DEER FOOD PRODUCTION IN CERTAIN SERAL STAGES OF THE COAST FOREST

by

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ABSTRACT

This study was designed to determine which seral stages of the regenerating coast forest are most efficient at converting radiant energy into energy available as seasonal deer foods, and if the most efficient stages are most intensively used by deer. Populations of Columbian black-tailed deer (*Odocoileus hemionus columbianus* Richardson) in coastal British Columbia have been reported to reach maximum levels soon after logging and slash-burning, and to decline as succession advances. The efficiency of a deer range in producing food has been suggested as a factor influencing reproductive success and thus, population density.

Seasonal forage preferences were determined through rumen content analysis. Cover composition up to four feet in height, and summer and winter estimates of quantity, variety and nutrient quality of the important food species were obtained in different seral stages. These data were then related to the intensity to which deer utilized each seral stage, as indicated by the abundance of pellet groups.

An early salal-catsear (*Gaultheria-Hypochaeris*) association develops three to five years after slash-burning. This type was preferred by deer during spring and early summer. Herbaceous plants formed 60 per cent of the spring-summer diet and were represented by more species, covered more surface area, and produced more available forage in this seral stage than in any other.

A salal-Douglas fir (Gaultheria-Pseudotsuga) association develops 12 to 15 years after slash-burning. This type was preferred during autumn and winter. Shrub and coniferous species formed 70 to 80 per cent of the autumn-winter diet and were represented by more species, covered more surface area, and produced more available forage in this seral stage than in any other. In addition, the crude protein, mineral, and ash contents of the important evergreen foods were higher when eaten (autumn-winter) than at other times. Heaviest deer use occurred in the seral stages where these evergreens were most available.

The nutrient content of key foods changed significantly with season, and there was evidence of selection by deer of the most nutritious plants available. Tests to demonstrate declines in nutrient levels as seral succession advanced between the fourth and fourteenth years were inconclusive, particularly since there is a likelihood of significant declines occurring in the initial four years. However, seasonal and successional changes in food quality are believed to be a factor influencing range selection.

It is concluded that the numbers of deer within a logged unit of coast forest are affected by the efficiency at which food is produced. Numbers within the whole community are affected by the availability of ideal food-producing units for each season. A further hypothesis is suggested which states that sustained populations cannot be expected in a logged coast forest because seral succession will inevitably cause regression of range quality.

TABLE OF CONTENTS

Page

LIST OF TABLES

TABLES IN APPENDIX

LIST OF FIGURES

FIGURES IN APPENDIX

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INTRODUCTION

It has been postulated that in the absence of wildfires and prior to the development of the logging industry, few blacktailed deer (Odocoileus hemionus columbianus Richardson) were supported by the moist coniferous forest biome of the Pacific Northwest (Cowan 1945, Leopold 1950, Dasmann and Hines 1959, and Brown 1961). Early in the twentieth century extensive logging operations developed, and a wide-spread conversion of climax forests back to early seral stages began. Marked increases in deer numbers were noted by these workers to coincide with the regeneration of new growth.

Reasons for favorable responses by ungulates to the creation of pioneer floral conditions have been discussed by DeWitt and Derby (1955), and have been attributed to an improved nutritional quality of the range. Increased variety and abundance of herbaceous plants and shrubs (Storer 1932, Buckland 1941, Cowan 1945, Leopold 1950, Dasmann and Hines 1959), as well as improved nutrient content of the preferred food species (Einarsen 1946, Cowan, Hoar and Hatter 1950, and Swank 1956) have been suggested as causative factors. In this regard, recent investigations with deer reveal that more rapid growth rates, larger body size, increased productivity, and greater population densities result from a better nutritional regimen (Taber 1956, Taber and Dasmann 1958, Severinghaus and Tanck 1964, Bandy 1965, Klein 1965, Murphy and Coates 1966, and Ullrey et al. 1967).

It can be hypothesized, therefore, that within regenerating units of land the numbers of deer are affected by the efficiency at which solar energy is converted into available food. Efficiency is believed to be greatest soon after deforestation, and to decline as climax conditions are approached (Brown, 1961). Deer numbers may be expected to vary accordingly. Therefore, if other factors such as predation, weather, and hunting are constant or have negligible effects, largest deer populations can be expected when the number of ideal food-producing units for each season is at a maximum.

Within regenerating units, optimum efficiency should be reflected by the greatest intensity of deer use. It should occur when the greatest variety of nutritious and productive food species occupies the greatest surface area. Decreasing efficiency should be reflected by a declining intensity of deer use. It should occur when variety, nutritive quality, and surface coverage of foods decrease, and when large amounts of energy become trapped in unpalatable or unavailable plants.

Studies of quality and quantity of forage, as related to blacktailed deer numbers, are limited to work by Taber and Dasmann (1958), Brown (1961), and Klein (1965). These investigations compare conditions on separate ranges of different biotic or seral structure, thus demonstrating biological differences in isolated deer herds. In order that extraneous influences were kept to a minimum, the present study attempted to measure these factors as they occurred within a single range.

Objectives

Specifically the purposes were to explore the nature of changes in vegetation growing in logged and burned areas of the coast forest, and to relate these changes to a pattern of range selection by blacktailed deer. In order to test the basic hypothesis, five aspects were investigated in detail: (1) the seasonal food habits of deer occupying the range - information essential for defining the relative importance of various plant species; (2) the changes in species composition and vegetative cover as seral succession progresses; (3) the annual production of deer foods in different seral communities; (4) the changes with succession and season in the nutritive content of important deer foods; and (5) the magnitude of use by deer of various seral communities.

Theoretically, each of these aspects could be studied within a single regenerating unit of land, but only over an extended period of time. In order to make the study practicable, the alternative of studying a number of adjacent, block-logged units, each at a different stage of regeneration, was chosen.

THE STUDY AREA

Location

The privately owned forest land of the Northwest Bay Division of MacMillan Bloedel Limited encompasses approximately 135 square miles on the east side of Vancouver Island, 18 miles northwest of the city of Nanaimo (Figure 1). The land lies on the south side of the Englishman River and includes the drainages of the south and middle forks of the Englishman River and Moriarty Creek. It is bounded on the west by Mt. Moriarty (5283 ft) and Mt. Arrowsmith (5962 ft), on the south by Mt. DeCosmos (4444 ft), and on the east by Okay Mt. (2826 ft).

The area selected for intensive study included ten square miles in the northeast corner, lying between the south and middle forks of the Englishman River. It is centered at coordinates 49° 13'N and 124° 18'W.

Topography and Soils

A general northerly aspect and gently rolling slopes prevail throughout. A few steep slopes are confined to the river banks and to minor areas of rock outcrop. Physiography is intermediate between that typical of the Georgia

