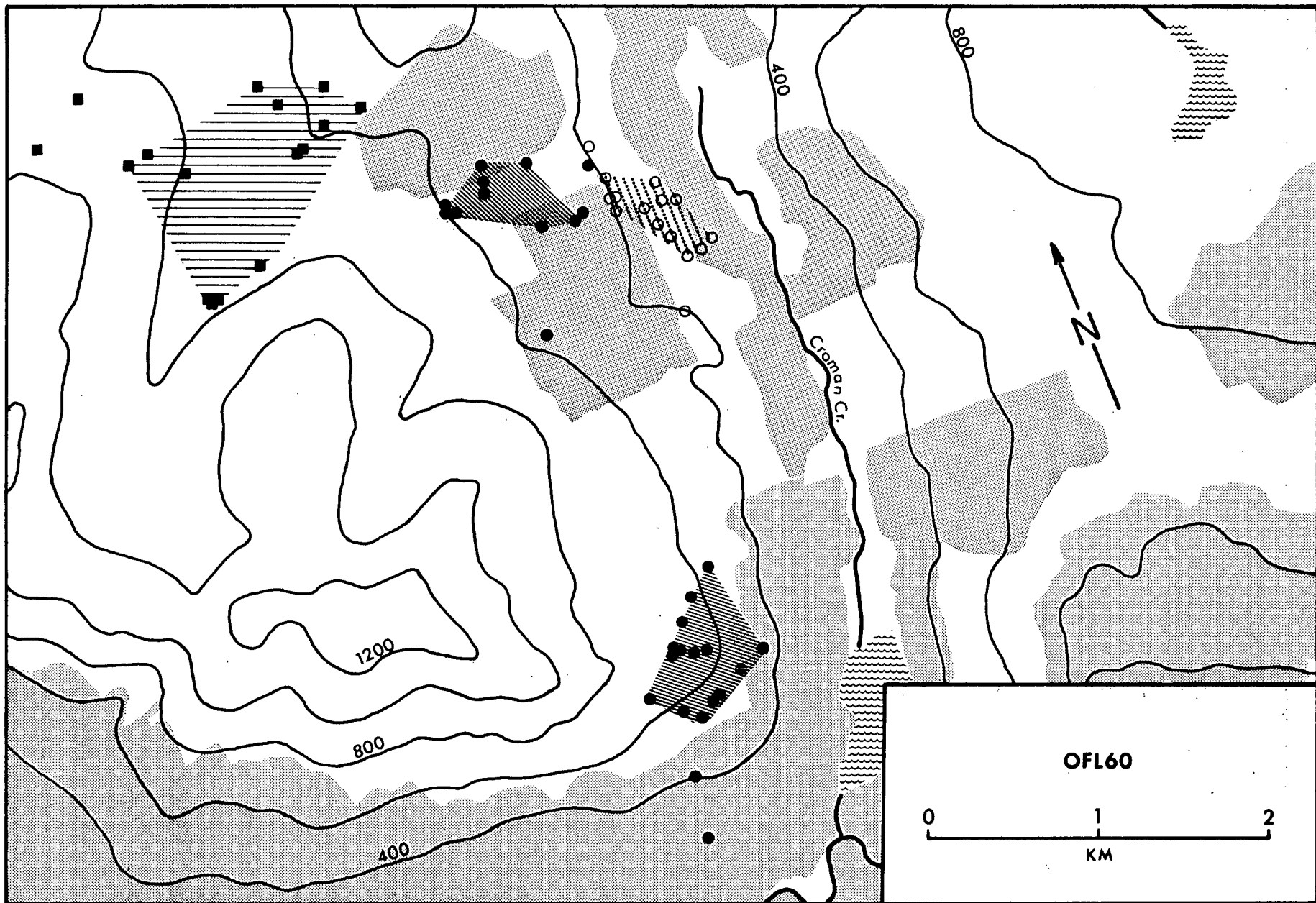
Figure 14. Seasonal 90% home ranges of horizontal migrator OPL71. Shaded areas are logged, unshaded areas are unlogged.

|||||||||| 90% spring home range   o spring location

≡≡≡ 90% summer home range   ■ summer location

▨▨▨ 90% winter home range   ● winter location

OFL71

Croman Cr.

Davie R.

0   1   2
KM
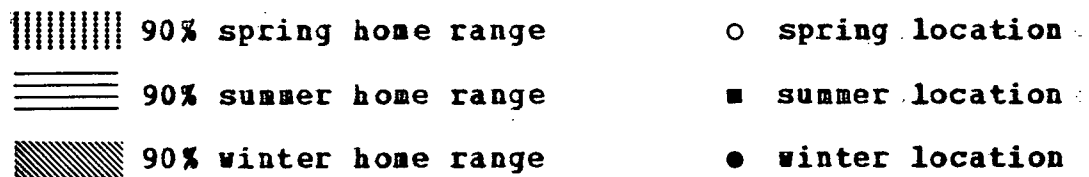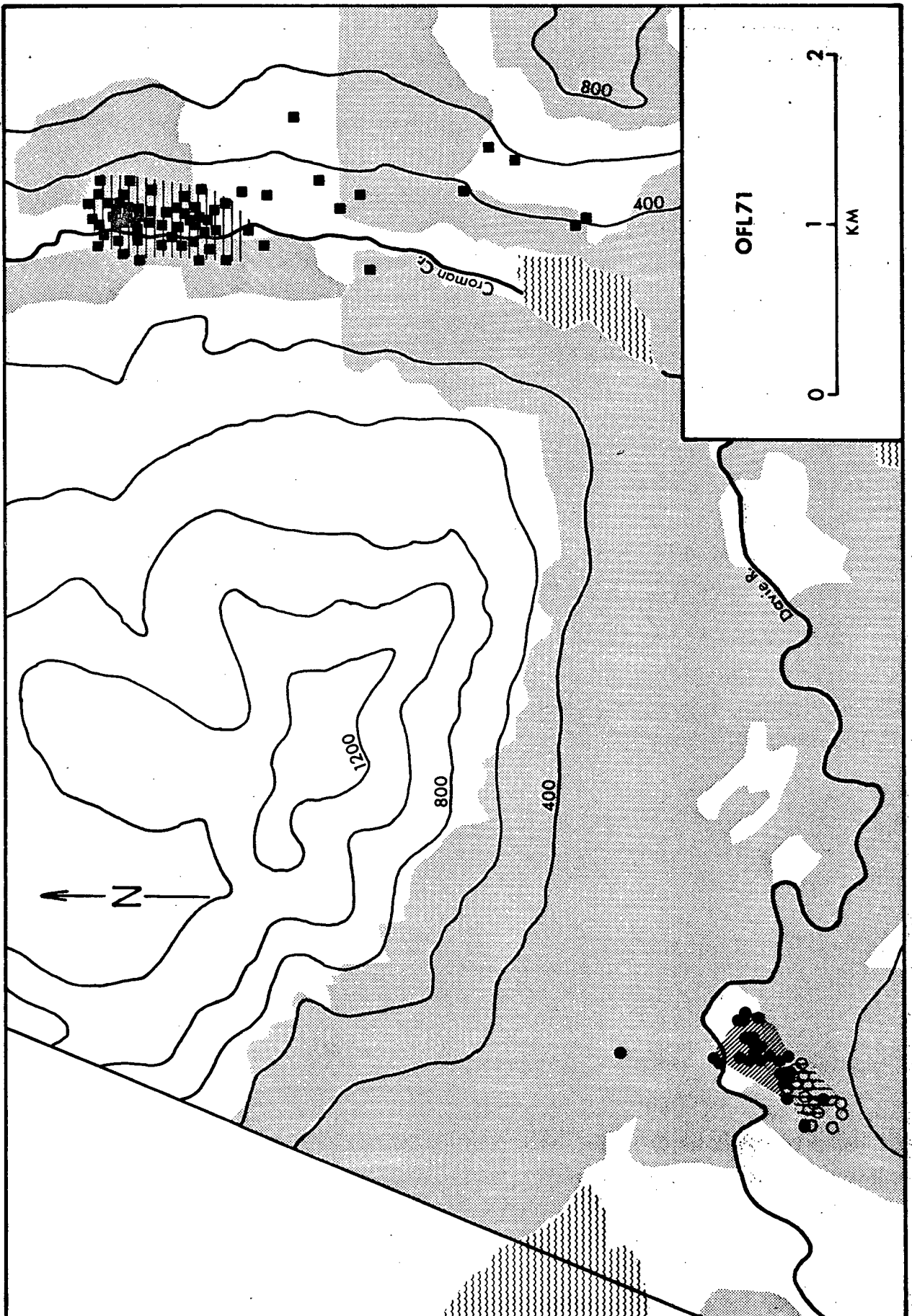
Figure 15. Seasonal 90% home ranges of resident OFL58. The 90% spring home range is not shown but it overlaps extensively with the 90% summer home range. Two extreme locations in summer are indicated with ■ ; other locations are not shown. Arithmetic mean centres of seasonal home ranges are indicated by:

☆ spring, ✪ summer, ★ winter. Shaded areas are logged, unshaded areas are unlogged.

≡ 90% summer home range

▨ 90% winter home range

Cain Cr.

1600

1200

N

800

Able Cr.

Davie R.

400

400

OFL 58

| 0 | 1 | 2 |

KM

81
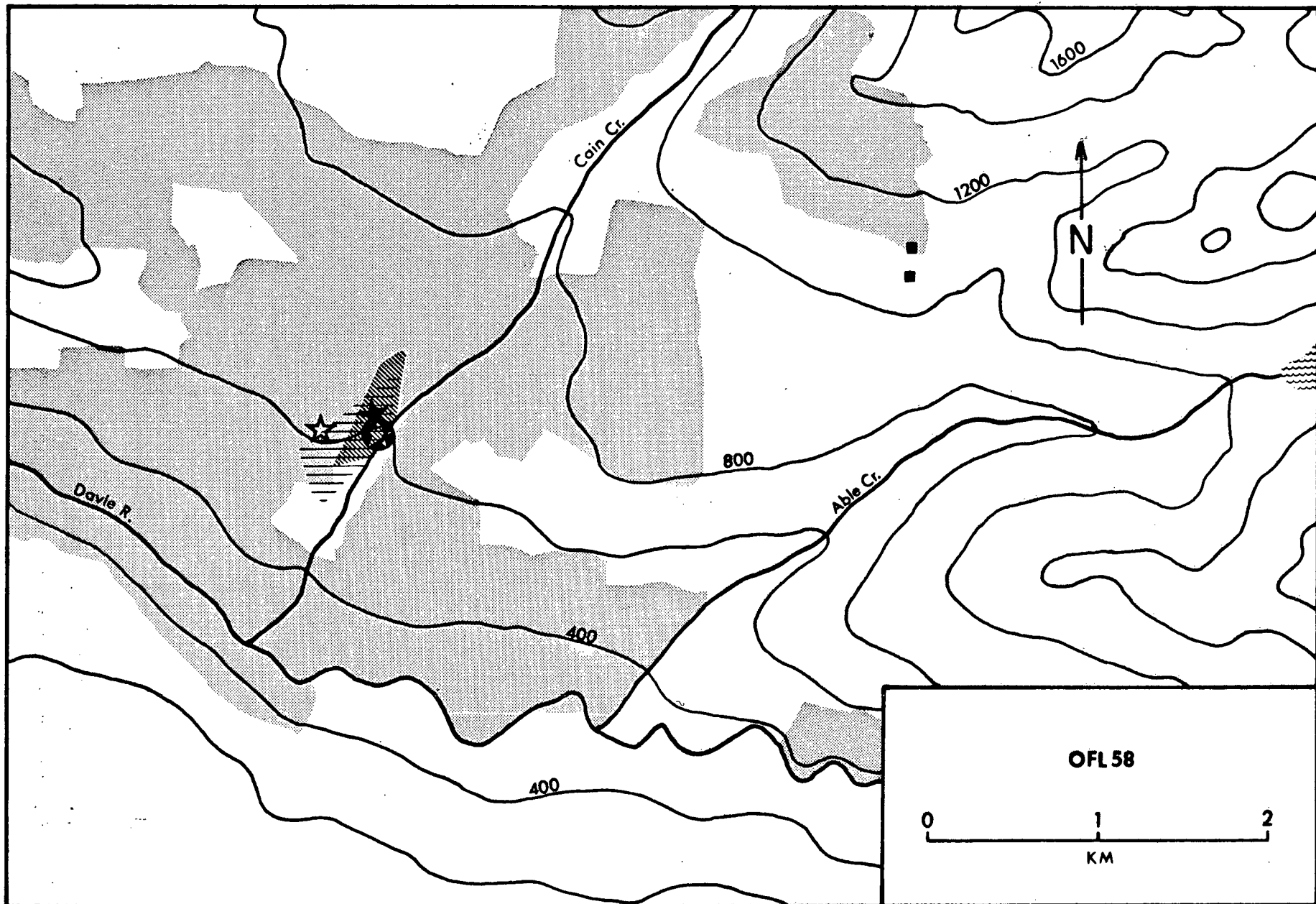
Figure   16.,   Seasonal   90%   home   ranges   of   resident   OFL62.
Arithmetic mean centres   of seasonal home   ranges   are indicated
by:

☆ spring,   ✪ summer,   ★ winter. Shaded   areas   are
logged, unshaded areas are unlogged.

|||||||||| 90% spring home range

≡≡≡ 90% summer home range

▧▧▧ 90% winter home range

Croman Cr.

Davie R.