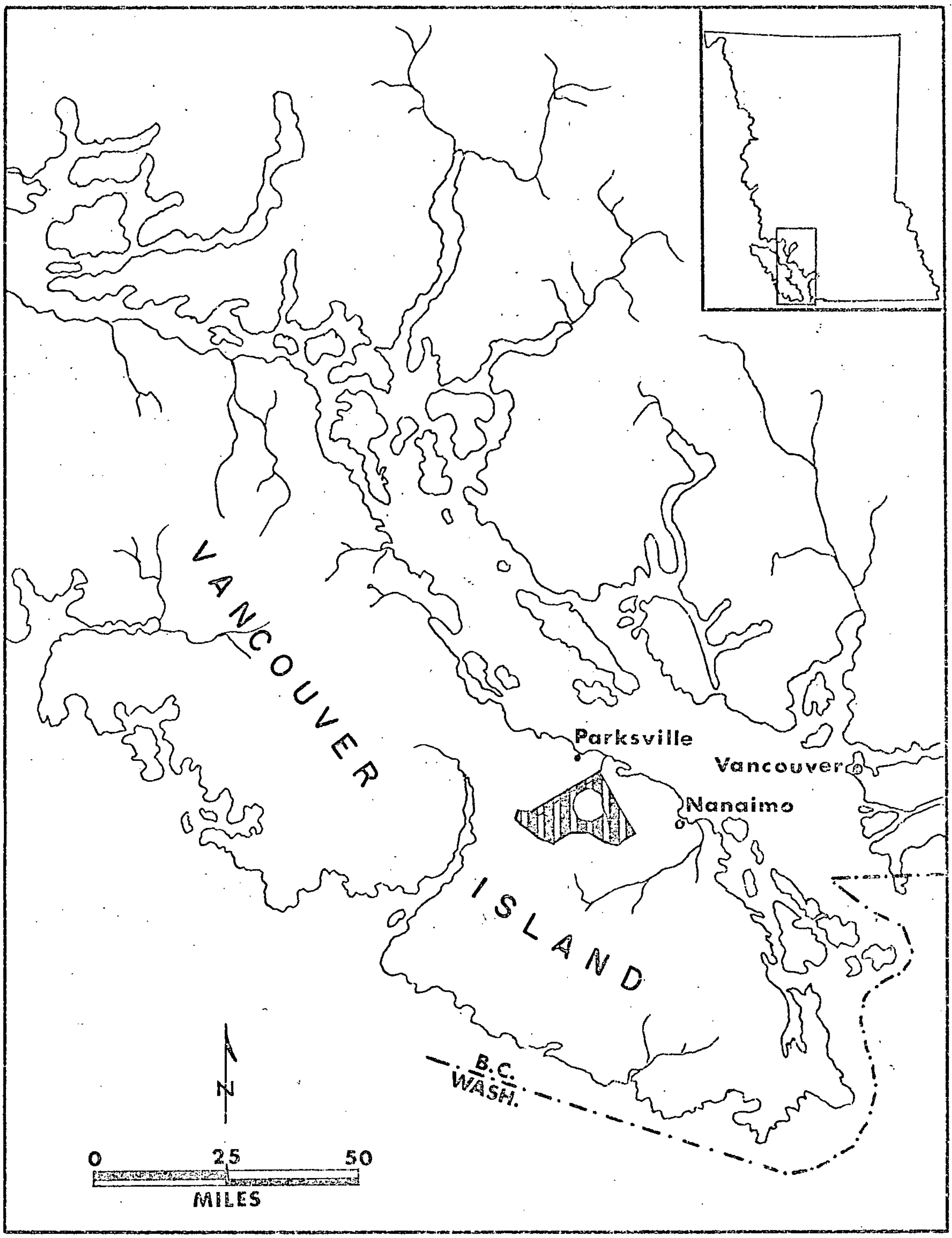


Fig. 1. Southwestern British Columbia showing the location of the Northwest Bay logging claim and the intensive study area (center).

Depression (Nanaimo Lowland) of the Coastal Trough and that typical of the Outer Mountain Area of Vancouver Island (Holland, 1964). Elevations range from 500 ft in the north-east corner to 1600 ft in the south-west corner.

Descriptions of soil profiles in the Nanaimo Lakes area ten miles to the south (McMinn 1957, Mueller-Dombois 1960) are considered representative of the study area. Parent materials are derived from Plutonic granite and Upper Cretaceous sandstone and sedimentary rock. Glacial drift and alluvial deposits have contributed most of the soil, with minor and localized contributions from rock-outcrop-colluvial materials. The soils belong to the Brown or Red-Brown Podzolic and Gley groups characteristic of warm, moist climates with dense vegetative cover. They are well drained, slightly acid and possess a relatively thin organic layer.

Climate

Northwest Bay lies in the rain shadow of the Vancouver Island Mountain Range 12 miles to the west (Cowan and Guiguet, 1965). Weather records taken at the Nanaimo Airport during the four year field study (Appendix A) provide a general indication of climatic conditions. Annual precipitation in the study area itself during that period was probably slightly higher than the average of 42.6 inches recorded at Nanaimo. This is based on the observations of Mueller-

Dombois (1960), who reported that in the Nanaimo Lakes area a significant west-east precipitation gradient exists, with as much as a 50 inch decrease in precipitation over a distance of 14 miles. Northwest Bay appears to experience the same gradient.

Temperatures are moderate throughout the year as indicated by a four year mean January temperature of 39.1 F and a four year mean July temperature of 64.7 F at Nanaimo Airport. Here again, mean temperatures and daily fluctuations are assumed to have been more extreme in the study area than at Nanaimo Airport, since the former is two miles further inland from the stabilizing influence of the sea and is 500 to 1600 ft higher in elevation.

Vegetation

Vegetation is typical of the Douglas Fir Bioclimatic Zone described by Krajina (1959) and Mueller-Dombois (1959). The climatic climax forest consists mainly of Douglas fir (*Pseudotsuga menziesii* var *menziesii*), with the edaphic climax species western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), balsam fir (*Abies grandis*) and lodgepole pine (*Pinus contorta*) comprising the remainder of the upper canopy. The timber yield from the area is approximately 50,000 feet-board-measure (f.b.m.) per acre, with a range of from 35,000 f.b.m. to 60,000 f.b.m. Species composition averages 70 per cent Douglas fir, 17 per cent western hemlock, 10 per cent western red cedar, 2 per cent balsam fir, and 1 per cent western white pine. (E. Touzeau, Forest Engineer, N.W. Bay Division of MacMillan Bloedel Ltd., pers. comm. 1963).

The climax and subclimax understory is dominated by salal (Gaultheria shallon), with lesser amounts of Oregon grape (Mahonia nervosa), dwarf rose (Rosa gymnocarpa), bearberry (Arctostaphylos uva-ursi), pipsissewa (Chimaphila umbellata), and twinflower (Linnaea borealis).

All seven of the associations of the virgin forest described by Krajina (1952) and Mueller-Dombois (1959) can be recognized in the study area, either in their natural form or in residual form following destruction. Two of these - the salal (Pseudotsuga-Gaultheria) and the salal-lichen (Pseudotsuga-Gaultheria-Peltigera) associations - completely dominate the others.

Logging and slash-burning have encouraged establishment of most of the edaphic and seral species listed by Krajina (1959) and Mueller-Dombois (1960). Noteworthy among these are red alder (Alnus rubra), trailing blackberry (Rubus vitifolius), black raspberry (Rubus leucodermis), willows (Salix species), hairy catsear (Hypochaeris radicata), pearly everlasting (Anaphalis margaritacea), vanilla leaf (*Achlys triphylla*), fireweed (*Epilobium angustifolium*), bracken fern (*Pteridium aquilinum*), and swordfern (*Polystichum munitum*).

Logging History

Logging first began in the study area in 1945, and except in 1946, some timber was removed each year until the end of the field work in 1962 (Table I). Sixty-four per cent of the mature forest was removed in that 18 year period, an average annual harvest of 3.5 per cent. The maximum annual harvest, in 1948, was 22 per cent. By June, 1962 slightly more than 2300 acres of mature forest remained.

Logging was by clear-cutting of selected 30 to 35 acre stands (settings), followed by drag-hauling with a spar cable or bulldozer to a roadside loading site. In the early years up to ten adjacent settings were cleared in a continuous operation. In the latter years this was reduced to a maximum of two or three adjacent settings, thus becoming more typical of patch-logging.

Slash-burning was practised regularly before and during the study. As a result, almost all settings were subjected to at least some degree of burning. The extent and intensity of the fires varied greatly, from effective and thorough broadcast burns in which almost all slash and vegetation was destroyed, to localized spot burns in which

TABLE 1 The logging history of the 10.1 sq. mile (6464 acre) study area at Northwest Bay.[1]

Year	Annual Cut Acres	Annual Cut %	Accumulated Cut %	Remaining Timber %
1945	99.9	1.6	1.6	98.4
1946	nil	nil	1.6	98.4
1947	266.2	4.2	5.7	94.3
1948	1436.8	22.2	27.9	72.1
1949	159.2	2.5	30.4	69.6
1950	494.1	7.6	38.0	62.0
1951	171.9	2.7	40.7	59.3
1952	390.1	6.0	46.7	53.3
1953	205.5	3.2	49.9	51.1
1954	73.8	1.1	51.0	49.0
1955	26.4	0.4	51.4	48.6
1956	179.1	2.8	54.2	45.8
1957	92.5	1.4	55.6	43.4
1958	184.4	2.8	58.5	41.5
1959	103.1	1.6	60.1	39.9
1960	121.0	1.9	62.0	38.0
1961	138.4	2.1	64.1	35.9
1962	14.3	0.3	64.3	35.7

[1]Data derived from logging company operations maps and from planimetric measurements of aerial photographs.

only portions of the light slash and vegetation were destroyed.

Conifer regeneration depended primarily upon natural seed drift from adjacent mature trees. Only portions of some large, exposed areas were reforested with two-year old Douglas fir seedlings (10-14 inches high) at densities varying from 370 to 450 trees per acre (E. Touzeau, Forest Engineer, pers. comm. 1963).

By 1962 a mosaic of discrete land units had been created. Seventeen different age-classes of seral communities, interspersed with irregular stands of virgin forest were present (Figure 2). A highly varied habitat with an abundance of edge was created for deer, and a wide choice of seral stages was available for the study of changing floral composition, food productions, and deer-use.

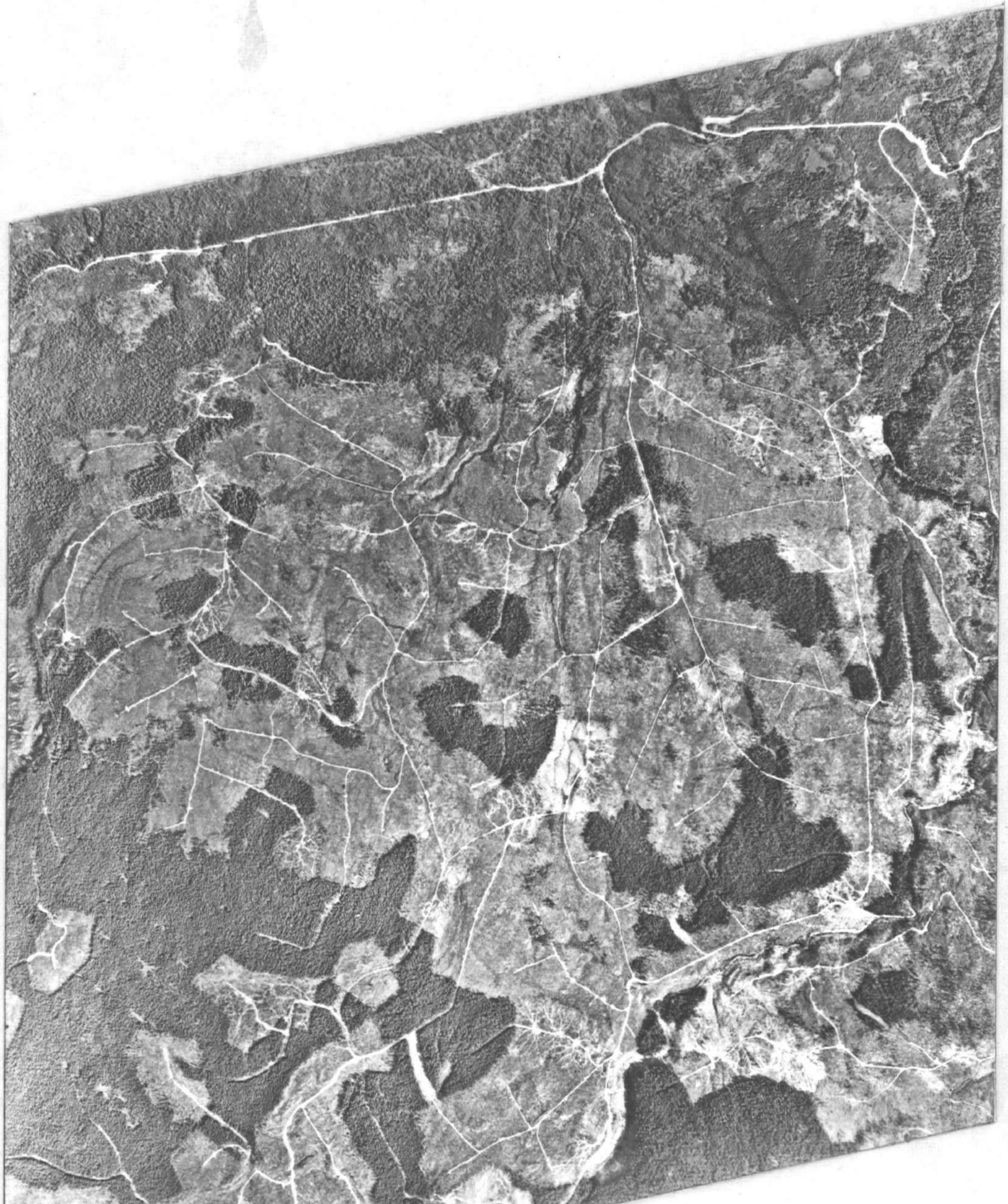


Fig. 2 Aerial photograph of approximately 15 square miles of the Northwest Bay logging claim, including the study area. Mature and submature forest stands occupied approximately one third of the area when the photograph was taken in June 1962. (Photograph by Air Division, Province of British Columbia).

METHODS OF SAMPLING AND ANALYSIS

Period of Study

Most field work was conducted in the summers of 1959 to 1962, with brief periods in March and December of 1962 devoted to the collection of plant samples for chemical analysis. Rumen samples were collected in 1963 and 1964.

Ruman Analyses

Rumen samples from seventy-five female deer were analysed to determine seasonal diets at Northwest Bay. The animals, representing all age-classes from five months to 12-1/2 years (Thomas, 1963), were collected in the autumn and winter, and in the transition between the spring and summer feeding seasons described by Cowan (1945).

One-pint samples of thoroughly mixed digesta were preserved in the field in 10% formalin (Taber and Dasmann, 1958) and subsequently washed over U.S. Standard No. 3-1/2 and No. 5 screens. The material remaining on both screens was separated manually and identified with the aid of a dissecting microscope and reference plant collection. Where possible, trees, shrubs, and forbs were identified to species while other plants were identified only to family. No attempt was made to identify grass and sedge species, and all fine residue was listed as "unidentified".

The separated fragments were sponge-dried and measured volumetrically to the nearest half millilitre by water displacement (Cowan 1945, Brown 1961). For each species and for each of the three collection periods, frequency percentages and average volume percentages were calculated.

The most important food plants, on the basis of the three periods sampled, were determined by a modification of the "consumption index" method described by Cowan (1945). For this calculation the spring-summer transition period was given a length of one and one-half months, from early May to mid-June. This corresponds closely with the mid-point of the combined spring and summer feeding seasons for Vancouver Island blacktailed deer (Cowan, op. cit.). The consumption indices obtained provided an importance rank for the food species consumed during a total period of nine months. Early spring and late summer forage preferences were not sampled, and therefore could not be entered into the computation.

Range Survey

Permanent range survey plots were established in representative stands of mature timber and in a chronological sequence of regenerating units. Sites exhibiting minimum slope, constant aspect, and a relatively homogeneous plant community were selected so that interactions between various environmental factors would be minimal. Replicates of age-classes were surveyed wherever possible.

The cover composition of each site was determined by a line-point survey method modified as follows from Dasmann and Blaisdel (1954) : transects were selected at random from all possible 100-foot intervals along a base line (usually a logging road) and were run at right angles to the base line through the depth of the plot; the number of transects selected was governed by the sample size requirements for pellet group counts (see Methods below); at each foot mark along a taut 100-foot tape only the uppermost plant or item "hit" between ground level and four feet above ground level (the normal maximum browsing height of deer) was recorded.

The successional age of burned-over sites was recorded as the number of growing seasons since burning, even though in those few plots burned in early spring an insignificant amount of growth may have occurred immediately after the burn. Those plots in which less than half the area had been subjected to fire were considered unburned sites, and their successional age was recorded as the number of growing seasons since logging.

Cover-percentages for each species and item were determined for each study plot and mean values were used to describe those age-classes for which replicate samples were obtained. Data for burned and unburned sites were treated separately. In the summer of 1962, selected plots were re-surveyed one, two, or three years after their original surveys, thus providing composition ratings for previously un-surveyed age-classes.