1200

800

400

800

800

400

400

OFL62

0   1   2
          KM

N
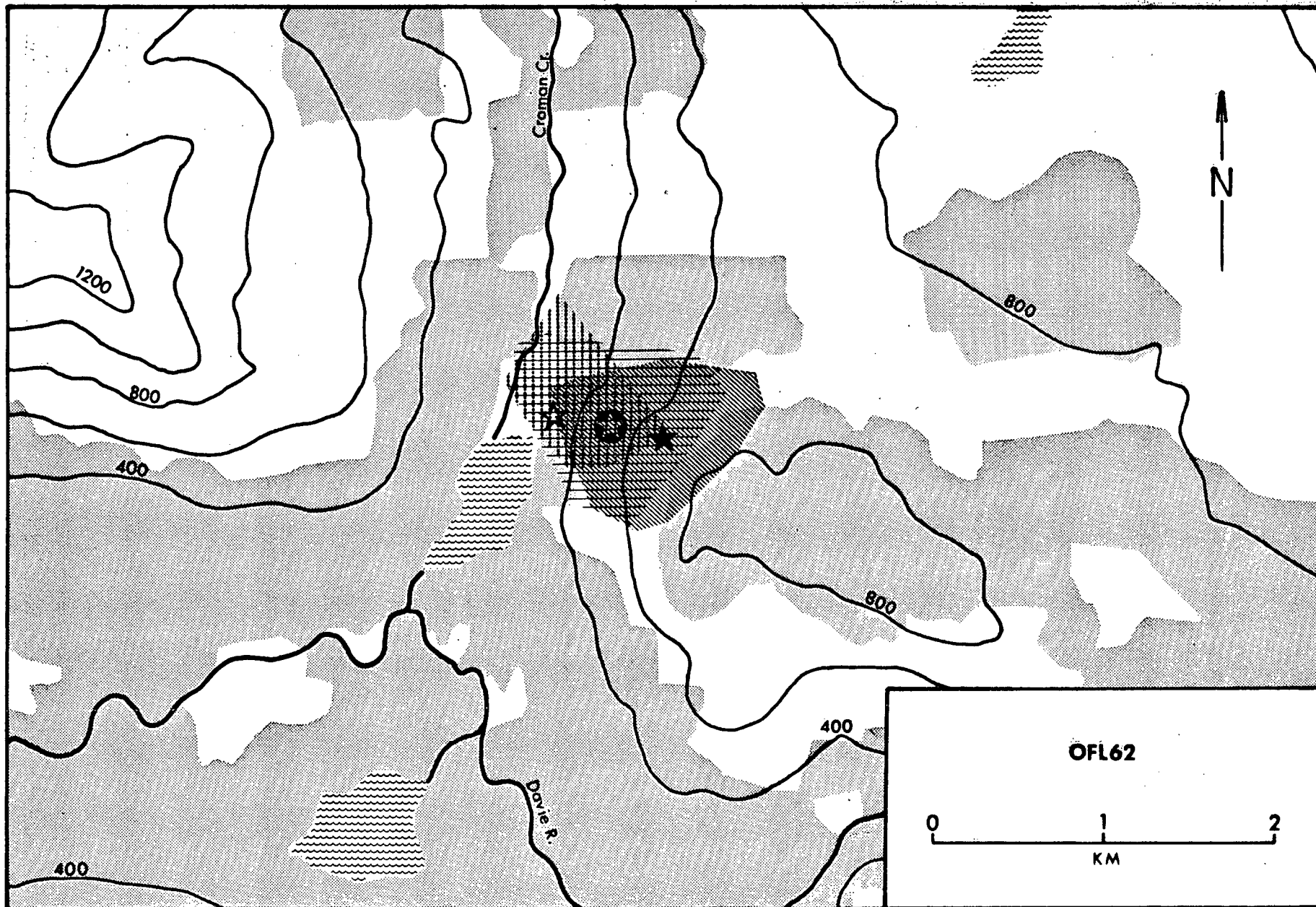
Figure 17. Relationship between standard distance deviation and size of 100% home range. $H = .000014 \ S^{2.52 \pm .97}$, $p \leq .05$, $r^2 = .61$, $n=21$; where H is home range size and S is standard distance deviation.
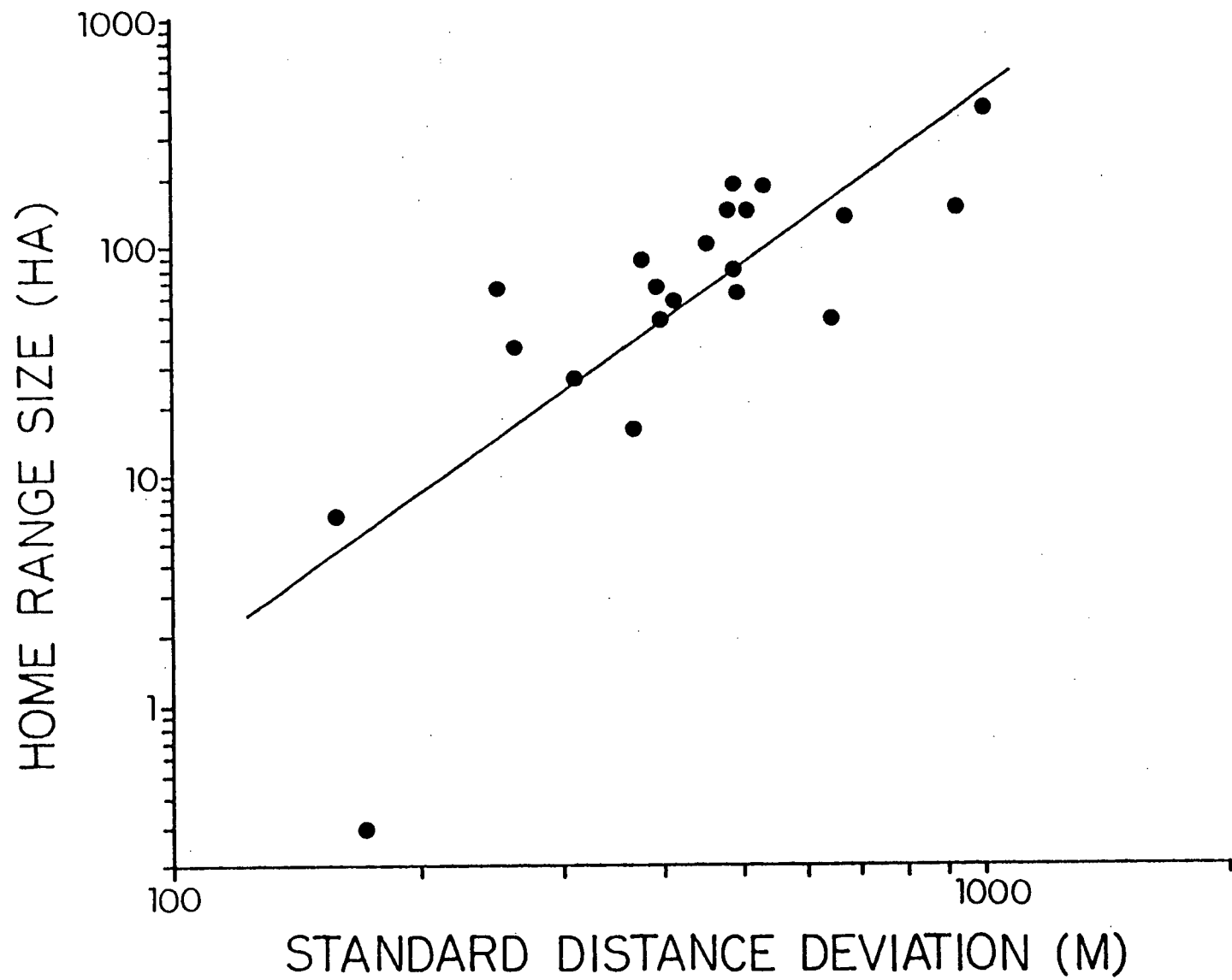
Table V. Differences in size of 100% home ranges using an F-test (Sokal and Rohlf 1969 :186) to compare standard distance deviations.

		Spring – Summer				Summer – Winter				Winter – Spring			
		d.f.	$f_c{}^+$	$f_t{}^+$	p	d.f.	f_c	f_t	p	d.f.	f_c	f_t	p
MIGRATORY	OFL61	38,33	7.07	1.69	$\leq$.05	38,32	3.51	1.79	$\leq$.05	32,33	2.01	1.84	$\leq$.05
	OFL68	–	–	–	–	9,25	2.70	2.28	$\leq$.05	–	–	–	–
	OFL67	9,49	3.92	2.12	$\leq$.05	9,37	1.02	2.12	>.05	37,49	3.84	1.74	$\leq$.05
	OFL60	19,14	4.75	2.46	$\leq$.05								
	" ———————————— winter range					19,11	2.91	2.65	$\leq$.05	11,14	1.63	2.57	>.05
	" ——————— auxiliary winter range					19,16	2.71	2.35	$\leq$.05	16,14	1.75	2.46	>.05
	" ———————————————————— between winter ranges					16,11	1.07	2.72	>.05				
	OFL71*	166,18	9.71	1.66	$\leq$.05	166,25	3.50	1.61	$\leq$.05	25,18	2.77	2.15	$\leq$.05
RESIDENT	OFL58	28,2	29.02	19.50	$\leq$.05	28,14	6.22	2.35	$\leq$.05	14,2	4.66	19.40	>.05
	OFL62	45,49	1.10	1.56	>.05	45,68	1.24	1.59	>.05	49,68	1.13	1.56	>.05

+ f_c= f calculated , f_t= f table

* horizontal migrator

summer home ranges were larger than either winter or spring home ranges.

Distance variances were not significantly different (p > .05) between the spring and winter home ranges of OFL58. This similarity in home range size probably results from the small sample size (n = 3) used to estimate the standard distance deviation of her spring home range. The similarity in size between summer and winter home ranges of OFL67 may be a result of inaccuracies in relocation as described in Section 3.1.1. Final exceptions to general trends in seasonal home range size were the home ranges of OFL62 which stayed the same size throughout the year. These similarities in home range size were largely a result of the more remote locations of OFL62. Comparison of his 90 or 50% home range sizes indicated that his spring home range was the smallest of his seasonal home ranges, and so was consistent with the general trends previously stated. Although the summer home range of OFL62 was larger than the winter home range , the difference was not as great as that observed in other deer.

The mean 100% home range size for the seven deer was 56.0 ha in spring, 165.7 ha in summer, and 72.7 ha in winter. Mean 90% home ranges were between 47 and 55% the size of mean 100% home ranges, and illustrated the concentration of locations about the arithmetic mean centre. Mean 50% home ranges were between 7 and 12% the size of mean 100% home ranges. Thus, in spring, half of a radio-tagged deer's locations were in areas averaging 4.1 ha. In summer, the area increased to 19.1 ha. During the winter, the core of deer use as delineated by the 50%

home range dropped in size and, on average, covered 7.4 ha. These comparisons of different percentage home range sizes were consistent with the results of Section 3.1.1. where home ranges were similar to bivariate normal distributions.

3.4.3. Position Of Home Ranges

As with univariate data, the locations, comprising two seasonal home ranges, can be compared in order to test the hypothesis that they come from populations with different arithmetic mean centres (Neft 1966). The conditions of the test are that the distributions are bivariate normal and that the variances are the same. In Section 3.1.1., it was shown that most home ranges were not different from a bivariate normal distribution and those that were significantly different, differed only in minor ways. Gilbert (1973) noted that the Student's t-test is fairly robust with regards to normality of the sample data. The t_r-test proposed by Neft (1966) is similar in derivation to the Student's t-test. Thus, I assumed it should also be robust with regards to bivariate normality.

With univariate data, if the variances are different, the Student's t-test can still be used to test for differences in the means of samples. However, the calculated t value must be outside of the interval between the critical t values derived from a table using the upper and lower sample sizes to obtain the degrees of freedom (Sokal and Rohlf 1969:375). This same constraint was applied to the t_r-test of Neft (1966).

For each radio-tagged deer, except for OFL58, arithmetic mean centres of the seasonal home ranges were significantly different (p ≤ .01) (Table VI and Figs. 10 to 16). For OFL58, no difference in the position of spring and summer home ranges or summer and winter home ranges could be detected. Lack of difference in position between her spring and summer home ranges was likely due to the small sample size (n = 3) used to calculate her spring home range . A second factor was the high standard distance deviation of OFL58's summer locations (Table III). This variability may also have contributed to the lack of difference between the arithmetic mean centres of her summer and winter home ranges. The high standard distance deviation in OFL58's summer locations was due to two extreme movements that may have resulted from disturbance by hunters (Fig. 15). OFL58 was accompanied by two fawns a few days previous to the extreme movements. After OFL58 moved to these extreme locations, I sighted her standing in the cutover, accompanied by only one fawn. Another fawn was found shot dead 400 m from OFL58. Within a few days after the extreme movements, OFL58 returned to her low elevation summer range and remained there until her signal was lost on the second day of the antlerless hunting season.

Distances between the arithmetic mean centres of winter and spring home ranges were much less than distances between summer home ranges and winter or spring home ranges (Table VI).

Distances between seasonal home ranges and the relative positions of home ranges were used to classify radio-tagged deer as either _migratory_ or _resident_ deer (Figs. 10 to 16 and Table VI). Migratory deer had separated summer and winter home ranges,

Table VI. Distance between arithmetic mean centres of home ranges and tests of differences in their positions.

	Spring – Summer			Summer – Winter			Winter – Spring		
	distance (km)	t_r	p	distance (km)	t_r	p	distance (km)	t_r	p
MIGRATORY									
OFL61	4.54	24.62	≤.01	3.64	18.46	≤.01	.91	7.99	≤.01
OFL68	–	–	–	4.30	23.42	≤.01	–	–	–
OFL67	2.23	20.76	≤.01	1.44	8.07	≤.01	.79	9.74	≤.01
OFL60	2.45	12.62	≤.01						
" ———————————— winter range				2.02	9.07	≤.01	.44	3.08	≤.01
" ————— auxiliary winter range				4.05	20.87	≤.01	2.79	20.68	≤.01
" ———————————————————— between winter ranges							2.93	18.45	≤.01
OFL71 *	6.16	54.15	≤.01	5.89	59.59	≤.01	.28	4.06	≤.01
RESIDENT									
OFL58	.40	.72	>.05	.09	.36	>.05	.31	2.68	≤.01
OFL62	.34	3.33	≤.01	.28	3.07	≤.01	.62	7.10	≤.01

* horizontal migrator

while their spring and winter home ranges were either separated or overlapped. Resident deer made seasonal shifts in their home range centres, although their home range boundaries remained basically the same throughout the year.

3.4.4. Occupancy Of Seasonal Home Ranges

The dates of occupancy in seasonal home ranges are shown in Figure 18. In the five migratory deer (Table VI) the dates of occupancy of home ranges were identified by distinct changes in the deer's locations. In the two resident deer (Table VI) dates of home range occupancy were based both on shifts in the core of the deer's locations and on dates of migration of other radio-tagged deer. The exact dates of occupancy of resident deer's home ranges were therefore arbitrary. However, during the periods chosen, different centres of activity were identified (Section 3.4.3.).

Individual differences occurred in the dates of occupancy of seasonal home ranges, but generally spring home ranges were occupied between March and June, summer home ranges between June and November, and winter home ranges between November and March. Thus, in the study area, black-tailed deer exhibited three migratory periods during the year. The distances of these migrations were presented in Section 3.4.3. Spring migration was the movement of deer between winter and spring home ranges. The distances moved were small, being usually less than 0.9 km, but were as great as 2.8 km. Summer migration was the movement from spring to summer home ranges, and was usually greater than the spring migration, with distances extending to 6.1 km. Winter

Figure 18. Periods of occupancy of seasonal home ranges. SP = spring, SM = summer, WT = winter, AW = auxiliary winter. Short vertical lines are dates when deer were located. Consecutive locations on a seasonal range are joined.
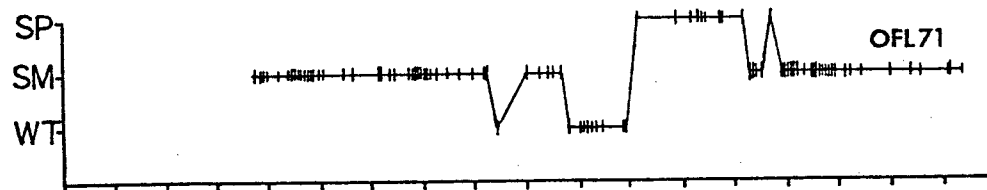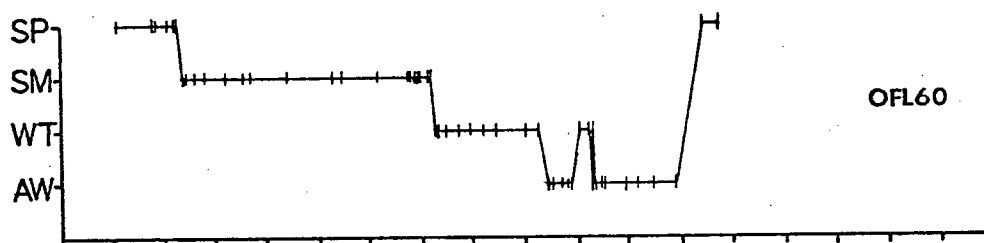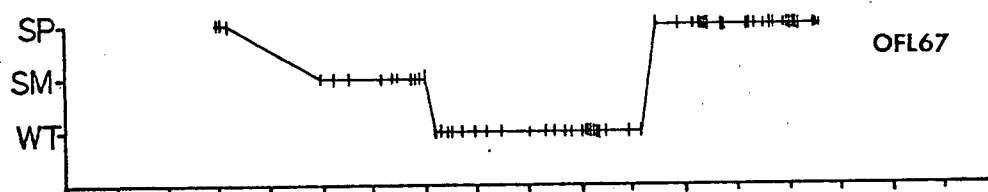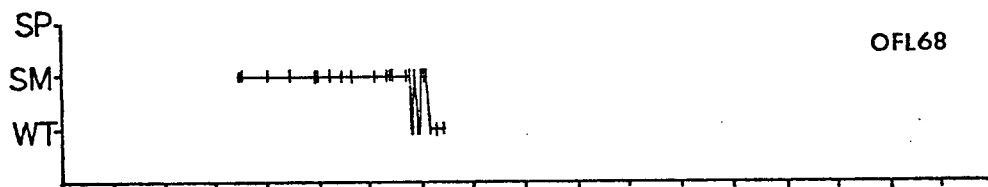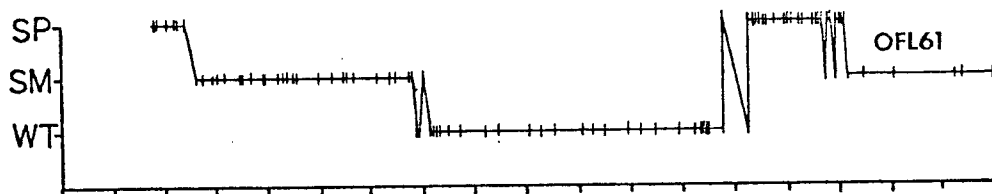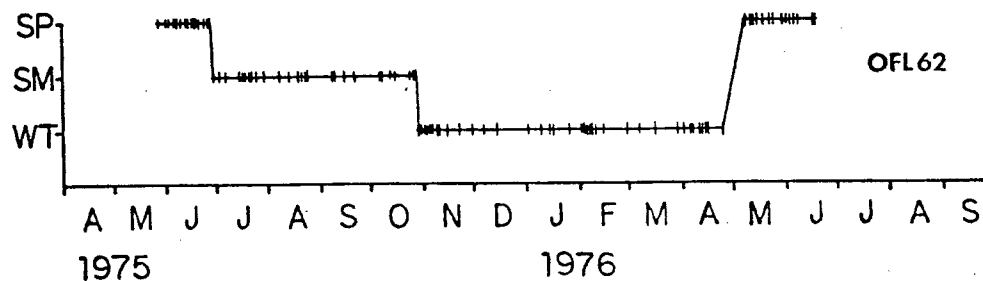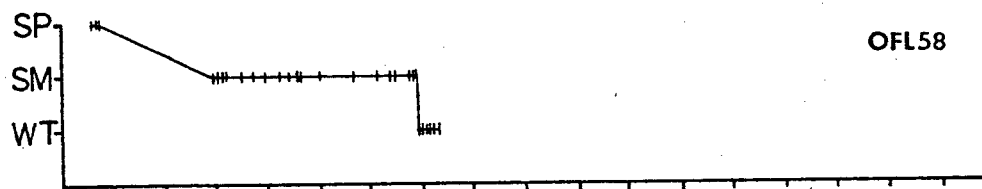
migration was the movement from summer to winter home ranges. The distances moved in the winter migration were usually slightly shorter than those moved during the summer migration.