Range Productivity

Annual plant productivity was estimated in ten of the burned survey plots representing six different age-classes. Four were sampled in July, two in August and four in December. In those plots sampled in July and December, the current year's growth was clipped from belt-transects 25 ft long, 2 ft wide and 4 ft high, each selected at random from one-quarter of the permanent 100 ft range survey transects. In those plots sampled in August, two randomly selected belts 100 ft long, 2 ft wide and 4 ft high were sampled. With both methods an average of 0.10 per cent of all new growth in the plot, which was available to deer, was clipped.

Clippings were placed in air-tight bags and transported to the laboratory for weighing. Each species was weighed separately and total production was expressed in pounds net weight per acre. Those species which appeared in greater than trace quantities in the rumen samples or which were rated no lower than "moderately palatable" by Cowan (1945) were included in calculating food production.

Chemical Composition of Food Species

To provide sufficient material for proximate analysis, specimens of important foods collected during the browse-production study were supplemented with annual growth collected randomly from the same survey plot. A representative sample was obtained by combining small sub-samples taken from many individual plants.

Four age-classes of seral communities were chosen for sampling, including sites which had undergone four, five, nine, and fourteen years of regeneration. Collections were made in June, July, August, December and March. Clippings were transferred to a laboratory within 12 hr of collection, and moisture contents were determined (Ohaus Moisture Determination Balance). Samples were dried for 24 hr in a temporary oven constructed of aluminum foil and heated by infra-red lamps. An average of less than five per cent moisture remained in the plants after the drying period. Subsequently, each sample was ground in a Wiley Mill to pass through a 40 mesh screen, thoroughly mixed, placed in an airtight bottle, and stored at room temperature until analysed.

Procedures outlined by the Association of Official Agricultural Chemists (1960) were followed for the proximate analysis. Nitrogen free extract (N.F.E.) was calculated as the difference between 100 per cent and the sum of the percentages of crude fat, crude protein, crude fibre and ash. Results were corrected for residual moisture remaining after the drying process and expressed on a dry weight basis.

Over-all differences in nutrient levels between species, between seral stages, and between seasons were tested for significance by arranging percentage values for each nutrient into a randomized design. Percentages were transformed by means of the arc-sine transformation and tested with an analysis of variance library program (MFAV) at the Computing Center of the University of British Columbia.

<u>Deer Use of Seral Stages</u>

Accumulated pellet group densities were used to determine the relative use by deer of various seral stages. Circular plots 100 sq ft in area (radius 5.64 ft) were centered at every hundred-foot interval along the permanent line-point transects and were marked for relocation by reference stakes. Sufficient plots were established to meet the 0.8 per cent sample size recommended by Robinette <u>et al</u>. (1958), an intensity designed to provide at least 70 per cent confidence with ten per cent sampling error.

When each plot was established, and again in May and September of each year, pellet groups were counted and removed. May counts provided measures of autumn to spring deer use; September counts provided measures of summer deer use. Each group counted in May was assigned an age classification of either "fresh", "moderately fresh", or "aged". Although somewhat arbitrary, these categories provided a means of determining the approximate season of deposition. The "fresh" and "moderately fresh" groups were assumed to have been dropped within two months of the counting period - subsequent to the start of plant growth; the "aged" groups were assumed to have been dropped between the time the plots were last cleared and early March. Age classification of groups counted in September was not necessary since the plots were cleared the previous May and thus, all groups were known to have been deposited in the summer.

Removal of groups facilitated calculation of the time taken to accumulate the groups recorded in each subsequent count (the "time-lapse", Hazzard, 1958). Since this factor was not constant for all plots, observed pellet group densities (groups per acre) were of no value in describing relative use by deer, and had to be converted to the time-constant index, deer per square mile. It is understood that this latter unit expresses relative deer use rather than the density of animals actually occupying any given study plot. Its calculation was by means of the following formula, modified from Hazzard (*op. cit.*):

$$X = \frac{a \times 640 \text{ acres}}{b \times c}$$

where : X = the number of deer per square mile (per day)

a = the number of pellet groups per acre

b = the time-lapse in days

c = the daily defecation rate of deer.

Factor c was given the value 13 pellet groups per deer-day based on work reported by Rasmussen and Doman (1943), Dasmann and Taber (1955) and Everhardt and Van Etten (1956). Initial counts in each plot were not included in the calculations because insufficient data were available regarding the decomposition rate of deer pellets in the coast forest, and thus the time-lapse could not be determined.

In an attempt to demonstrate differences in deer exploitation attributable to slash-burning, results for burned sites were analysed separately from those of unburned sites. Between-treatment differences in deer use for sites of equal age were tested for significance with a *t* Test for paired observations.

Trends in use with advancing seral succession were determined by plotting mean use-indices against successional age. Regression curves were fitted through these points by means of a polynomial library program (PFIT) at the Computing Center of the University of British Columbia. The analysis was programmed for regression through the origin on the premise that deer do not make significant use of a site immediately after logging and burning.

Estimation of Deer Numbers

A method was derived for estimating total numbers of deer in the study area and for measuring the ecological potential of the land to support deer. It made use of the pellet group density information and was based upon the following assumptions: (1) that sample sizes for obtaining deer density indices in the 18 age-classes of land within the study area were adequate, and (2) that any logged or burned site of a given age was capable of supporting the density of deer derived for that age-class by the polynomial equation. The calculation required was the product of the number of deer per square mile for each age-class of land by the number of square miles occupied by that age-class. Planimetric measurements from an aerial photograph taken in 1962 (Fig. 2), combined with logging history information provided the acreage estimates needed. As an example of the calculation, it was found that in the summer of 1962 there were 184.4 acres (0.29 square mile) of land which had undergone four years of regeneration. According to the polynomial results, four-year old sites were used by deer at an intensity equivalent to 140 deer per square mile. Therefore,

0.29 square miles x 140 deer per square mile = 40.6 deer,

or about 41 deer were potentially supported by the four-year old sites. The sum of the products so derived for all age-classes provided the estimate of total herd size.