One deer, OFL60, exhibited a fourth migration. This deer had a winter home range along the sidehill in the Croman sector near its spring home range (Fig. 13). OFL60 occupied this home range for the first part of the winter and then moved in mid-January to her auxiliary winter range on the sidehill at the mouth of Croman Valley. She remained there approximately two weeks until a very mild spell in the weather with consequent snowmelt, and then returned to her early winter home range. When snow began to accumulate again in early February on the early winter home range, she returned to her auxiliary winter range and remained there until the spring migration.

Another deer, OFL71, may also have a mid-winter migration similar to OFL60's. The extreme locations included in the summer home range of OFL71 (Fig. 14) were mainly observed during the first part of winter before OFL71 moved to her winter home range in the Hoomak sector. Insufficient locations were taken during this movement to identify an auxiliary winter home range.

The movement of a deer between two of its seasonal home ranges may occur more than once during a particular migratory period. In several deer, movement between seasonal home ranges was characterized by short duration visits before permanent occupancy of the new seasonal home range occurred (Fig. 18). For example, OFL61 was located on his spring home range on June 21, 1976. On June 23 he was located on his summer home range. Twelve hours later, he was back on his spring home range where

he remained until at least June 27. Later on June 29, OFL61 was relocated on his summer home range during the day , but by that night he had moved to his spring home range and was located there daily until July 4. Then on July 6 he returned to his summer range and remained there through to November.

Short duration visits prior to permanent seasonal occupancy were also observed during the winter migration. In OFL61 and OFL68, these movements corresponded with snowfalls at the elevations of their summer home ranges (Fig. 19). Although the lower limit of snow deposition during initial visits was well above the winter home ranges, deer moved below the snow line to their winter home ranges. Some movements between summer and winter home ranges occurred in less than 12 hours. The distances travelled were about 3.6 km by OFL61 and 4.3 km by OFL68. Even though these deer were sometimes monitored every 12 hours few locations were obtained between their summer and winter home ranges. This lack of locations along the migratory routes suggests that migration was performed in less than 12 hours and was a direct movement between seasonal ranges.

Comparison of the winter migrations of OFL61 and OFL68 merits further consideration since substantial blocks of forest are reserved for migration corridors. OFL61 inhabited an area that was virtually unlogged, while OFL68 inhabited an area that was extensively logged and did not have a direct forested connection to low elevations. Cutover areas along the direct route between the summer and winter home ranges of OFL68 were between five and six years old and vegetated mainly by Epilobium angustifolium . OFL68 was located only once outside of its

Figure. 19. Movements between summer and winter home ranges by migratory deer, OFL68 and OFL61, showing the correspondence of their winter migrations to snowfalls on their summer home ranges. The summer home range of OFL68 was close to the 915 m snow-depth station, while the summer home range of OFL61 was close to the 1098 m snow-depth station.
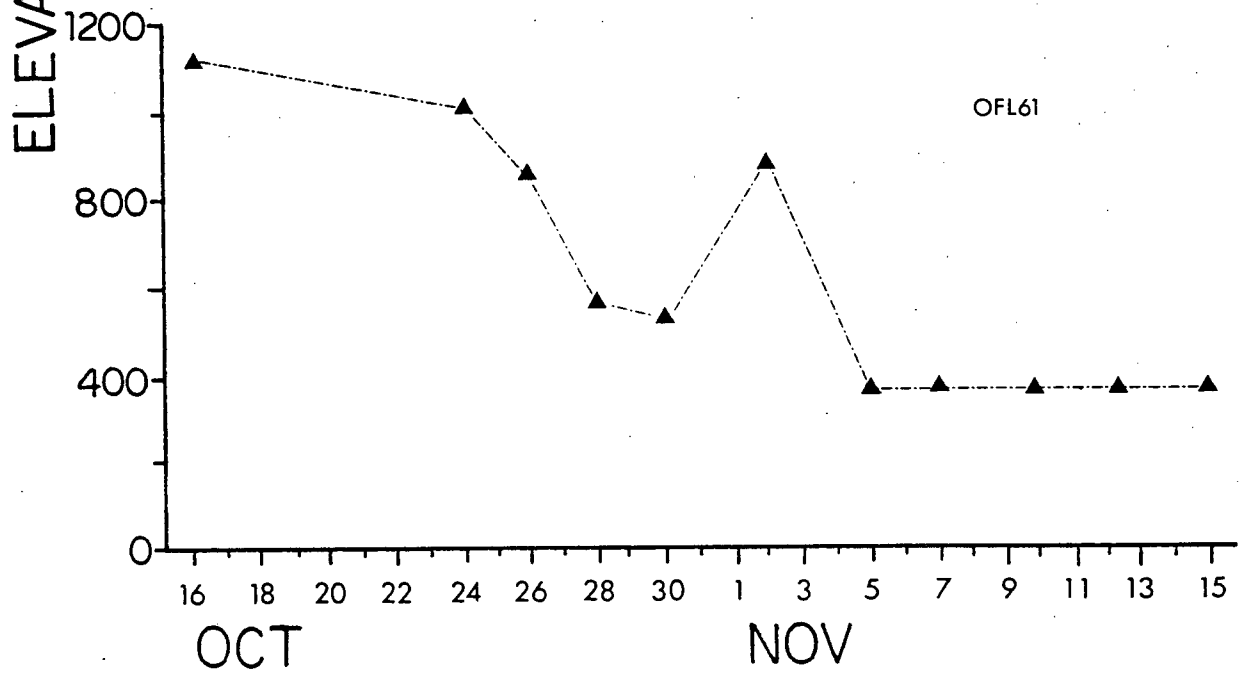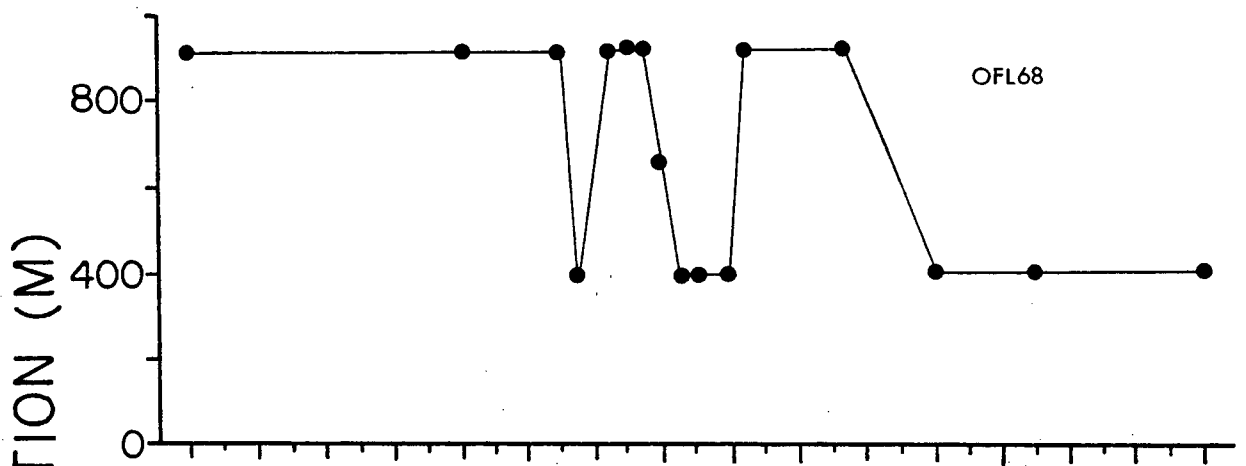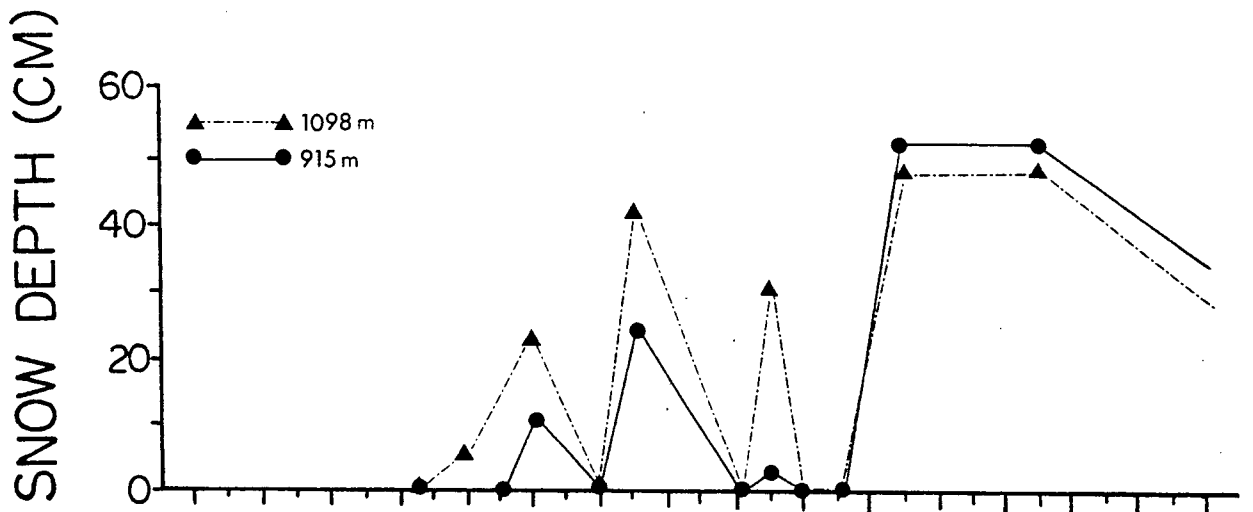
summer or winter home ranges. Since this location was in the cutover about half way along the direct route between these home ranges, it appears that she moved through the cutover in order to reach her winter home range . No snow was on the ground in the cutover where she was located, although the summer home range was covered by about 15 cm of snow. Comparison of the migratory patterns of OFL68 and OFL61 (Fig. 19) suggest that these deer behaved similarly even though one deer inhabited an extensively logged area while the other deer inhabited an almost completely forested area.

The date of permanent seasonal occupancy of spring home ranges by migratory deer reflect the severity of the local climates on the spring home ranges. OFL71 occupied its spring home range at the beginning of March. There, the local climate in the valley bottom of the Hoomak sector is milder than other portions of the study area. Less snow fell in the Hoomak sector during winter, and shrubs budded and flushed earlier than they did in other sectors. OFL67 was the next radio-tagged deer to occupy its spring home range. This slightly later spring migration reflected the longer persisting snowpack since the climate in the Davie River valley bottom is more severe than in the Hoomak sector but milder than in the Croman sector. OFL60, whose spring home range is about half way up Croman Valley, occupied its spring home range by mid-April, later than did OFL67. OFL61 occupied its spring home range in mid-May. The climate in Croman Valley was colder and snow persisted longer in the northern portion of the valley than in the southern portion. The late occupancy of the spring home range by OFL61 was

consistent with this variation in local climate.

Differences in the date of summer home range occupancy were similar to although not as great as those observed for the occupancy of spring home ranges. The occupancy of the winter home ranges reflected the occurrence and severity of the first snowfalls. In high elevations where snow occurred earlier than at low elevations (Fig. 2), deer moved to their winter home ranges earlier than deer with summer home ranges at middle and low elevations (Figs. 10 to 13 and 18). The time differences involved were much shorter than those observed for the occupancy of the spring and summer home ranges. These shorter differences are likely due to the abrupt nature of snowfalls compared to the longer periods involved in snowmelt and the gradual uncovering and phenological development of forage plants during spring and early summer.

3.4.5. Topographical Features Of Seasonal Home Ranges

The two patterns of seasonal movements described in Section 3.4.3 were those of migration and of minor seasonal shifts in centres of activity. These patterns were defined by the degree of difference between centres of activity (Table VI) and the degree of overlap of the home range boundaries (Figs. 10 to 16).

For migratory deer, two types of seasonal movements were evident, altitudinal migrators and horizontal migrators. These types were identified by the magnitude of changes in elevation made during migration (Table VII). For the three altitudinal migrators with spring locations, spring home ranges were lower in elevation than either their summer or winter home ranges.

Table VII. Elevations at the arithmetic mean centres of home ranges showing altitudinal (OFL61, OFL68, OFL67, OFL60) and horizontal (OFL71) migratory patterns. Although resident deer can make altitudinal changes in their home range centres their home ranges overlap and so are not altitudinal migrators.

	Elevation (m)			Change In Elevation (m)		
	spring	summer	winter	spring to summer	summer to winter	winter to spring
OFL61	304	1094	408	+790	−686	−104
OFL68	−	878	437	−	−441	−
OFL67	358	686	488	+328	−198	−130
OFL60	480	725	−	+245	−	−
"	------------------ winter range		559	------------	−166	−79
"	------ auxiliary winter range		670	------------	−55	−190
OFL71*	282	286	276	+4	−10	+6
OFL58	570	555	681	−15	+126	−111
OFL62	288	431	628	+143	+197	−340

MIGRATORY (rows OFL61 through OFL71*)

RESIDENT (rows OFL58, OFL62)

* horizontal migrator

Summer home ranges of the altitudinal migrators were higher in elevation than both their winter and spring home ranges (Table VII). In OFL60, the late winter home range was only 55 m lower in elevation than the summer home range. However, the climate and vegetation of these home ranges were different since the late winter home range of OFL60 was on a southern aspect while her summer home range was on a northern aspect. The centres of winter home ranges of all altitudinal migrators were on valley sides at low elevations. The general pattern of altitudinal migrators is that they summer at high elevations and move down to winter on sidehill slopes adjacent to the valley floor. Some deer then move down further to spend spring on the valley floor, while other deer stay on the valley sides for spring. This pattern corresponded to the altitudinal pattern of snow depth and duration of snow cover (Fig. 2). Summer ranges were at elevations where there was deep snow and continuous snow cover over winter, while winter ranges were at elevations where there was shallow snow and intermittent snow cover. Spring home ranges were areas where snow was deeper and snow cover longer lasting than on winter ranges but of shallower depth and shorter duration than on summer ranges.

Elevations at the centres of the seasonal home ranges of horizontal migrator OFL71, were all within 10 m of one another. Although OFL71 did not make an elevational change during migration, she did accomplish a change in local climate by moving from Croman Valley, where temperatures are colder and the snow deeper and more persistent, to the Hoomak sector where the climate was milder.

The resident deer, OFL58 and OFL62, did not exhibit the patterns of changes in elevation and home range separation characteristic of altitudinal migrators. Although based on only three locations the spring home range of OFL58 was close to the elevation of her summer home range . The winter home range of OFL58 was higher in elevation than her summer home range . OFL62 exhibited a different pattern. His spring home range was located in the valley bottom at an elevation of 288 m. Although some of this valley bottom area used during the spring, was also included in the summer home range , the centre of the summer home range was on the lower sidehill, 143 m higher than the spring home range centre. The winter home range of OFL62 was centred higher on the sidehill than his summer home range .

The resident deer differed from the altitudinal migratory deer in that the centres of their winter home ranges were higher in elevation than the centres of their summer home ranges. This pattern may occur because cutover areas in low elevations provide foraging habitat for deer during summer (Fig. 5). If more resident deer were tagged I would expect some of them to shift their home range centres laterally and others downwards between summer and winter.

Slopes on the spring and summer home ranges of most deer were not as steep as those on their winter home ranges (Table VIII). Exceptions were the spring home ranges of OFL58 and OFL60 and the summer home ranges of OFL58 and OFL62 which were on steep sidehills, and the winter home range of OFL71 which was gently sloped. No clear trends in the aspects of seasonal home ranges were evident (Table VIII). All aspects were represented

Table VIII. Slope and aspect near the arithmetic mean centres of home ranges. No consistent trends are evident.

		Slope (degrees)				Aspect		
		spring	summer	winter		spring	summer	winter
MIGRATORY	OFL61	≤ 1	9	24		N-NW	SW-N	SW-W
	OFL68	-	8	22		-	S-SE	SW-SE
	OFL67	3	7	29		S-SE	N-NE	NW-W
	OFL60	23	6	-		W-S-E	NW-NE	-
	"	------------------ winter range		15		-----------------------		E
	"	------- auxiliary winter range		24		-----------------------		S-E
	OFL71 *	10	≤ 1	10		NW	W-S-E	NW
RESIDENT	OFL58	23	14	11		W-SE	W-SE	SW-SE
	OFL62	4	34	33		W	NW-W	NW-W

* horizontal migrator

in spring and summer home ranges. In winter, home ranges were located on aspects varying southerly between northwest and southeast.

Seasonal movements of radio-tagged deer are summarized in Figure 20. In general, altitudinal migrators moved downward at the beginning of winter and occupy winter home ranges below 650 m in elevation. Their spring ranges were usually in valley bottoms adjacent to their winter home ranges. In summer, these deer moved to high elevations. Resident deer inhabited low elevations throughout the year and made relatively small shifts in their home ranges between seasons. Where local climate changed substantially over a horizontal distance, such as between the narrow tributary valley and the wide main valley, deer made horizontal migrations and attained differences in local climate similar to those experienced by altitudinal migrators.

3.5. Indirect Measures Of Seasonal Movements

The movements made by the radio-tagged deer were corroborated by indirect measures of movements made by the deer population. These measures were employed to evaluate if individual movements were broadly based and representative of the deer population.

Deer tracks were observed along Mount Cain road from February to July in 1975 and from October 1975 to May 1976. The data were combined and the elevation of the highest deer track on Mount Cain road during winter and spring is shown in Figure 21. The elevation of the highest deer track decreased from 1200

Figure 20. Seasonal Movement patterns of deer in the study area. Arithmetic mean centres of seasonal home ranges are joined for each deer. $\boxed{S}$ = spring, $\textcircled{S}$ = summer, $\textcircled{W}$ = winter, $\textcircled{A}$ = auxiliary winter. Cutover areas are stippled.
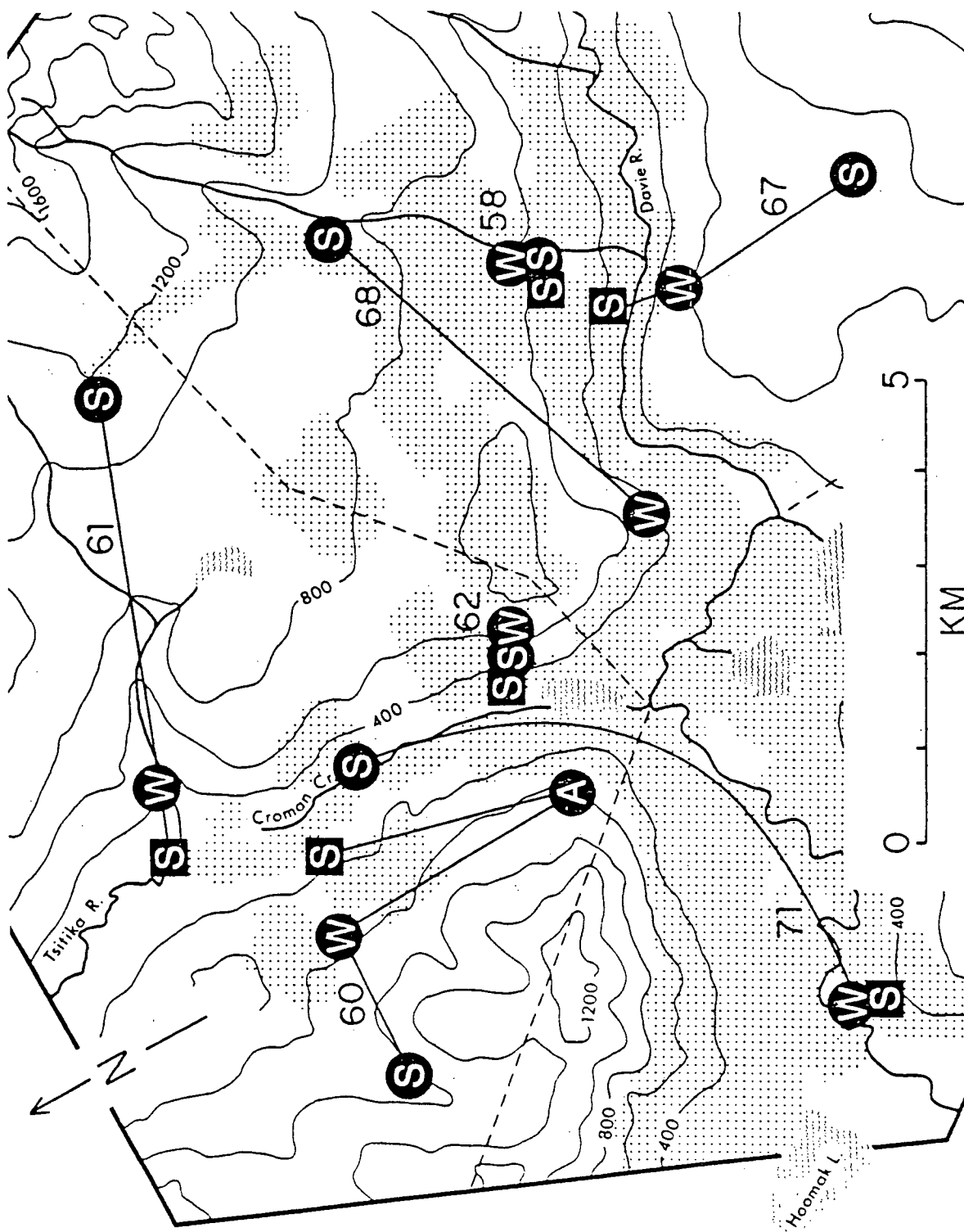
Figure. 21. Elevation of highest deer track observed along Mount Cain road.
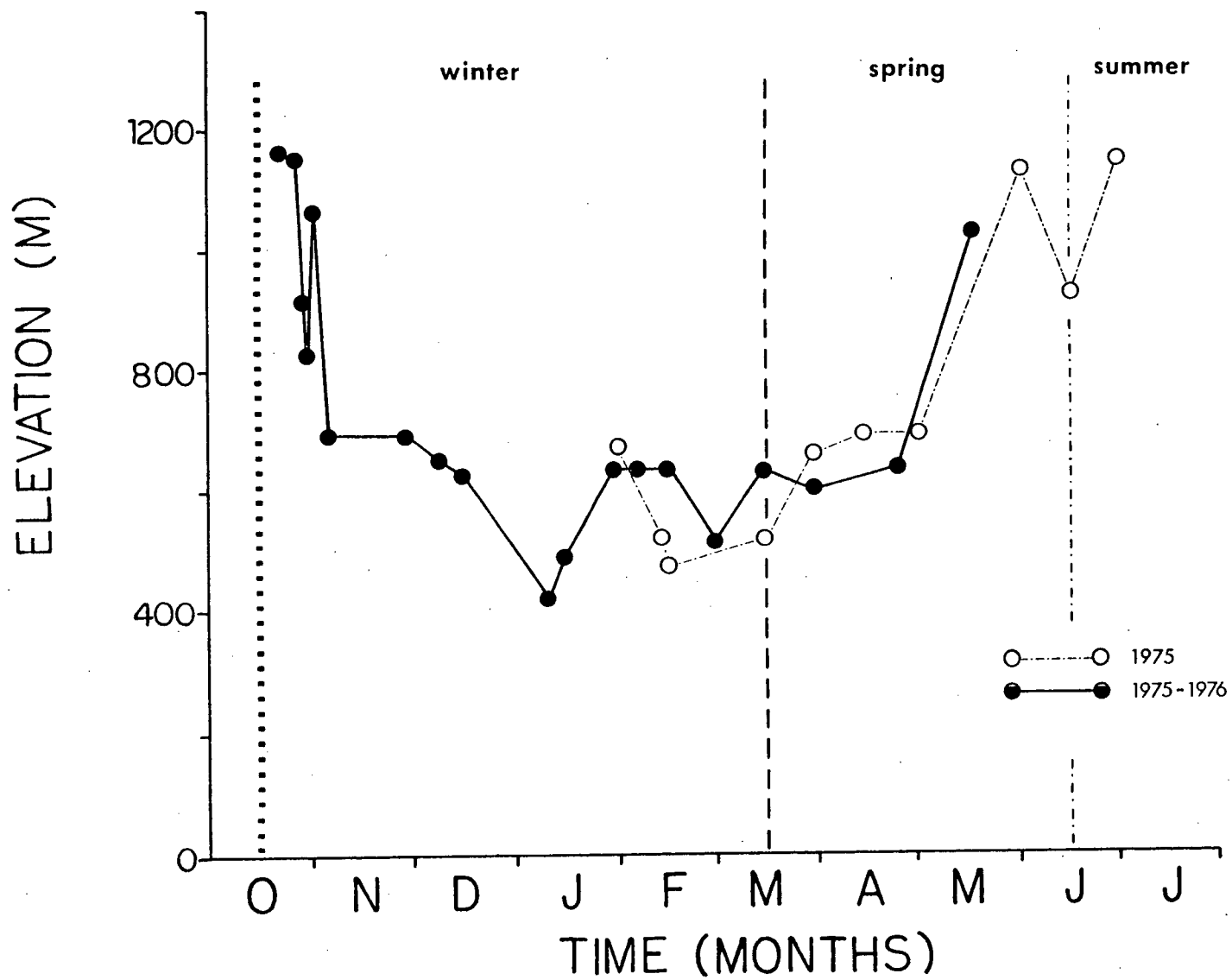
m in early October to 700 m in November. This decrease in
elevation of deer tracks coincided with the descending snow line
and increasing snow depths in high elevations (Fig. 2). During
winter, deer inhabited low elevations in the study area (Fig. 20
and Table VII). In spring, the highest occurrences of deer
tracks were higher in elevation than those observed in winter.
The elevation of the highest deer track increased throughout
spring and on into summer.

Night counts conducted in the Mount Cain sector showed that
the dates of first sightings of deer increased with increasing
elevation as spring progressed (Fig. 22) and were consistent
with track counts (Fig. 21). The first appearances of deer in
night counts at middle and high elevations occurred soon after
snow cover was reduced to about 50% in the cutover areas. The
first observations of tracks (Fig. 21) and sightings of deer
(Fig. 22) in the higher transects may be caused by deer making
temporary visits to high elevations similar to the spring
migratory behaviour exhibited by OFL61 (Section 3.4.4).

Although track counts (Fig. 21) indicate when the first
deer moved into high elevations after wintering in low
elevations, they do not indicate when the majority of deer
moved. Night counts showed when the majority of deer make
altitudinal movements. Since deep snow prevented vehicular
travel, night counts indicate relative abundance of deer within
transects during periods with shallow or no snow. The magnitude
of the number of deer km^{-1} cannot be compared between all
transects since visibility, and thus the area censused, differed
between transects. However, within a transect, the number of

Figure 22. Mean number of deer and 95% confidence limits
(vertical bars) counted at night along road transects in the
Mount Cain sector. The number of transects counted are given
above the 95% confidence limits. Transect 22-B was adjacent to
the low elevation sidehill forest that was used intensively by
deer during winter. Transect A was further from the forested
winter range than B and situated in the valley bottom next to
Davie River. Elevations are indicated and increase from A to E.
Transects A and B were through conifer seral stages, while C, D,
and E were through herb seral stages. Data for 1975 and 1976 are
combined.
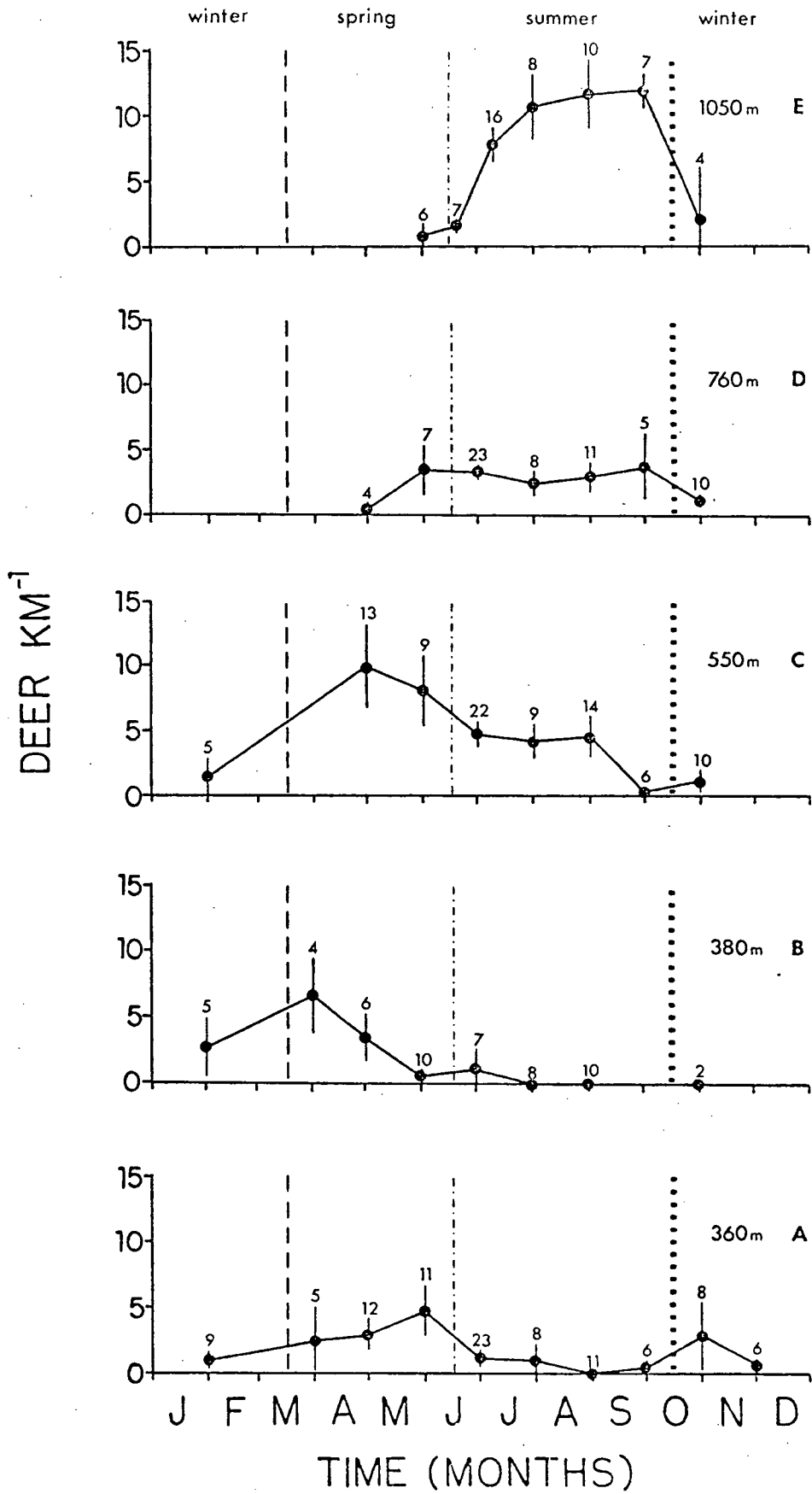
deer km⁻¹ gives a relative index of population density. Seasonal
trends between transects show the movement patterns of the deer
population.

The altitudinal pattern of deer use in logged areas at
night (Fig. 22) was consistent with movements of radio-tagged
deer and pattern of snow accumulation and melt (Fig. 2). At low
elevations, deer densities were greatest in spring but decreased
by early summer. This intense use of low elevation logged areas
in spring was also evident from the locations of radio-tagged
deer (see section 3.6). The decrease in deer use at lower
elevations by early summer corresponds to migrations of radio-
tagged deer (Fig. 18) and increased deer use of forested areas
(Section 3.6). Some deer inhabited low elevations throughout the
year (Fig. 22) and are represented by the radio-collared
resident deer OFL62 and OFL58 (Figs. 15 and 16).

The date of first deer use in an area was progressively
later as elevation increased (Fig. 21 and 22). First deer use in
high elevations was probably not a result of deer that had made
their final spring migration but, rather, a result of short
duration visits by deer to their summer home ranges (Fig. 20).
The peak in intensity of deer use also was progressively later
with increasing elevation (Fig. 22). This peak represents deer
moving from their spring home ranges directly to their summer
home ranges. Individual deer moved directly from their spring to
summer home ranges. Complete, one-step migration was exhibited
by OFL61, OFL67, OFL60, and OFL71 (Figs. 10 and 12 to 14). At
the beginning of winter, deer use decreased in the high
elevation transects 22-D and 22-E (Fig. 22). This decrease

coincided with the first snowfalls. As deer use at high elevations decreased, deer use increased at low elevations (transects 22-A and 22-C), indicating a downward movement by some deer. This downward movement was consistent with the documented movements of OFL61, OFL68, and OFL67. The increase of deer numbers at low elevations was small. The reason for this small increase in numbers was that deer use of forests was greater during winter than in the other seasons (see section 3.6) and differences between transects in visibility (lower cutovers were older and had taller and denser vegetation than the higher cutovers).