RESULTS

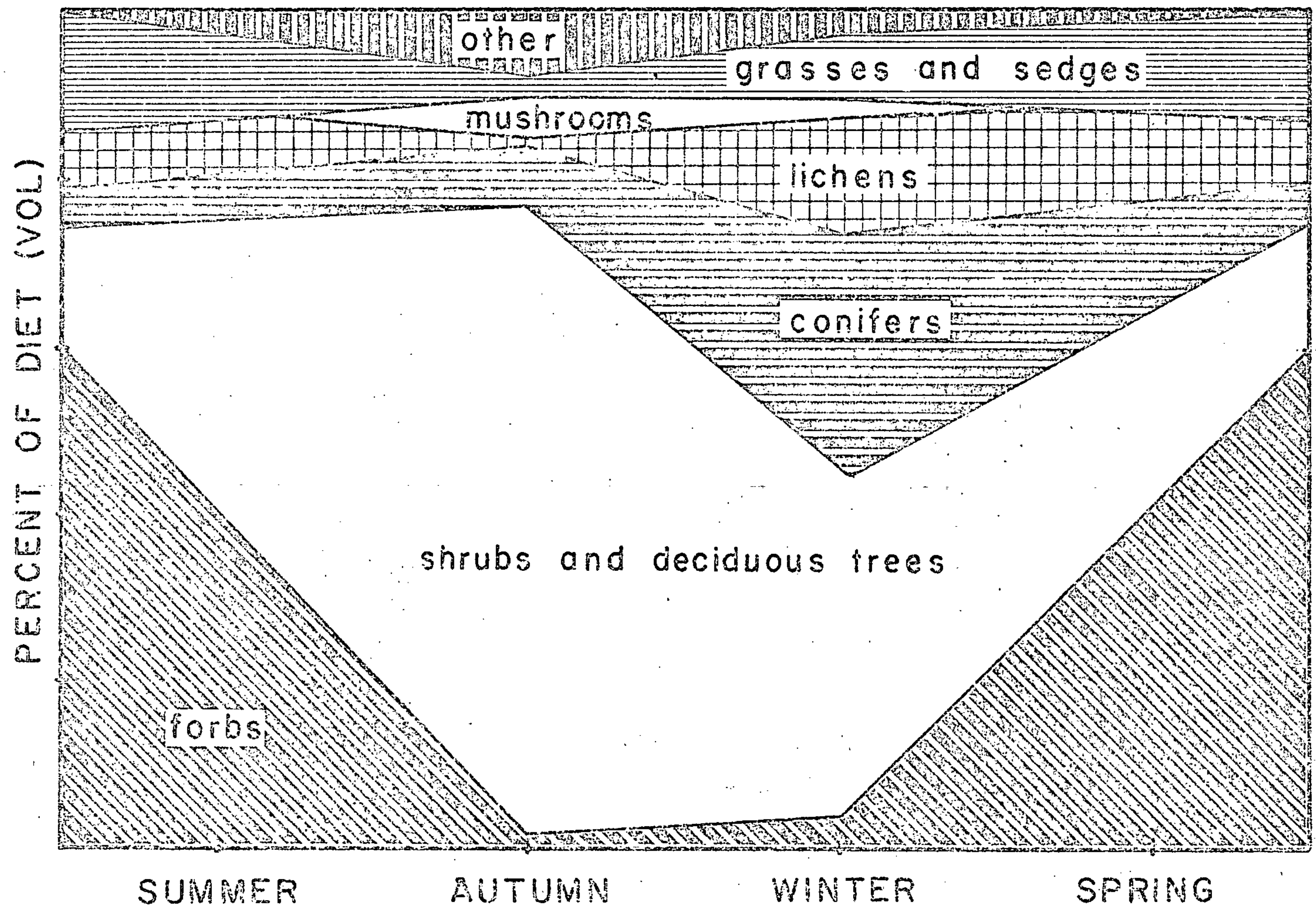
Food Habits

Interpretation of factors dealing with range composition, seral succession, and the production and availability of nutrients depends upon a knowledge of the annual and seasonal diets of the animal under investigation. The analysis of digesta from 75 rumens provided sufficient knowledge to demonstrate that blacktailed deer at Northwest Bay, as on other ranges (Cowan 1945, Chatelain 1947, Taber and Dasmann 1958, Brown 1961, McCullough 1961) depend primarily upon shrubs and deciduous trees for food. Herbaceous plants are preferred when succulent, and coniferous trees are taken in quantity during the winter. These and other plant types undoubtedly supply necessary and otherwise unavailable nutrients. But by volume, shrubs make the greatest year-round contribution to the diet.

Seasonal use of the major plant classes is shown in Fig. 3. During the spring-summer transition period newly available forbs dominated the rumen samples, contributing 59 per cent of the bulk. Grass and sedge consumption reached an annual peak, while shrub, conifer and lichen use were low.

During the autumn, shrubs replaced forbs as the main

Fig. 3. Seasonal pattern of use of the major vegetation types by Northwest Bay deer, as indicated by rumen content analysis.



component, the latter becoming largely unavailable or unpalatable. Mushrooms made up only seven per cent of the autumn diet but were important in that they were present in 73 per cent of the samples. The consumption of conifers increased slightly, and the consumption of grasses and sedges decreased slightly, between the transition and autumn periods.

In winter the greatest diversity in the use of the five plant categories was noted. Shrubs remained dominant but provided less bulk than in autumn. Conifers and lichens increased markedly in importance, with both forms reaching annual high levels. Grasses, sedges, and the few perennial forbs available were more abundant in winter samples than in autumn samples but were still relatively unimportant in terms of bulk.

Annual diet - The application of Cowan's (1945) "consumption index" method to the seasonal food habits data present in Appendix B, gives the relative importance of foods consumed during a nine-month period. The results of the computations are shown in Table 2.

The top eleven sources account for approximately 92 per cent of all food consumed in that period. Salal formed more than a third of the total diet and was three times more important than any other species. Red cedar (11 per cent)

Table 2 The relative importance of food items to blacktailed deer at Northwest Bay as indicated by stomach contents of 72 animals sampled in three different seasons.

Season	Spring-Summer Transition	Autumn	Winter	Total	
Length of season in months	1-1/2	3	4-1/2	9	
Item	Seasonal Consumption Factors[1]			Consumption Index	
				Actual[2]	%
Salal	8.1	167.7	136.4	312.2	34.7
Red Cedar	2.9	6.9	94.0	103.8	11.5
Arboreal lichens	11.0	T	59.4	70.4	7.8
Pearly everlasting	69.0	0	0	69.0	7.7
Grasses	22.6	7.2	36.9	66.7	7.4
Trailing blackberry	6.9	21.9	16.6	45.4	5.0
Catsear	12.2	4.5	17.6	34.3	3.8
Mushrooms	T	21.0	12.6	33.6	3.8
Douglas fir	3.5	11.7	18.0	33.2	3.7
Bearberry	4.1	3.3	23.0	30.4	3.4
Red alder	T	21.6	3.2	24.8	2.8
Other vegetation	9.8	34.2	32.4	76.4	8.4
Totals				900.2	100.0

T = Trace

[1] Product of average volume % for each season by the number of months represented by that season.

[2] Sum of Seasonal Consumption Factors. See Cowan (1945).

ranked second, followed by arboreal lichens (8 per cent), pearly everlasting (8 per cent), and grasses and sedges (7 per cent). Of the total volume contributed by the 11 key foods, shrubs and deciduous trees made up 46 per cent, conifers 15 per cent, herbaceous plants 11 per cent, lichens 8 per cent, and mushrooms 4 per cent. The balance of 8 per cent was grouped as mixed vegetation.

Cowan (1945) and Brown (1961), in their studies of coastal blacktailed deer, found heavy use of Douglas fir, trailing blackberry, willow and grasses in early spring, and of salal, red alder, and trailing blackberry in late summer. Since these are the two periods during which rumen samples were not obtained at Northwest Bay, it is likely that these species rate higher in the annual diet than they appear in Table 2. For this reason a tentative list of the ten most important annual foods at Northwest Bay was derived from the combined data of Cowan (1945), Brown (1961) and the present study. This and comparable lists presented by the other two authors are given in Table 3.

Salal, Douglas fir, red alder, and grasses are very important in all three areas. Four other species important at Northwest Bay (red cedar, trailing blackberry, arboreal lichens and willow) are also important in one of the other areas. Only pearly everlasting and catsear are unique to the Northwest Bay diet and it is possible that these would not have ranked in the first ten if sufficient data were available on late summer food habits. Mushrooms, for example, ranked eighth on the basis of the consumption index (Table 2), and since some are available to deer by late summer, it is possible that they are more important in the annual diet than either of these forbs.

Table 3 The ten dominant items in the annual diets of Columbian blacktailed deer occupying three separate ranges.

Northwest Bay[1]	Southern Vancouver Island[2]	Western Washington[3]
Salal	Douglas fir	Trail.blackberry
Red cedar	Salal	Salal
Trail.blackberry	Arboreal lichen	Grasses
Arboreal lichens	Red alder	Red alder
Grasses and sedges	Willow	Vine maple
Douglas fir	Mushrooms	Western hemlock
Pearly everlasting	Bracken	Douglas fir
Red alder	Grasses and sedges	Huckleberry
Willow	Thimbleberry	Fireweed
Catsear	Equisetum	Red cedar

[1]From present study with interpolation from Cowan (1945) and Brown (1961). See text.

[2]From Cowan (1945).

[3]From Brown (1961).

Western hemlock, an important food to western Washington deer, was never observed to have been browsed at Northwest Bay. Dzubin (1951) reported that it formed less than one per cent of the diet during winter feeding tests with blacktailed deer, and Cowan (1945) rated it as apparently unpalatable to deer on southern Vancouver Island. Vine maple was not present in the study area and red huckleberry was of limited distribution. Where available, however, the latter was severely hedged. Bracken, thimbleberry, and Equisetum, rated important by Cowan, were eaten at Northwest Bay but were found in only small amounts in the stomach samples analysed.

Spring-summer transitional diet - Pearly everlasting was the most important food item during the late spring and early summer, forming 46 per cent of the diet (Fig. 4). The new leaves and flower buds were the preferred portions and were found in 79 per cent of the stomachs sampled. Cowan (1945) reported that this species was apparently not eaten by deer in Southern Vancouver Island. Grasses and sedges, at 15 per cent, were the second most important item. Among the species present in the area upon which grazing was recorded were Hulcus lanatus, Agrostis exerata, and Luzula multiflora. Catsear, rated third by volume, formed 15 per cent of the diet and occurred in more than half the samples.

The arboreal lichens Usnea barbata and Alectoria sp. were abundant in May samples but occurred less frequently as the transition period progressed. Salal, trailing blackberry, bearberry, Douglas fir and red cedar each made up

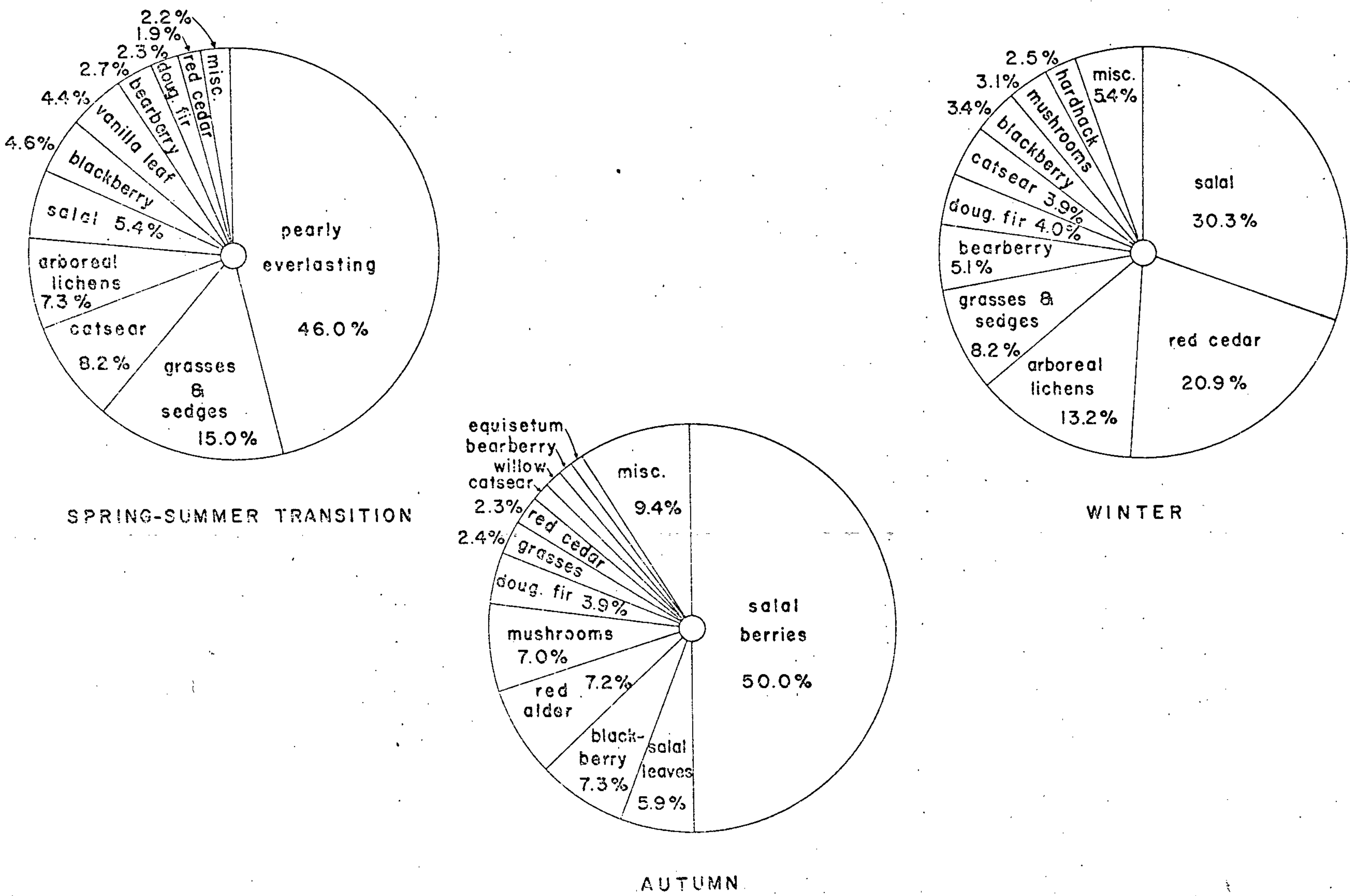


Fig. 4. Seasonal diets of Northwest Bay deer.

less than six per cent of the diet but are considered important because each was present in from 50 per cent to 71 per cent of the samples. As with lichens, each of these species was taken in decreasing quantities, while pearly everlasting, catsear and vanilla leaf were taken in increasing quantities as the transition period progressed. Thus, a shift in preference from browse to succulent forbs is indicated as soon as the latter become available in the spring.

Bracken was not recorded in the spring rumen samples but the tender sprouts were noted to be extensively browsed. High moisture and low fibre content of the new growth may leave it, as well as other succulent plants, unidentifiable in the rumen soon after consumption (Bruggemann, Giesecke, and Walser-Kärst, 1968).

Autumn diet - When available, both green and ripe salal berries formed an average of 79 per cent of the autumn diet. After the berries had dropped in early November, the leaves alone contributed 16 per cent of the diet. For the three-month autumn season as a whole, therefore, salal contributed an average of 56 per cent by volume (Fig. 4).

Trailing blackberry leaves were present in 91 per cent of the samples but made up only 7.3 per cent of the bulk. Brown (1961) found this the most important autumn and year-round food in Western Washington, Chatelain (1947) found it of moderate autumn importance in Oregon, and Cowan (1945) found it of little importance at any time of the year on southern Vancouver Island.

Red alder leaves (7.2 per cent), mushrooms (7.0 per cent), Douglas fir (3.9 per cent) and grasses (2.4 per cent) were other important items during the autumn, with mushrooms and Douglas fir occurring in more than half the stomachs. A variety of browse species and a few forbs made up the balance.

Winter diet - The consumption of salal from December through March was about half that of the autumn period but the species was still eaten by almost all deer and was still the key food (Fig. 4). Red cedar, at 21 per cent, rated second by volume and it too was present in almost all samples. Arboreal lichens, made available by strong winds and by snow and logging damage to mature trees, contributed 13 per cent by volume. Grasses and sedges contributed 8 per cent. Douglas fir and trailing blackberry were taken in moderate amounts by at least 70 per cent of the animals, while bearberry, catsear and mushrooms were taken in slightly greater amounts but by only one third of the animals. Many other plants were eaten in minor amounts during this season.

Range Composition and Changes with Seral Succession

Cover and species composition of various seral communities were derived from 27 permanent study plots established and surveyed during 1959-61. Figure 5 shows the location and relative size of each plot, and the direction of transect lines; Table 4 lists descriptive features of each. The logged patches studied included 17 burned sites representing eleven age-classes, eight unburned sites representing six age-classes, and two stands of 180-200 year old subclimax forest. The sizes of the plots ranged from 4.1 acres (Plot V) to 69.0 acres (Plot 2) and averaged 14.5 acres.

Average cover-composition by major plant categories and the rank of dominant species in sites of increasing successional age are given in Appendix C (burned areas) and Appendix D (unburned areas). Detailed data for the 27 individual plots are on file with the Wildlife Research Division of the British Columbia Fish and Wildlife Branch.

Seral communities at Northwest Bay - The major seral communities developing after logging or burning are basically similar to those described for southern Vancouver Island by Cowan (1945). Four distinct associations were recognized:

(1) *Senecio-Epilobium* association.
(2) *Gaultheria-Hypochaeris* association.
(3) *Gaultheria-Pseudotsuga* association.
(4) *Pseudotsuga* consocies.