In the Croman (1) sector (Fig. 1), seasonal changes in dispersion of the deer population also occurred (Fig. 23). Shifts in the population occurred over a narrower elevation interval than was observed in the Mount Cain (2) sector (Fig. 22). Transects in Figure 23 were arranged in order of distance from the mouth of Croman Valley beginning with transect 23-A adjacent to a forested winter range.

Deer use in Croman Valley was greatest during early spring near the valley mouth. As spring progressed, deer moved further up the valley. Near the beginning of winter, deer use decreased in upper portions of the valley while it increased near the mouth. The movements of OFL60 and OFL71 were consistent with movements of deer along Croman Valley observed through the night counts. OFL61 did not move horizontally along Croman Valley but stayed on the sidehill for the winter (Fig. 10). Most of the deer population migrated horizontally in Croman Valley, south towards Davie River. These shifts in the deer population

Figure 23. Mean number of deer and 95% confidence limits (vertical bars) counted at night along road transects in the Croman Sector. The number of transects counted are given above the 95% confidence limits. Distance from the valley mouth increases from A to D. Elevations are indicated. All transects were through herb seral stages. Data for 1975 and 1976 are combined.
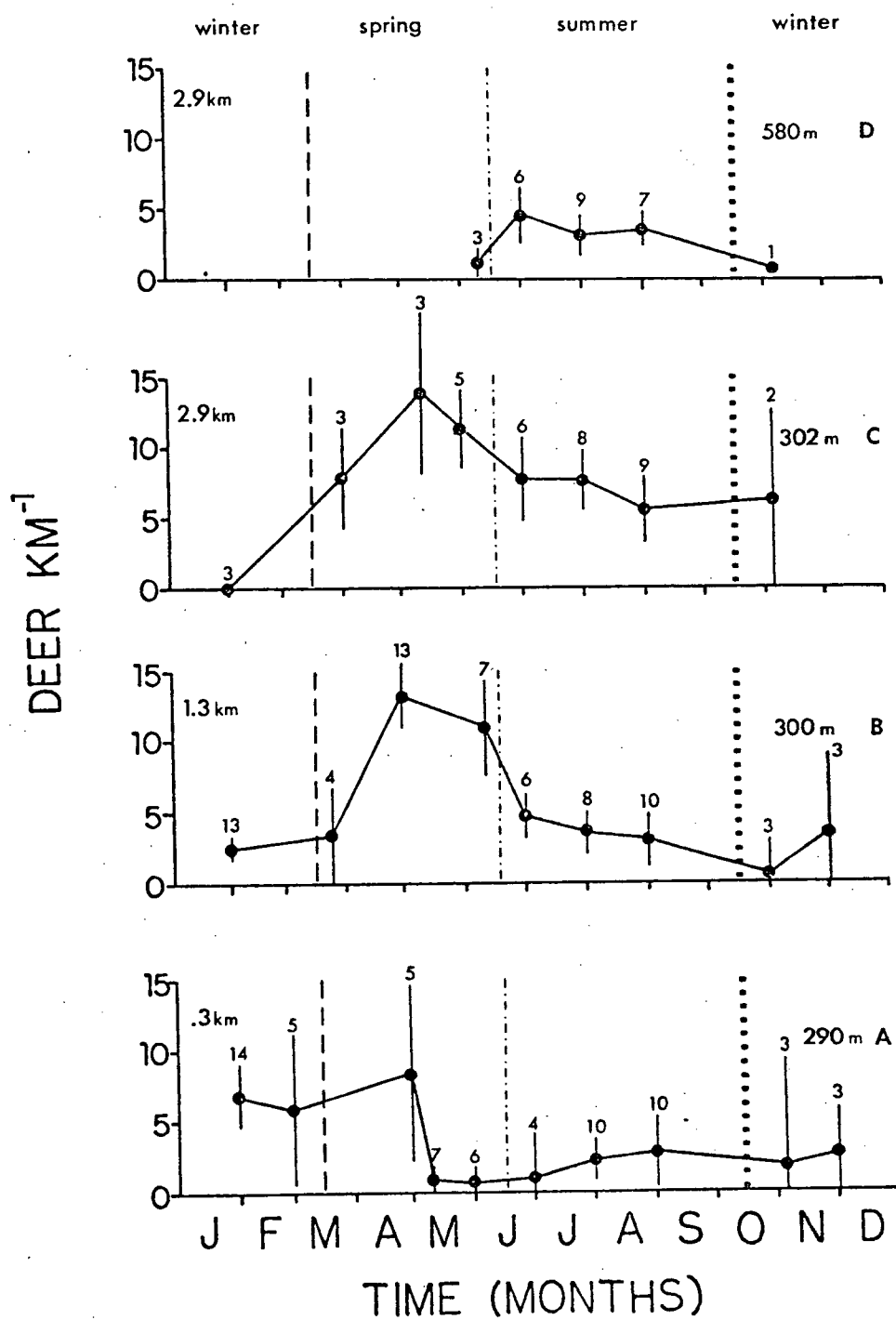
corresponded to patterns of snow melt in spring and snowfall and snowpack accumulation in winter.

3.6. Seasonal Use Of Habitats

Use Of Unlogged And Logged Habitats

Day and night locations of radio-tagged deer were classified as being in either forested or cutover areas (up to 27 years of age) during the three seasons and indicated the relative use made of these habitats by deer throughout the year. The percent use of habitats was averaged for each seasonal movement pattern (Fig. 24). Resident deer increased their use of forest during both day and night between spring and winter. The opposite trend occurred in use of cutovers. Within each season, use of forest was greater during day than at night, while use of cutovers was greater at night than it was during the day.

Comparison of the two types of migratory deer to the resident deer show some similarities in use of forested and cutover habitats. Forests were used more during day than at night, while cutovers were used more at night than during day (Fig. 24 and Table IX). Daytime and nighttime use of forested habitats during summer by migratory deer was greater than that by resident deer (Table IX).

When all radio-tagged deer were considered together, use of forests was greater during the day than at night, while cutovers were used more frequently at night. Daytime use of forests was lowest in spring and almost doubled in summer. Use of forests during winter decreased slightly from that during summer. In

Figure 24. Percent use of forested and cutover habitats during each season (SP = spring, SM = summer, WT = winter). Unshaded histograms are daytime use, shaded histograms are nighttime use. Number of deer from which the percent use of forested and cutover habitats in each season was calculated are indicated above the histograms for forested habitats.

PERCENT

altitudinal migrators

horizontal migrator

residents

all deer
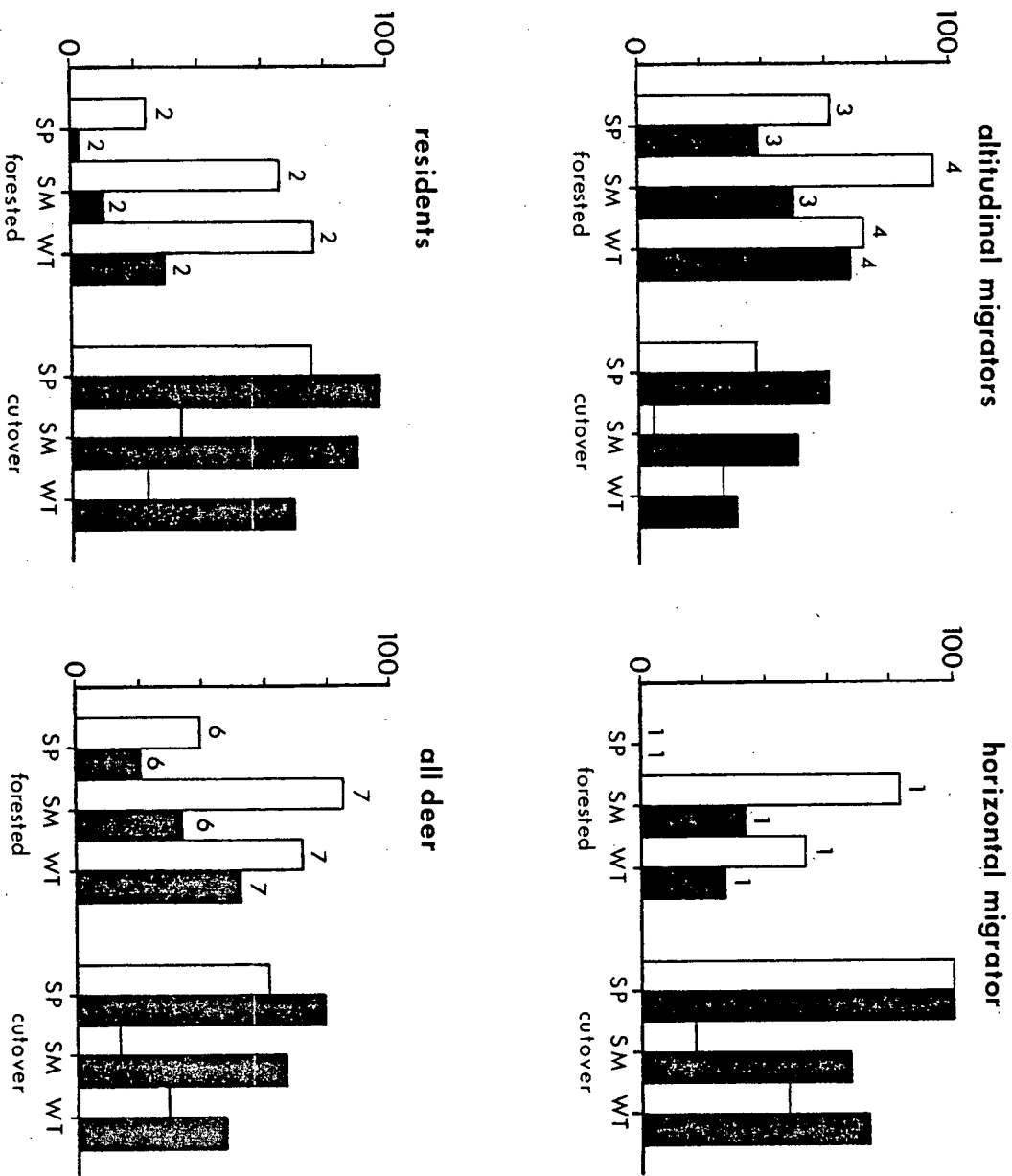
Table IX. Comparison of use of forested and cutover habitats by
migratory and resident deer during summer. Migratory deer were
in forested habitats more frequently than were resident deer.

| | Daytime | | | | | Night time | | | |
	n	forested	cutover	% in forest		n	forested	cutover	% in forest
migratory	181	162	19	89.5		81	26	55	32.1
resident	58	40	18	69.0		17	2	15	11.8

$$x^2 = 12.6 \ , \ \ p \le .05$$

Fisher's Exact Probability Test
p= .059

cutovers, daytime use was greatest during spring, lowest in summer, and increased again in winter, but not to the intensity observed in spring. At night, use of forests increased from spring through summer to winter, while use of cutovers showed a comparable decrease.

Use Of Forested Plant Associations And Seral Stages

Locations of radio-tagged deer were combined and a frequency of use calculated for each forested plant association and seral stage (Fig. 25). Individual variation in the use of these habitats is discussed where appropriate. Daytime and nighttime locations were considered separately. Caution must be used in interpreting these frequency distributions in terms of habitat selection and preference. Since the proportion of the study area covered by each plant association or seral stage is not known, habitat preferences cannot be calculated. Some insight into preference can be obtained through comparison of deer use with cursory estimates of the extent of each habitat type. Regardless of habitat preferences, the locations of deer do indicate the various habitats used during different seasons.

Spring

In spring, all deer use during both day and night was in forested plant associations or seral stages in the Coastal Western Hemlock Zone. The Vaccinium-Skunk Cabbage association was the most frequently used forested habitat during daytime. The Amabilis Fir-Western Hemlock and Salal-Western Hemlock associations were the next most intensively used forested

Figure 25. Percent use of forested plant associations and seral stages by radio-tagged deer during each season. Unshaded histograms are daytime use, shaded locations are nighttime use. Number of deer from which the percent use of forested and cutover habitats in each season was calculated are indicated above the histograms for forested habitats. Forested plant associations :   VS = Vaccinium - Skunk Cabbage,   SC = Sword Fern - Western Red Cedar,   DW = Deer Fern - Western Hemlock, WP = Western   Hemlock - Plagiothecium,   AW = Amabilis   Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock,   AT = Amabilis   Fir - Twisted   Stalk,   MC = Mountain Hemlock - Copperbush . Immature Seral   Stages :   N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.
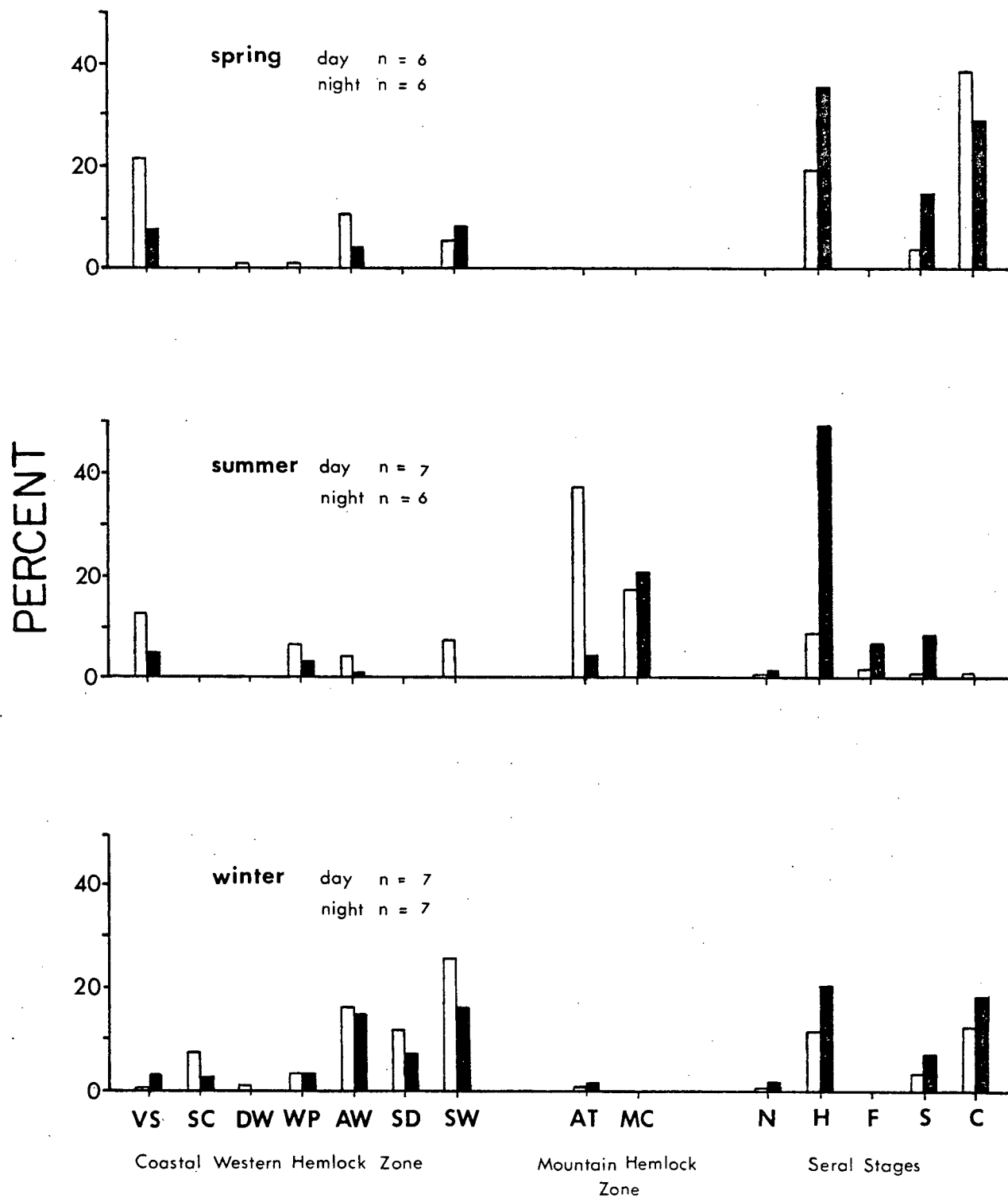
habitats. Deer Fern-Western Hemlock and Western Hemlock-Plagiothecium associations had only minor use, each accounting for less than 6% of the daytime use. There was no daytime use of Salal-Douglas-fir or Sword Fern-Western Red Cedar associations nor of any associations in the subalpine Mountain Hemlock Zone.

Use of forested plant associations was generally less at night than during the day. However, the pattern of use was similar in that the Vaccinium-Skunk Cabbage association was used the most intensively while secondary use was made of the Amabilis Fir-Western Hemlock and Salal-Western Hemlock associations.

In cutovers, the greatest daytime use was in herb and conifer seral stages, while less than 5% of the deer use was in the shrub seral stage. Use of seral stages was greater at night than during the day. The herb seral stage was the most intensively used habitat at night. The conifer seral stage was the second most commonly used cutover habitat, while the shrub seral stage was the third. No use was made of fern or newly logged seral stages by radio-tagged deer during spring.

Summer

In summer, daytime use of the Vaccinium-Skunk Cabbage association was again greater than the use of other forested plant associations in the Coastal Western Hemlock Zone (Fig. 25). This high use of the Vaccinium-Skunk Cabbage association was mainly due to horizontal migrator OFL71 (Fig. 26). However, resident deer OFL62 also used this association. In summer, use was still made of Amabilis Fir-Western Hemlock, Western Hemlock-

Figure 26. Percent use of forested plant associations and seral stages during summer by altitudinal and horizontal migrators, and residents. Unshaded histograms are daytime use, shaded histograms are nighttime use. Number of deer from which the percent use of forested and cutover habitats in each season was calculated are indicated above the histograms for forested habitats. Forested plant associations : VS = Vaccinium - Skunk Cabbage, SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal - Western Hemlock, AT = Amabilis Fir - Twisted Stalk, MC = Mountain Hemlock - Copperbush . Immature Seral Stages : N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

PERCENT

altitudinal   day   n = 4
              night n = 3

horizontal   day   n = 1
             night n = 1

resident   day   n = 2
           night n = 2

VS   SC   DW   WP   AW   SD   SW   AT   MC   N   H   F   S   C

Coastal Western Hemlock Zone   Mountain Hemlock   Seral Stages
                                        Zone
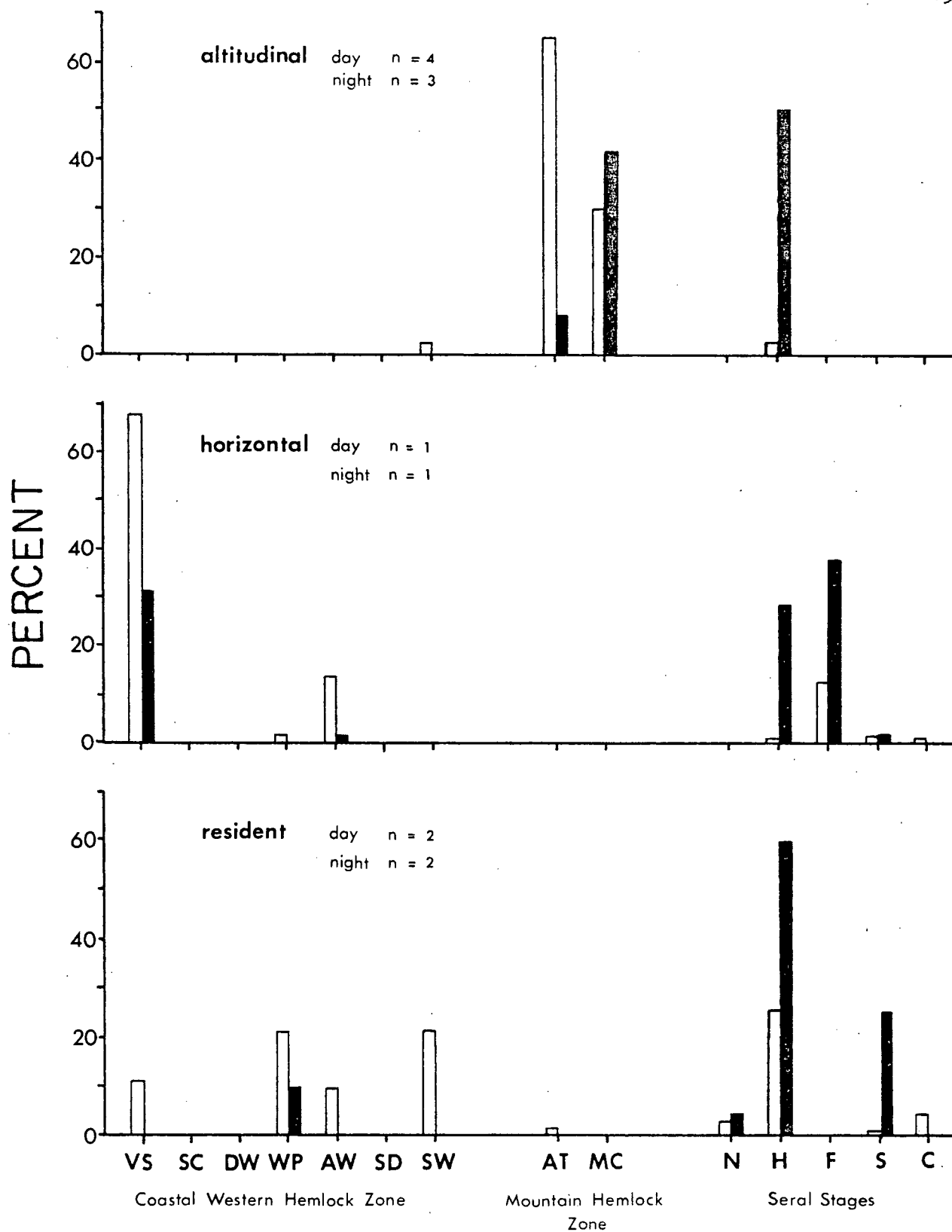
Plagiothecium, and Salal-Western Hemlock associations. Most daytime use of these associations resulted from the resident deer (Fig. 26). Two plant associations used in summer, but not in spring, were the Amabilis Fir-Twisted Stalk and Mountain Hemlock-Copperbush associations (Fig. 25). Use of these associations in the subalpine Mountain Hemlock Zone was mainly due to altitudinal migrators (Fig. 26).

Nighttime use of forested plant associations in summer was similar to that in spring. Use of forested plant associations was generally less at night than during day and the same associations were used during both periods.

Seral stages were used in different intensities in summer than in spring (Fig. 25). The conifer seral stage, in which almost 40% of the daytime use in spring occurred, had less than 5% of the daytime use in summer. Some of this drop in use of the conifer seral stage was a result of the lack of old seral stages at high elevations. Thus, the altitudinal migrators did not have access to this seral stage in summer. However, the decrease in use of the conifer seral stage is not wholly due to movement of deer away from the conifer seral stage. OFL62 is a resident deer with access to the conifer seral stage during spring and summer. Use of the conifer seral stage by this deer was high in spring but much lower in summer (Table X), suggesting other factors are responsible for the reduction in use of the conifer seral stage. Daytime use of the herb seral stage was less in summer than in spring. Use of the fern seral stage resulted from only one deer, OFL71. Although the cutover classified as a fern seral stage was used by OFL71, she used the area near Croman Creek more

Table X. Daytime use of the conifer seral stage by resident deer OFL62, during spring and summer. $X^2=9.64$, $p \leq .05$

	Spring	Summer
Conifer Seral Stage	13	3
Other Habitats	16	33
Number of Locations	29	36
% in Conifer Seral Stage	44.8	8.3

intensively than the rest of the cutover. This stream bank area was greater in shrub and herb cover than were central portions of the cutover.

Trends in nighttime use of seral stages were similar to trends in daytime use, although the intensity of use was much greater (Fig. 25). As in daytime, nighttime use of the fern seral stage resulted solely from OFL71 (Fig. 26). The conifer seral stage was not used at night in summer by radio-tagged deer. This contrasts markedly with the high use it received in spring. Use of herb and fern seral stages was higher in summer than spring, while use of the shrub seral stage was lower.

Winter

In winter, daytime use was greatest in Amabilis Fir-Western Hemlock and Salal-Western Hemlock associations (Fig. 25). Secondary use was made of Salal-Douglas-fir, Western Hemlock-Plagiothecium, and Sword Fern-Western Red Cedar associations, but use of these habitats was much less than that of the former two associations. Use of the Sword Fern-Western Red Cedar association was due to OFL71 when she migrated into the valley bottom along the Davie River near Hoomak Lake (Fig. 14). This association was not an important type of habitat for deer in the Croman and Mount Cain sectors of the study area. The Vaccinium-Skunk Cabbage association was used only occasionally during winter. This low use contrasts sharply with the high use it received during spring and summer. The associations in the subalpine Mountain Hemlock Zone were used incidentally during winter in contrast to the high use they received during summer.

Although use of forested habitats at night was generally less than that in daytime, trends in use of plant associations at night were similar to those in the day.

Daytime use of cutovers during winter differed from that in summer by the higher use of shrub and conifer seral stages. Nighttime use of herb and fern seral stages in winter was less than that in summer. The conifer seral stage was used more at night in winter than in summer. Herb, shrub, and conifer seral stages received about the same amount of use in winter and did not exhibit the large differences apparent during spring and summer.

4. Discussion

4.1. Size Of Home Ranges

Black-tailed deer inhabiting coastal forest environments in British Columbia were found to have three primary seasonal home ranges corresponding to the spring, summer, and winter. Although summer and winter home ranges have been observed in a non-migratory population of black-tailed deer (Dasmann and Taber 1956), the existence of seasonal home ranges for migratory deer are not consistent with existing concepts of migratory behaviour for black-tailed deer that were proposed by Klein (1965).

Home ranges were largest in summer and the mean 100% home range size was 165 ha , similar to the estimate predicted by Harestad and Bunnell (in press). Home range size is related to the animal's energy requirements and habitat productivity (McNab 1963, Schoener 1968, Harestad and Bunnell, in press). The variability in home range size is likely a result of differences in body size and spatial differences in food abundance. Home ranges during winter were smaller than they were in summer. This decrease of home range size during winter has been observed in other North American cervids (Leopold et al. 1951, Sparrow and Springer 1970, Van Ballenberghe and Peek 1971, Alexander 1973, Craighead et al. 1973, Phillips et al. 1973). The decrease is attributed by Harestad and Bunnell (in press) to the ruminant's lower apparent energy requirements (Nordon et al. 1970) and lower rate of food processing during winter because of reduced quality of their forage (Cameron et al. 1975, Person et al. 1975).

The spring home ranges of black-tailed deer were smaller than both the summer and winter home ranges. Energy and productivity relationships with home range size can also explain these small spring home ranges. The spring home ranges were located in habitats with greater amounts of food than the habitats used during winter. Also during spring the new growth at the lower elevations would be higher in quality than the food available in winter. The abundance of high quality food during spring would result in a smaller area being needed to obtain energy and nutrients than would be necessary during winter.

Although the amounts of food available on spring and summer home ranges are similar, home range size increased in summer. The decrease in food quality over time from spring to summer would mean a decrease in the amounts of energy and other nutrients available to deer on these areas. Further, not only would the density of energy and nutrients available to deer be lower in summer than in spring but the deer's energy and nutrient requirements would be increasing because of growth, fat deposition, late foetal growth, and lactation. These changes in requirements, and availability of energy and nutrients, would result in the expansion of home ranges during the summer from the small home ranges used during the spring. The trends in sizes of seasonal home ranges in this study are consistent with the energy : productivity home range model proposed for mammals by Harestad and Bunnell (in press).

4.2. Seasonal Movements and Nutrition

Alterations of home range size is one way by which deer can respond to environmental changes. However there appears to be a maximum limit to the extent which home range size can be increased (Covich 1976, Harestad and Bunnell, in press). Another way by which deer can respond to environmental changes is by altering the position of their home ranges. In the study area three patterns of seasonal movement were observed; altitudinal migration, horizontal migration, and residency. Together, these patterns provide a general description of the seasonal movements of the black-tailed deer population inhabiting the study area. Black-tailed deer wintered in forested habitats on sidehills at low elevations using nearby cutover habitats when they were available. During spring deer moved down into the valley bottoms or used the cutovers nears their winter home ranges more intensively. In summer, some deer remained at low elevations but changed the intensity of use of portions of their home ranges; other deer migrated to mid-elevations or high elevations; still other deer migrated into tributary valleys.

Although there are differences in the proximate factors inducing the seasonal movements of North American ungulates, the ultimate factor is generally accepted as seasonal fluctuation in food availability (Orr 1970, p. 24). In the study area, black-tailed deer used different seasonal home ranges during spring, summer, and winter. Movements of black-tailed deer between these seasonal home ranges are proposed to occur because of habitat selection resulting from the relative abundance of food supplies in habitats encompassed by the home ranges. Where food

availability fails to account for patterns of seasonal movements, other factors are suggested which could contribute to the relative favourability of habitats.

Winter

During winter, snow affects food availability by burial of food sources and through locomotory restrictions on deer. The burial of food items by snow can be direct or snow can cause downward displacement of the forage and permit their burial by subsequent snowfalls. At high elevations (above 900 m), the snowpack was deep enough by late November to reduce food availability. This reduction in availability occurred for both herbs and shrubs. Herbs were covered sufficiently by 8 cm of snow to eliminate this forage component from diets of white-tailed deer, *O. virginianus* (Zimmermann) (Coblentz 1970). Similar effects may be imposed on black-tailed deer because no evidence of deer digging through the snowpack was observed in the study area. Besides herbs, the snowpack was deep enough to bury directly the shorter shrub stems. If the effect of bending of shrub stems is also considered, then the amount of food available at high elevations would be less than that at low elevations.

Food availability during winter also depends on the effect of snow on deer mobility. Snow depths at which the mobility of black-tailed deer is hampered can be estimated from observations of the mobility of Rocky mountain mule deer and white-tailed deer in snow. In these species, snow depths of over 40 to 60 cm seriously hampered or prevented locomotion (Hosely 1956,

Loveless 1967, Kelsall 1969, Gilbert et al. 1970), while shallower snow depths (25 to 35 cm) reduced mobility (Hepburn 1959, Loveless 1967). Kelsall (1969) observed that snow depths of greater than 70% of the chest height of moose (Alces alces (Linnaeus)) and white-tailed deer seriously impeded their movements. Assuming this same relationship for black-tailed deer, then with their average chest heights between 50 and 58 cm (Jones 1975), the depth at which their mobility would be seriously impeded is about 37 cm. Snow depths were frequently greater than 37 cm at mid and high elevations of the study area over most of the winter. Snow density determines the degree to which snow depth affects deer mobility. Snow densities decrease with increasing elevation (Fitzharris 1975), so high elevations would be more likely to have densities of snow that would not support deer and so restrict their movement. This decrease of deer mobility would result in increased energy costs for movements while foraging in areas of deep snow (Jacobsen 1973).

The burial of food and the deer's reduced mobility in areas of deep snow would result in a decreased density of available food, and an increased energy cost of obtaining food. For migratory deer, these snow-dependent effects on foraging efficiency mean that winter home ranges with shallow snow or snow-free areas would be more favourable than the summer home ranges in winter with deep snow cover.

Resident deer would also experience lowered food densities on their summer home ranges during winter. This reduction would occur because of the characteristics of food plants on summer home ranges, and differences in snow depth and density between

forests and cutovers. Use of cutovers by resident deer was greater in summer than in winter (Fig. 24). In summer, most of the food in these cutovers was in the form of herbs. In winter, herbs were dormant or dead and their availability reduced or eliminated by even shallow snowdepths. Forested areas have more food available since food here is mainly shrubs which are less affected by shallow snow depths. Cutovers have snowpacks of greater depths than nearby forested areas and have higher energy costs for locomotion (Jones 1975). At low elevations under the observed snow conditions, forested areas have greater food densities than most cutovers and energy costs for locomotion are lower. Winter home ranges of resident deer, being predominantly forested habitats, are more favourable in winter than their summer home ranges which have greater amounts of cutovers and poorer snow conditions.

As with summer home ranges in winter, differences in snow depths between the winter and spring home ranges modify the amount of food available to deer and their energy cost of locomotion. Spring home ranges of most deer were located in valley bottoms. These areas had snowpacks that accumulated to greater depths and persisted for longer periods than did the snowpacks in winter home ranges on adjacent low elevation sidehills. Spring home ranges also included large portions of cutover. Snow depths in the valley bottom were frequently deeper than the 37 cm depth estimated to restrict locomotion of black-tailed deer. Although burial by snow of forage on spring home ranges would not be as great as on summer home ranges, more forage would be covered on spring home ranges than on winter

home ranges. On spring home ranges, the herb component in the amount of food available during winter would be much less than that available in summer or spring. Given the absence of herbs and the higher costs of locomotion on spring home ranges during winter, winter home ranges would be the most favourable habitats.

Although differences between individual deer were observed, the locations of seasonal home ranges were similar in their snow characteristics. Winter home ranges were in areas subjected to less snowfall and periodic snow cover of shorter duration than were other seasonal home ranges. Abundance and availability of food during winter are a function of both the amount of food present and the snowpack. On winter ranges snow accumulation is less and more food is available than on the other seasonal habitats. The winter ranges are the only habitats where food is available and the energy cost of locomotion is low.