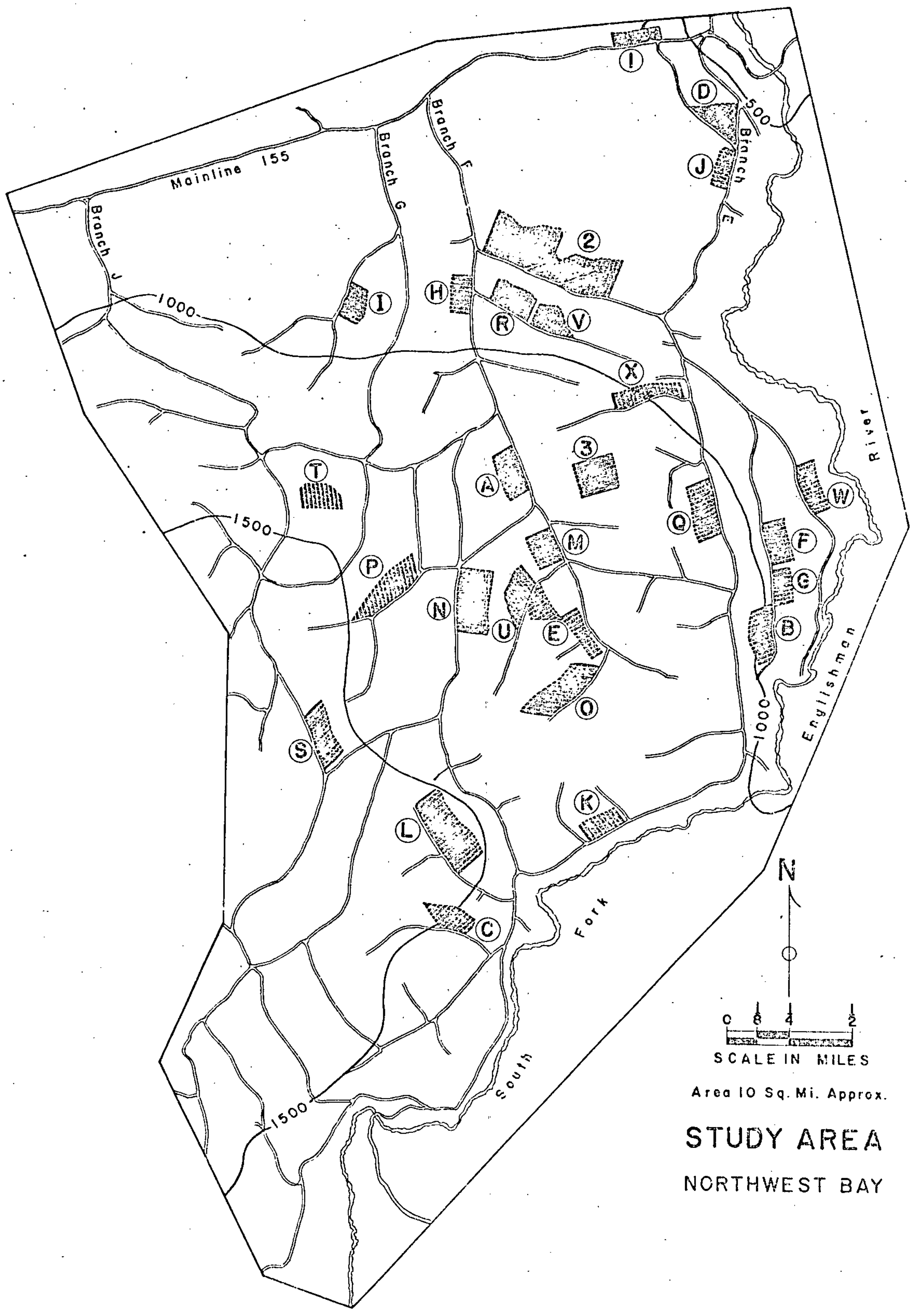


Fig. 5. The Northwest Bay Study Area showing the major logging roads and the location and relative size of the 27 permanent study plots.

Table 4 The permanent range survey and pellet-group study plots established at Northwest Bay, 1959 to 1961.

Plot	Year Logged or Burned	Age in Years at: Initial Survey	Age in Years at: Resurvey	Area (Acres)
A. Burned-over sites				
A	1958 A*	1	-	9.7
B	1957 A	2	-	13.1
C	1957 A	2	-	13.6
R	1958 A	3	4	9.5
S	1958 A	3	-	11.5
E	1956 S	4	-	21.7
G	1954 A	5	-	8.9
H	1953 A	6	9	8.9
U	1956 S	6	-	11.4
P	1952 A	8	-	17.5
J	1949 A	10	-	8.8
N	1950 A	10	-	23.2
O	1950 A	10	-	17.4
L	1948 A	12	-	23.3
M	1948 A	12	14	9.8
W	1948 A	13	-	11.4
1	1945 A	15	-	9.3
B. Unburned sites				
D	1957	2	-	9.4
T	1956	5	-	8.8
Q	1954	6	-	16.2
I	1951	8	-	8.9
V	1953	8	-	4.1
K	1947	12	-	9.7
X	1948	13	-	13.2
2	1947	13	-	69.0
C. Subclimax forest sites				
F	-	180-200	-	8.3
3	-	180-200	-	15.0
			Average	14.5

*A - Autumn burn

S - Spring burn

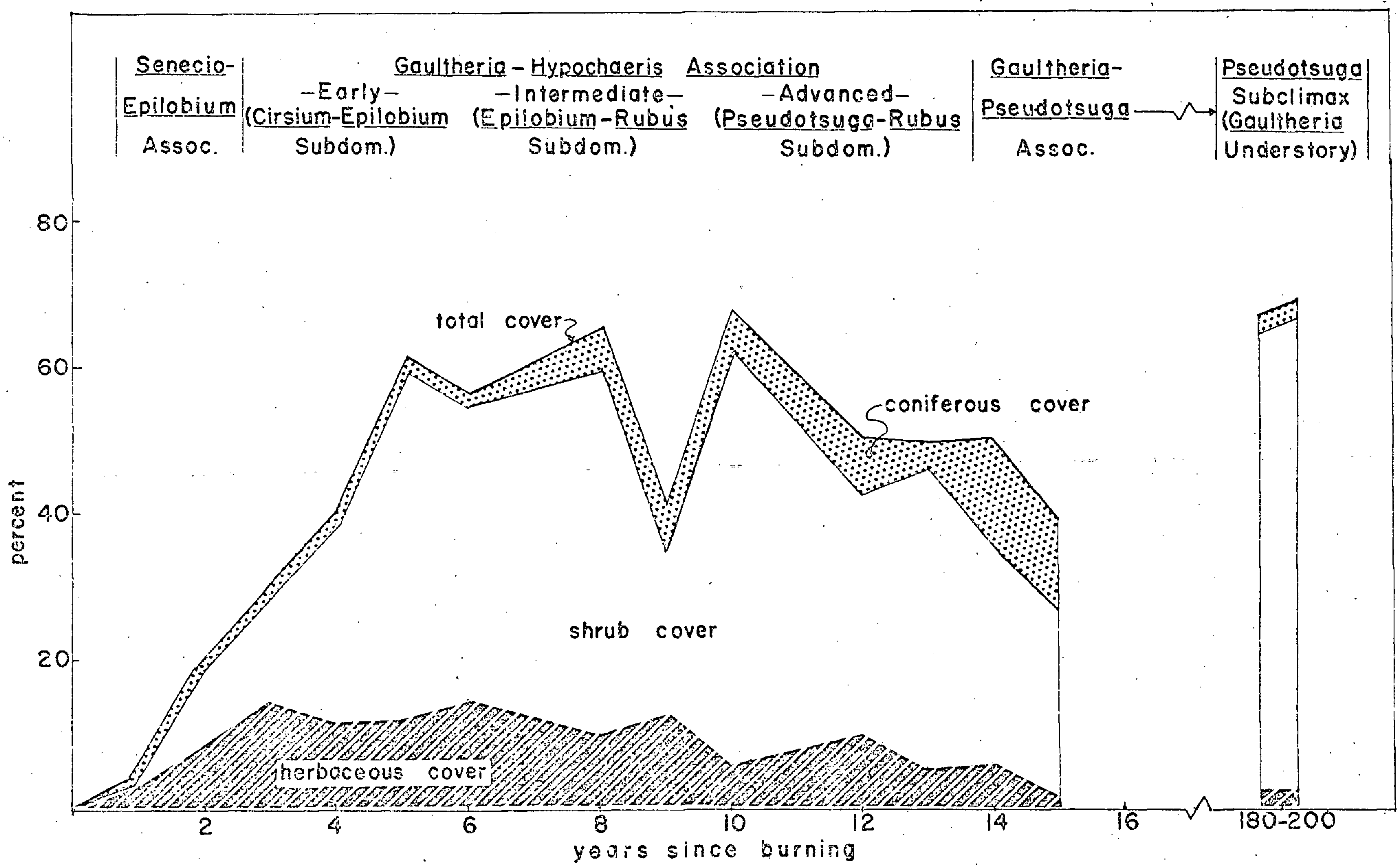
Cowan's "rock bluff", "sedge meadow", and "alder-willow" communities were of such limited distribution that they were not considered in detail.