Altitudinal migrations from summer home ranges to winter home ranges coincided with, or occurred soon after, the first snowfalls of 12 cm or more. Snowfalls of 3 and 5 cm were not sufficient to cause migration. Thus, the winter migration was not a direct response to the availability of food. This is also implied by the observation that deer did not move to elevations just below the lower extent of snow, but moved directly to their winter home ranges well below the snow line.

The coincidence of snowfall and winter migration is common in North American ungulates (Edwards and Ritcey 1956, Blood 1963, Capp 1968, Phillips et al. 1973, LeResche 1974, Sweeney 1975, Hoskinson and Mech 1976, Leege and Hickey 1977). Other

studies observed winter migrations correlated with climatic factors such as temperature and humidity (Wright and Swift 1942, McCullough 1964), and water availability (Ashcraft 1961). Ashcraft (1961) and McCullough (1964) observed migrations occurring up to several weeks before actual snowfalls. The occurrence of winter migrations before the food supply is reduced to densities below that on winter ranges does not mean that food availability is not the ultimate factor inducing migration. Adaptation to unpredictable or highly variable factors may include either an immediate or premature response (Cohen 1967). Ungulate populations that make their winter migration before snow covers their food supply may only be reacting to the probability that a snowfall may occur which will cover their food as well as prevent their migration to winter range (Bergerud 1974). In places where deer migrations occur before the first snowfalls, distances between summer and winter ranges may be up to 160 km. In these situations, the probability of an early snowfall deep enough to impede migration may be sufficient to select for deer that are sensitive to environmental variables which are precursors of snow.

In situations where distances between summer and winter home ranges are short, snowfall is implicated as the trigger for migration. In only one area is a winter migration of deer described that occurs several months before the first winter snowfalls (Dealy 1959, McCullough 1964). In this apparent anomaly, night counts were made only on the summer range. Changes in deer abundance were interpreted as migrations. Although in late summer there was a decline in deer numbers, a

migration to the winter range was not demonstrated. McCullough (1964) was unable to detect increases in deer abundance in other portions of his study area, and interpreted the decline in deer population as an early migration to the winter range. In nearly all other studies in areas where there is snow during the winter, snow is reported as the initiator of the winter migration (Russell 1932, Dixon 1934, Leopold et al. 1951, Longhurst et al. 1952, Gruell 1958, Moir 1976, Bertram and Rempel 1977). Depending on the risks and benefits of these movements, selection would favour deer that were sensitive to factors which induce migrations before they are necessary from a foraging perspective. Over long distances, the chances of being trapped on the summer range may be sufficient to outweigh the loss in fitness imposed by not staying on the summer ranges as long as is possible (Cohen 1967).

Spring

During spring, when winter and spring home ranges are snow-free, and thus not subjected to the burial of forage and locomotory restrictions of deer by snow, spring home ranges would have greater densities of available food than winter home ranges. Snow melts on spring home ranges early in spring and uncovers new sources of food. Use of these spring home ranges with higher densities of food results in movement of deer from their winter home ranges.

During spring, summer home ranges would still be covered with snow. Locomotion would therefore be impeded, and although the snowpack could be less than the snow-free heights of shrubs,

the snowpack on summer ranges still covers shrubs because of stem displacement. This displacement and consequent burial of shrubs result in densities of available food on summer home ranges during spring that would be less than those on spring home ranges.

In this study, locations of deer in spring were different from their locations in winter. This contrasts with the results of Dasmann and Taber (1956) who do not recognize spring home ranges as spatially different from winter home ranges, but do describe "seasonal drifts" of the deer population during the spring. Some authors state or imply that migrations must be of a certain magnitude (Einarsen 1946, Longhurst et al. 1952). This assumption has led to discussions of "seasonal drifts", when actually short distance seasonal movements were observed. Lack of recognition of spring home ranges by earlier studies probably results because seasonal movements have been determined usually from changes in the seasonal dispersion of the deer population, rather than from locations of individual animals.

Summer

Energy is a major factor influencing the size of home range (McNab 1963, Schoener 1968, Harestad and Bunnell, in press) and the use of habitats (Klein 1965, Jarman 1974). Foraging models predict that animals should forage in habitats where the density of available energy is greatest (MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). For ruminants, the caloric need is a primary one to which requirements of other nutrients are linked (Blaxter 1962, Oldemeyer 1974) and the available

energy in forage is indicative of its nutritive value (Swift 1957, Hardison 1959, Reid 1968). Given the relationships between energy, foraging behaviour, and home ranges, it follows that seasonal movements should place deer in habitats where the density of available energy and nutrients would be greater than in habitats used in the previous season. Thus selection of seasonal habitats should be based on the relative availability of energy and nutrients.

Estimates of digestible energy were not available for the major forage types used by black-tailed deer in the study area. However, digestible dry matter values were available from Rochelle (in prep.) and used in place of digestible energy. Digestible dry matter is directly proportional to digestible energy with r^2 of .98 (Moir 1961) and .93 (Rittenhouse et al. 1971). This correlation is supported by studies of wild ruminants (Ammann et al. 1973, Hebert 1973). Digestible dry matter is also proportional to the protein content of a forage, since forages high in protein are usually low in crude fibre (Crampton and Harris 1969). Because of these interrelationships the density of digestible dry matter of the available food was used to evaluate home ranges, and is an expression of the density of energy and nutrients available to deer.

During summer, the amount of energy and nutrients available to deer on their seasonal home ranges was estimated in terms of the density of digestible dry matter. The mean density of digestible dry matter per location was calculated for the three seasonal home ranges of each deer, under conditions of the summer food supply for the appropriate habitat types listed in

Table II. Mean densities of digestible dry matter for the day and night locations were weighted according to average length of day and night at 50°N between June and October (List 1966), and a mean daily density of digestible dry matter per location calculated (Table XI).

The locations of radio-tagged deer in summer were situated in habitats significantly greater (p ≤ .05) in density of digestible dry matter than their winter ranges contained in summer (Table XI). For only one out of the seven radio-tagged deer was the habitats used during summer less abundant in digestible dry matter than habitats this deer would have encountered had it stayed on its winter home range during summer. This deer, OFL62, was a resident and the lower density of digestible dry matter for his summer home range was due to his greater use of the Western Hemlock - Plagiothecium association during summer than in winter.

Densities of digestible dry matter available on summer and spring home ranges were not significantly different (p ≤ .20). Three of the four migratory deer encountered greater densities of digestible dry matter by moving to their summer home ranges than they would have encountered had they stayed on their spring home ranges for summer. The fourth migratory deer and the two resident deer used habitats in summer that had lower densities of digestible dry matter than habitats they used in spring. In one resident deer, the sample size of locations was small and density of digestible dry matter on the spring home range may have been overestimated. Part of the spring home ranges of the other two deer included the Vaccinium-Skunk Cabbage association.

Table XI. Mean density of digestible dry matter per location
available during summer on seasonal home ranges. Wilcoxon signed
ranks test.

H_o: summer $\leq$ winter ; T=1, n=7, p$\leq$.01

H_o: summer $\leq$ spring ; T=6, n=6, p$\leq$.20

H_o: spring $\leq$ winter ; T=3, n=6, p$\leq$.05

Food Available On Seasonal Home Ranges
During Summer

$(\text{ kg digestible dry matter ha}^{-1})$

		Spring Range	Summer Range	Winter Range
MIGRATORY	OFL61	360.4	144.9	106.1
	OFL68	-	208.5	166.2
	OFL67	197.8	503.6	179.8
	OFL60	99.2	256.9	142.8
	OFL71*	163.8	326.2	124.6
RESIDENT	OFL58	288.8	210.0	172.0
	OFL62	190.6	126.4	142.8

* horizontal migrator

This association has a high density of digestible dry matter but is small in area relative to other types of forested plant associations . Migration of deer away from the Vaccinium-Skunk Cabbage association and reduction in use of this habitat by resident deer may result from the concentration of deer in spring and use of this habitat throughout the year by Roosevelt elk (*Cervus elaphus roosevelti* Merriam). This concentration and associated feeding by deer and elk may reduce the amounts of food available in spring habitats.

While the effect of feeding in spring habitats could reduce food density, another potential factor, that could explain why deer leave the spring habitats and go to summer home ranges, is predation. If deer predators selected their hunting habitats on the basis of prey density and foraging efficiency, then during spring they would focus their hunting in deer spring ranges. Not only are the deer concentrated on the spring range but fawns are born in June adding further to the prey available to predators. Risk of predation would be less on high elevation summer ranges because wolves (*Canis lupus* Linnaeus) are tied to den sites at this time (B. Scott, personal communication) and black bears (*Ursus americanus* Pallas) are tied to low elevation habitats because of their dependence on vegetative food. Attraction of predators to spring ranges would increase the risk of predation to deer inhabiting these areas and make spring home ranges less favourable than summer home ranges. If deer moved off spring home ranges and into the much larger area of summer range when it was snowfree, the risk of predation may be reduced because of lower prey densities (Tinbergen *et al.* 1967).

Movement from spring to summer home ranges coincide with the melting of the snowpack and the uncovering of forage on summer ranges. For migratory deer, this movement was not immediate but occurred up to several weeks after the first bare patches of ground appear. Short term visits to the summer home ranges prior to permanent seasonal occupancy were observed in some migratory black-tailed deer and have been reported by Bertram and Rempel (1977) for California mule deer (O. h. californicus (Canton)) and by Hoskinson and Mech (1976) for white-tailed deer. Occasional visits to suboptimal habitats are proposed as functioning to keep an animal aware of changes in the food supply of potential habitats (Smith and Sweatman 1974, Davies 1977). These visits suggest that black-tailed deer reconnoitre their summer home ranges and provide a mechanism through which their summer home ranges can be occupied when they are more favourable. Short term visits provide deer with an up-to-date assessment of conditions on their summer home ranges.

Early studies implicated both the abundance of food and its nutrient content as factors in migrations of mule deer (McLean 1930, Russell 1932, Dixon 1934, Leopold et al. 1951, Longhurst et al. 1952). Where nutritional factors are suggested as important in causing seasonal movements, protein content in the forage was proposed as the inducing agent (Dealy 1959, Hebert 1973). Although protein is necessary for growth and body maintenance, it also facilitates increased forage digestibility and food intake and thus the benefits of high protein diets to ruminants are mainly in terms of energy (Jones 1972, Verme and Ullrey 1972, Baile and Forbes 1974). Relative availability of

energy and nutrients on seasonal home ranges of migratory animals depend on both the quality and quantity of forage. Studies relating seasonal movements to protein content of forage (Dealy 1959, Klein 1965, Hebert 1973) have found nutritive disparities between seasonal ranges, but since food abundance was not assessed, evaluation of the advantages of migratory behaviour cannot be made. The nutritive value of the forage cannot be singled out as the driving variable in migration. Both quantity and quality of the forage combine to give a density of digestible dry matter and it is this density of digestible dry matter to which black-tailed deer appear to respond.

In coastal areas where summers are wet and moisture deficiencies do not cause early senescence of the forage plants at low elevations, altitudinal differences in the nutritive content of forage would not differ as much as it does in drier interior and alpine areas. In the study area on Vancouver Island, the principal forages of deer are herbs and shrubs. These classes of forage maintain their nutritive quality over a longer portion of the phenological cycle than do grasses (Cook 1972). Both the summer-long succulence of herbs and shrubs and their prolonged high quality would result in less nutritional difference in the forage between altitudes on the coast than would be observed in interior areas.

If only differences in quality, and not quantity, of the forage were responsible for the seasonal movements of black-tailed deer in the study area, then several major differences would be expected from the observed patterns of movements. If black-tailed deer were exploiting a phenological state of their

forage in order to maximize their intake of some nutrient, such as protein, then a slow progressive migration would be observed. Deer would be expected to leave their spring home ranges and move upwards in elevation or into tributary valleys following the best phenological condition of the forage. This pattern of movement was not observed. The final migration of black-tailed deer from their spring to summer home ranges was not a gradual process over many days, but occurred in a period of less than a day.

If black-tailed deer were migrating in order to exploit some phenological stage of their forage, then the deer population would be concentrated within the area where this stage occurs. On Mount Cain, the population would be expected to be in a horizontal strip that moves altitudinally in response to the changing phenological state of the forage. This pattern was not observed. Both radio-telemetry and night count observations indicate that some deer move from low elevations into mid-elevations and remain there throughout summer. Other deer, whose home ranges were at high elevations, remained on their low elevation spring ranges until the high elevation habitats were snowfree and plant growth had begun. Under the observed system of migratory behaviour, deer left the spring ranges where they were concentrated and spread out over the habitat made available during summer with the melting of the snowpack.

If deer were migrating in order to exploit a particular phenological stage of their forage, then since nutritional advantages would exist for migratory deer, non-migratory deer would be selected against. Hence, a third expectation is that if

black-tailed deer were responding to solely a nutritional factor, the population should be primarily migratory and few resident deer would occur. This expectation is not confirmed by my observations. There are substantial numbers of resident deer.

Rather than nutritional factors being invoked for explaining some migrations and forage availability invoked for others, my approach can be used as the basis for a single model of seasonal movements that focuses on energy, nutrients, and security factors. By addressing these factors, assessment of seasonal home ranges in terms of the benefits and costs to the animal's fitness permits a more general explanation of seasonal movements made by black-tailed deer.

4.3. Seasonal Movements And Social Organization

Mammalian societies are complex systems influenced and modified by external environmental variables and species parameters (Crook et al. 1976). Crook et al. (1976) argue that particular social structures arise because they provide an optimal context within which the individuals comprising them carry out vital functions including primarily: resource exploitation, predator avoidance, mating, and rearing of young. The importance of the spatio-temporal distribution of resources to the social organization of ungulates is discussed by Estes (1974), Jarman (1974), and Geist (1974), and is relevant to the seasonal movements of black-tailed deer. In this study, the use of home ranges rather than territories by black-tailed deer confirm predictions of Geist (1974) concerning the spatial organization of ungulates in environments with seasonal

fluctuations in availability of resources.

Group size is one of the principle social systems variables used to describe social organizations (Crook et al. 1976). In "chaparral" habitats, black-tailed deer form small groups for most of the year (Dasmann and Taber 1956). These groups consist mainly of mothers and young or up to three adult males. During the rut more males become solitary and more male-female groups are observed. The "chaparral" habitat would be classed as a closed habitat by Jarman (1974), who observed a negative correlation between group size visual density of the habitat. Forested and conifer seral stage habitats are also closed habitats so small groups sizes would be expected. In the study area deer occurred mainly in small groups or were solitary, similar to those described by Dasmann and Taber (1956) and agree with the predictions made by Jarman (1974). In cutovers which have little lateral cover (newly logged, herb, fern, and shrub seral stages), the habitat would be more open and group sizes would be larger than in the visually dense habitats (Jarman 1974, Hirth 1977). The increased use of the more open habitats by black-tailed deer during spring and summer should result in larger sized aggregations in these seasons than in winter. These aggregations would affect other aspects of social behaviour such as interaction rates and activity.

The seasonal movements of black-tailed deer would impose further influences on their social organization. In a population where some members are migratory, the seasonal concentration and spacing out of deer would affect stable hierarchical relationships because of the addition and loss of social

partners. Seasonal movements by a portion of the population to summer home ranges at high elevations or to tributary valleys would result in the breaking of social relationships that were established between individuals during winter and spring. After the summer migration, new relationships would have to be established with the unfamiliar deer encountered on the summer home range. Even on low elevation areas inhabited by resident deer some social disruption would occur. Migration away from the low elevations by migratory deer would result in the loss of some participants and this would alter relationships between the remaining social partners.

The rut occurs in November and early December (Thomas 1970), and overlaps with the winter migration period. The shuffle of the deer population resulting from the winter migration would affect the dominance hierarchy among the males and so have direct repercussions on the mating system of deer (Kucera 1978). Mixing of migratory and non-migratory deer would result in a less stable male hierarchy. The social organization of black-tailed deer in the study area would be based on transient hierarchical relationships rather than on stable social relationships such as in resident populations described by Dasmann and Taber (1956) and Miller (1970).

4.4. Model Of Seasonal Movements

A more succinct statement of the seasonal movements and habitat use by black-tailed deer can be made through a conceptual model (Fig. 27). This model is derived from observations of deer movements and the factors proposed to

Figure 27. Model of seasonal movements and habitat selection.

Benefits To Fitness

- ENERGY
    quantity and quality of food,
    requirements, expenditures.

NATURAL SELECTION FOR
GREATER FITNESS

HABITATS
AVAILABLE

Habitat Evaluation

- experience
- habitat predictability
- exploration
- natural selection for
    surrogates of fitness

HABITATS
SELECTED

HABITATS
USED

**Seasonal
Movements**

Costs To Fitness

- PREDATION
    security cover, mobility,
    other prey.

**Seasonal
Environmental Changes**

depth and density of snow,
growth and dormancy of
vegetation.

elicit these movements. The model illustrates the process of habitat selection by black-tailed deer in the study area. In this model, seasonal movements are a response by deer to changes in the relative favourability of different habitats. Given a number of habitats which are available to deer, the use of these habitats can be evaluated on the basis of the benefits and costs to the user's fitness. The benefits to fitness of a habitat are represented by a single parameter, net energy acquisition. This parameter integrates the effects of nutrient requirements, weather, competition, locomotion, and foraging costs occurring within a particular habitat. The costs to fitness express the effects of changes to the risk of predation within a habitat and incorporates the impacts of alterations in prey density, security cover, and predator avoidance.

Among heterogeneous habitats potentially available to deer, some will be more favourable than others. This favourability is evaluated in terms of the deer's fitness. The evaluation can be based on the deer's experience, selection for the appropriate behaviour, or possibly even direct evaluation. Experience could provide deer with a means to anticipate imminent environmental changes (Bouckhout 1972). No conscious anticipation is needed as long as deer respond appropriately to the environmental signals. Tradition may also contribute to this "experience". In black-tailed deer, tradition probably helps to maintain migratory or resident behaviour in individuals once their seasonal movement patterns have been established.

Habitat evaluation can also be made by migratory explorations to potential habitats. This process may be occurring in black-tailed deer and could explain their short visits to summer and winter home ranges prior to their seasonal occupancy of these habitats. When habitats have been evaluated, then those that are the most favourable can be selected. Although some habitats may have different benefits and costs to fitness, they may have the same net contribution to the deer's fitness, and thus more than one type of habitat may be used by deer. These differences would be observed as variability in the patterns of habitat use.

As habitats are evaluated, deer select and use the more favourable ones. Depending on the location of these habitats the observed patterns of seasonal movements could occur. The use of these new habitats would continue until their food and cover resources were altered. These alterations would be primarily a function of snow and phenological changes in the food sources. In the study area these processes are seasonal and thus change the relative favourability of the habitats. As habitats are altered, further habitat selection would occur and the response observed as another seasonal movement.

The movements of black-tailed deer from one seasonal home range to another as a response to the benefits and costs to fitness accrued through exploiting the most favourable habitats is an explanation consistent with the observed patterns of seasonal movements. The causal differences between vertical and horizontal migrations as well as seasonal shifts in use of different habitats within home ranges of resident deer can be

resolved by this model of habitat selection.

The model has broader application than just accounting for the behaviour of black-tailed deer in the study area. The seasonal movements of mule deer throughout its geographical range can be attributed to the seasonal availability of food. This variation in food availability is largely due to the effects of precipitation in the form of both rain and snow. Four climatic regions based on the amount of rain and the depth and duration of the snowpack exist within the geographical range of mule deer in North America. Among these climatic regions the patterns of seasonal movements are between extremes of completely resident populations to completely migratory populations. In the dry south-west there is little if any snowfall and precipitation is low, occurring mostly in winter. In areas away from ground water this pattern of precipitation results in the drying and senescence of forage during the summer with green forage occurring in winter. At the beginning of summer deer do not migrate up into the mountains but instead move down into the valley bottoms where green forage is available in the riparian habitats and irrigated agricultural land (McLean 1930, Longhurst and Chattin 1941, Longhurst et al. 1952). After the winter rains and growth of forage in the areas away from the valley bottoms the deer leave these areas and migrate into the surrounding habitats where they remain until the dry summer.

In moister parts of California, Oregon, and Washington where there is little snowfall, mule deer tend to be mainly resident (Dasmann 1953, Dasmann and Taber 1956, Brown 1961,

Lauckhart 1948). The food supply although seasonally changing does not have the extreme spatial differences in quantity and quality as occurs in the dry or high snowfall areas. In this region deer make seasonal shifts of their home range centres (Dasmann 1953) but there are few migratory deer. The preponderance of resident deer occurs because their requirements are met within their home ranges for the whole year and there are not more seasonally attractive habitats nearby.

The third climatic region in the range of mule deer has deep snowpacks during the winter in high elevations and low rainfall during the summer. These conditions occur in interior areas like Colorado, Utah, eastern California, and parts of Washington and Oregon. In this climatic region there is a downward altitudinal migration in winter coinciding with snowfalls in higher elevations and this migration is attributed to the covering of forage by snow. In spring there is an upward migration which occurs because the food in the lower elevations matures and dries out by summer and so the forage in the high elevations becomes more nutritious relative to that at the low elevations. Deer in this climatic region are primarily migratory (Russell 1932, Dixon 1934, Leopold et al. 1951, Longhurst et al. 1952, Robinette 1966, Loveless 1967, Bertram and Rempel 1977).

The fourth climatic region is in the north-coastal areas and represented by this study. Here rainfall is abundant and occurs throughout the year, snowpacks are deep at high elevations but low elevations are snowfree or have shallow snowpacks. The rain allows green forage throughout the summer at all elevations. In winter, snow covers forage at high elevations

and the low elevations are the only habitats where food is available. Under these climatic conditions deer populations have both resident and migratory components. The resident deer stay in the low snowfall areas throughout the year but make seasonal shifts in their home range centres. The migratory deer move from winter ranges to summer habitats that were unavailable during the winter. They return to the winter ranges after the initial snowfalls on their summer ranges. The seasonal movements of mule deer in the four climatic regions can be explained by the habitat selection model. Although the patterns of movements are different, the reasons for them appear to be the same.

4.5. Seasonal Habitats and Forest Harvesting

The concept of seasonal movements and subsequent habitat use as a function of energy and nutrient availability and predation is useful in evaluating forest management practices with regard to the abundance of black-tailed deer . In forest types where there is little shrub and herb food , removal of the forest canopy results in an increase of forage and is thought to be beneficial to deer (Einarsen 1946, Leopold 1950, Brown 1961, Gates 1968, Hines 1973). In the study area, some forested summer range habitats have equal or greater food densities than is found in adjacent cutovers (Fig. 5). Also, these forested habitats are more extensive in area than are the cutovers and are used by deer during day and night. Forest habitats thus represent a large amount of the potential summer foraging area for deer. Because of greater food abundance in high elevation and some valley bottom forest types (Fig. 5), the benefits to

deer of logging in the study area are likely not as great as those enjoyed by deer in regions further south or with lower snowfall. In the study area removal of the forest canopy at high elevations probably does not affect deer abundance to any great extent, since food can be provided by either forested or logged habitats.

On summer ranges, where food can be provided by either forested or cutover areas, the use of these habitats by deer will depend upon satisfaction of the deer's other habitat requirements (Bunnell and Eastman 1976). Although initially logging usually results in the lack or reduction of cover for the first 15 to 20 years after the forest is removed, some harvesting practices could be employed which would provide the deer with cover. One obvious way to provide cover in the summer ranges would be to leave patches of old-growth. Since these patches are only intended to provide cover, non-merchantable stands would suffice.

Logging of low elevation forests could either benefit or constrain deer populations depending upon the season in which the evaluation is made. In summer, logging may appear beneficial to deer. However, since extensive summer ranges already exist at high elevations in the study area, replacement of forests by cutovers at low elevations may only result in the redistribution of the deer population. Logging in low elevation forests essentially results in the provision of summer ranges adjacent to winter ranges. Provision of this habitat may encourage an increase in the proportion of the resident component, but not necessarily in an increase of the total deer population.

In winter, forest harvesting at low elevations may have a detrimental effect on the deer population (Edwards 1956, Robinson 1956, Jones 1974 and 1975, Bloom 1978). The magnitude of this effect will depend upon the severity of the winter , the forest type that is logged, and the availability of other winter habitat. Some low elevation, forested plant associations provided little available digestible dry matter for deer (Fig. 9) and were used incidentally during winter (Fig. 25). Logging in these forest types should not be detrimental to the deer population and the cutovers created may provide foraging areas which deer could use during low snow depth or snow-free periods in winter. The value of these cutovers as winter foraging areas would be greatest once they had reached the shrub and conifer seral stages (Fig. 9).

Other forested plant associations at low elevations provide deer with greater densities of available digestible dry matter (Fig. 9) and reduced snow depths during periods of deep snow in winter. Use of forested winter ranges by black-tailed deer in deep snowfall regions was observed by Robinson (1956). He noted that during periods with deep snowpacks, deer were in old-growth forests. Robinson (1956) suggested that in deep snowfall regions logging of these forested winter ranges would be detrimental to the deer population. Edwards (1956) observed that deep snow was a factor in a die-off of black-tailed deer and recognized the importance of forested winter ranges. The value of forested winter ranges to black-tailed deer was apparent in the extensively logged Sayward Forest where only deer inhabiting the small patches of remaining old-growth survived the winter

(Edwards 1956). The necessity of old-growth forest as winter habitat for black-tailed deer was further acknowledged by Cowan and Guiguet (1965) and Alaska Dept. Fish and Game (1973). Jones (1974,1975) and Bloom (1978) were more specific about the types of forest habitat that were used by deer during winter. The habitats they identified are similar to those used by radio-tagged deer in this study.

In recent years preservation of "critical winter range" has taken priority in deer habitat management. The assumption is that preservation of "critical winter range" means preservation of the deer population. This is not necessarily true since "critical winter range" is not an isolated component of the habitat requirements of black-tailed deer and other seasonal habitats may be important in providing deer with adequate energy reserves with which they can survive the winter (Mautz 1978). It does not follow that if all "critical winter range" is preserved then the deer population will be maintained.

The importance of severe winter ranges may be overestimated because even though severe winter ranges have greater deer densities , mild winter ranges may provide the population with a greater total number of deer days of use. During periods of shallow snow depths mild winter ranges can have greater food densities than some forested plant associations used as severe winter range. In evaluating an area as winter range, consideration should be given to the contribution of the habitat towards meeting the winter energy and nutrient requirements of the deer population, and not just the density of deer in that habitat.

Failure to provide mild winter range may be just as detrimental to the deer population as failure to provide severe winter range. If only severe winter range habitat is provided for deer then during each winter they would be on their severe winter diet for the entire winter. Provision of mild winter ranges which would be available during periods of shallow snow may allow deer to reduce their rate of energy loss or it may even permit them to secure a positive energy balance, thus increasing their chances of over-winter survival. If mild winter ranges are not provided along with severe winter ranges, then deer would be restricted to severe winter ranges for the entire winter. This concentration of the deer population could cause an over-utilization of the forage and lead to a degradation of the severe winter range's carrying capacity.

If winter range habitat is to be provided for black-tailed deer then it must include areas of both mild and severe winter range. Severe winter ranges are described by Jones (1974 and 1975) and in the study area are primarily in the Salal - Douglas-fir association. Deer used this association type mainly during the more severe periods in winter. When weather was milder and snow depths shallower, deer left the Salal - Douglas-fir association and moved into Salal - Western Hemlock and Amabilis Fir - Western Hemlock associations. Since deer moved from severe winter ranges during mild periods it suggests that mild winter ranges met their requirements better at these times than did the severe winter ranges. Stevenson (1978) has shown that lichens are more abundant on mild winter ranges than on severe winter ranges. This difference in lichen abundance

combined with greater amounts of shrubs and conifers and greater area of mild winter ranges, would provide deer with a more substantial food source than that on severe winter ranges. Because of their potential as foraging areas, mild winter ranges may be just as important as severe winter ranges to the over-winter survival of the deer population.

4.6. Migration Corridors

Jones (1975) proposed that continuous strips of mature forest be maintained between subalpine summer ranges and low elevation winter ranges in order to facilitate downward winter migration of deer. These corridors are also suggested by the British Columbia Fish and Wildlife Branch (1976) who recommend that "long term firebreak - deer corridors" extending from valley bottoms to heights of land be established to connect winter ranges with summer ranges. The provision of these corridors in the management of deer habitat are implemented by the B. C. Forest Service through its input into forest harvesting plans (Young 1977).

Results of this study suggest that the concept of "deer corridors" and their value in facilitating black-tailed deer migrations should be reassessed. Migration of some deer from their summer to winter home ranges occurred soon after the first snowfalls. These snowfalls were ephemeral and not deep enough to prevent deer movement. Several times during the initial part of the winter deer moved to their winter home ranges below the snow line and returned to their summer home ranges a few days later when the snow melted. Great mobility is also evident in that

migratory movements were accomplished in less than 12 hours. Given the sensitivity to snow by black-tailed deer , the speed with which migration can occur, and the short distances involved, it is unlikely that substantial numbers of black-tailed deer would be trapped at high elevations by deep snow and thus be unable to move to their winter ranges, if no forested corridors existed.

Sensitivity to weather and early snowfalls has been reported in mule deer (Russell 1932, Leopold et al. 1951, Wallmo and Gill 1971). Although die-offs of ungulates on winter ranges have been reported (Severinghaus 1947, Leopold et al. 1951, Longhurst et al. 1952, Robinette et al. 1952, Edwards 1956, Klein and Olsen 1960, Cumming and Walden 1970, Verme and Ozoga 1971), no instances of mass die-offs of mule deer caused by entrapment on their summer ranges have been observed, even in populations where migrations of over 80 km are common. The mobility of black-tailed deer and their sensitivity to snow suggest that provision of forested corridors as migratory routes are unnecessary. If cover for migrating deer or habitat for other wildlife species is desired then it could be provided by segmented or staggered forested blocks, or by the appropriate placement and enhancement of residual strips.

Forested corridors were also proposed by Jones (1975) to function as mild winter range. The potential for winter use of these corridors decreases with increasing altitude. If the function of corridors is to provide mild winter range then forested areas allotted for this purpose would be more effective if they were horizontally deployed and bordered severe winter

ranges. This orientation would make mild winter ranges accessible to a greater proportion of the deer population for a longer time in winter and be more beneficial than the present corridors between high and low elevations.

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Appendix I. Estimates of shrub annual growth available in
forested plant associations and seral stages during summer.
Actual heights were used for stems over 30 cm. For stems less
than 30 cm the mean stem height was set at 0, 10, and 30 cm.
Forested plant associations : VS = Vaccinium - Skunk Cabbage,
SC = Sword Fern - Western Red Cedar, DW = Deer Fern - Western
Hemlock, WP = Western Hemlock - Plagiothecium, AW = Amabilis
Fir - Western Hemlock, SD = Salal - Douglas-fir, SW = Salal -
 Western Hemlock, AT = Amabilis Fir - Twisted Stalk,
MC = Mountain Hemlock - Copperbush. Immature Seral Stages :
N = Newly Logged, H = Herb, F = Fern, S = Shrub, C = Conifer.

Association or Seral Stage	Plot No.	Annual Growth (kg ha^{-1}) For Various Mean Heights Of Stems $\leq$ 30 cm		
		0 cm	10 cm	30 cm
VS	7	974.2	1005.7	1095.6
VS	20	666.3	700.7	800.4
VS	41	136.8	156.8	209.4
SC	13	10.1	10.5	11.6
DW	19	16.3	18.0	25.2
WP	3	t	.1	.3
WP	39	1.1	1.4	2.8
AW	10	5.7	6.4	8.8
AW	18	4.6	5.3	8.0
AW	44	261.5	269.7	299.0
AW	45	154.2	159.8	182.4
SD	2	297.4	359.4	521.3
SD	5	575.3	643.9	823.3
SW	4	121.8	218.0	471.8
SW	6	190.4	218.1	302.0
SW	8	239.5	253.6	296.0
SW	17	19.6	21.4	28.6
SW	46	160.5	164.4	191.5

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Association or Seral Stage	Plot No.	Annual Growth (kg ha^{-1}) For Various Mean Heights Of Stems ≤ 30 cm		
		0 cm	10 cm	30 cm
AT	1	309.5	323.5	369.4
AT	28	992.1	1018.0	1104.8
AT	29	263.6	279.4	331.1
MC	32	364.4	406.5	545.4
MC	33	471.1	531.0	727.6
N	38	5.1	5.4	7.4
H	9	1.5	5.7	21.8
H	11	t	.3	1.6
H	14	t	.3	1.3
H	15	.1	.5	1.7
H	16	t	t	.2
H	21	13.3	20.1	52.9
H	23	67.3	83.8	137.9
H	24	11.3	12.1	17.2
H	30	7.2	55.5	214.0
H	31	2.7	3.3	5.8
F	12	t	t	.2

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Association or Seral Stage	Plot No.	Annual Growth (kg ha^{-1}) For Various Mean Heights Of Stems $\leq$ 30 cm		
		0 cm	10 cm	30 cm
S	27	122.8	234.0	524.6
S	34	32.8	39.6	62.2
S	36	.1	.2	.5
S	37	7.4	7.5	8.1
S	40	2.9	3.0	3.5
S	43	268.7	290.0	361.8
C	22	12.5	12.7	14.1
C	25	257.0	469.4	1027.2
C	26	306.2	461.2	866.3
C	35	195.7	515.8	1351.7
C	42	139.8	141.3	146.7

t = trace