The sequence of the four dominant associations as they develop in burned-over sites, and the relationship to the amount of surface covered by plant types are shown in Fig. 6. Irregularities in the graph are attributable to sample size and to site variability, the latter being partially a result of differences in burning intensity. The general pattern of succession, however, is apparent.

Herbaceous plants reach peak cover-densities about three years after burning, usually in the early *Gaultheria-Hypochaeris* association. Thereafter they decline gradually through competition and shading and are of minor importance by the fifteenth year (the early *Gaultheria-Pseudotsuga* association). Under the mature forest, forbs cover less than one per cent of the surface.

Shrubs and young deciduous trees dominate the low stratum from the third year through to at least the fifteenth year. They develop rapidly, cover 60 to 65 per cent of the surface by the fifth year, maintain that level until the tenth year, and then decline. By the fifteenth year only 30 per cent of the community consists of shrubs, and it is likely that the downward trend continues beyond the fifteenth year as

Fig. 6. Sequential development of four major seral associations and related cover percentages by three vegetation types; slash-burned sites only.



shrubs are shaded and replaced by coniferous trees. Under the mature timber, shrubs (principally salal) regain dominance and reach a peak cover density of almost 70 per cent.

Conifers comprise almost insignificant proportions of the *Senecio-Epilobium* and early *Gaultheria-Hypochaeris* associations. Coniferous ground cover increases very gradually, remaining below five per cent for the initial 12 to 13 years. In the fourteenth and fifteenth years, a marked increase occurs and it is at this time that the *Gaultheria-Pseudotsuga* association develops. This type, in turn, quickly advances into dense second-growth Douglas fir with little subordinate vegetation, and eventually into a closed-canopy forest with a salal or moss understory.

The structural characteristics and the chronology of the four fire-induced seral stages follow. Representative photographs of each are presented in the Appendix.

(1) *Senecio-Epilobium* association

Immediately after logging and intensive slash-burning, a sparse and ephemeral forb association develops. In the first year (Appendix C) it is dominated by wood groundsel (*Senecio sylvaticus*), with the principal associates, lettuce (*Lactuca muralis*), thistle (*Cirsium lanceolatus* and *C. arvense*) and willowherb (*Epilobium minutum*). Shrubs and coniferous trees are rare and total plant cover may be less than four per cent (Fig. 6).

In the second year, fireweed, thistles, catsear and a variety of woody species including salal, black raspberry and western hemlock become well established. Plant cover increases markedly to approximately 20 per cent with shrubs and forbs contributing equally. Wood groundsel maintains a relatively constant density, but since it grows best on scorched soils and is intolerant of changing soil conditions (Mueller-Dombois 1959), it and the association itself rarely thrive in the third season.

(2) Gaultheria-Hypochaeris association

From approximately the fourth to fourteenth year (Appendix C), a mixed shrub and forb community dominated by salal and catsear is recognizable. Both of these species are far more abundant than any of the principal associates. Rubus species, including trailing blackberry, black raspberry and salmonberry (Rubus spectabilis) are usually represented, and become more abundant with advancing years. Willows, twinflower and Oregon grape are other common shrubs.

Associated herbaceous plants vary greatly with soil and moisture conditions and with the intensity of burn. Most prominent are thistles (Cirsium spp. and Carduus spp.), lettuce, pearly everlasting, fireweed, and vanilla leaf. Wood groundsel is greatly reduced in cover percent from its first year abundance, and grasses and sedges are only locally distributed. Bracken fern develops vigorously in moist, sun-exposed pockets (Fig. 7) and frequently prevents development of the typical forb stratum. Salal, however, may persist under the bracken.

The earliest stages of this association are represented by the three- and four-year-old sites (see Fig. 6). Typically, one-third or less of the surface is shaded by plants. Forbs and shrubs are equally abundant, each occupying an average of 15 per cent of the surface. Grasses are more abundant than in any other seral stage but still occupy less than two per cent of the area. Salal is the dominant species, with catsear and trailing blackberry the important associates, and black raspberry, willows, thistle and lettuce present in moderate quantities.

The more advanced stages are recognizable in five- to thirteen-year-old burns, areas in which total plant cover ranges from 40 to 70 per cent. Shrubs dominate and may cover six to eight times more of the surface than herbaceous plants. The important coniferous species are generally present but frequently occupy an average of less than five per cent of the surface. Only under ideal soil and moist-

Fig. 7 Dense bracken fern growing in the moist lower end of Plot J, 14 years after slash-burning. In this site salal persisted under the bracken.

Fig. 8 An early Gaultheria-Pseudotsuga association fifteen years after logging and burning (Plot M). Douglas fir regeneration was particularly rapid in this site, even though reforestation was not attempted. When surveyed three years earlier this plot was classified as an advanced Gaultheria-Hypochaeris association.

ure conditions is Douglas fir dominant (Fig. 8). Salal is usually most abundant, occupying an average of 38 per cent of the surface. Catsear covers only four per cent of the surface but ranks second or third in all areas where fire was intensive. Trailing blackberry (2 per cent), along with Douglas fir, western hemlock, willow, black raspberry, lettuce and pearly everlasting (each averaging approximately 1 per cent) are the other principal components.

(3) Gaultheria-Pseudotsuga association

Approximately fourteen years after burning, Douglas fir becomes the principal associate with salal. Dense salal common in the earlier seral stages does not seriously hamper the establishment of conifers (Mueller-Dombois, 1959) and once established in sufficient numbers they soon surpass forbs and shrubs in abundance. The fourteen- and fifteen-year-old sites (Appendix C) represent the earliest stage of this association. Structurally it is little different from the advanced Gaultheria-Hypochaeris association, the distinctive features being reduced salal and total shrub cover, and increased Douglas fir cover. Trailing blackberry, Oregon grape, willow and catsear remain as subdominants but become less abundant with time.

Since the earliest logging occurred only fourteen years before the start of field investigations, more advanced stages of this association were not available for survey. However, under average conditions it is presumed that Douglas fir surpasses salal as the dominant species 18 to 20 years after burning.

(4) _Pseudotsuga_ subclimax

The mature, subclimax forest community, or "_Pseudotsuga_ consocies" (Cowan 1945), was represented by two stands of 180- to 200-year-old timber. A dense canopy consisting mostly of Douglas fir and western hemlock restricts growth in the understory to only the most shade-tolerant species. Tall-growing salal dominated the two sites studied, covering an average of 65 per cent of the surface. Rock-outcroppings were present in both sites, and supported a moss community similar to that described by Mueller-Dombois (1959). Twin-flower, Oregon grape, dwarf rose (_Rosa gymnocarpa_) and pipsissewa were present on these shallow soils but, together, covered only two per cent of the surface. Limited regeneration of western hemlock was noted in the salal zones and a few low-hanging branches of western red cedar made up the remainder of the low stratum. As noted by Cowan (1945), plant variety in this association is very limited.

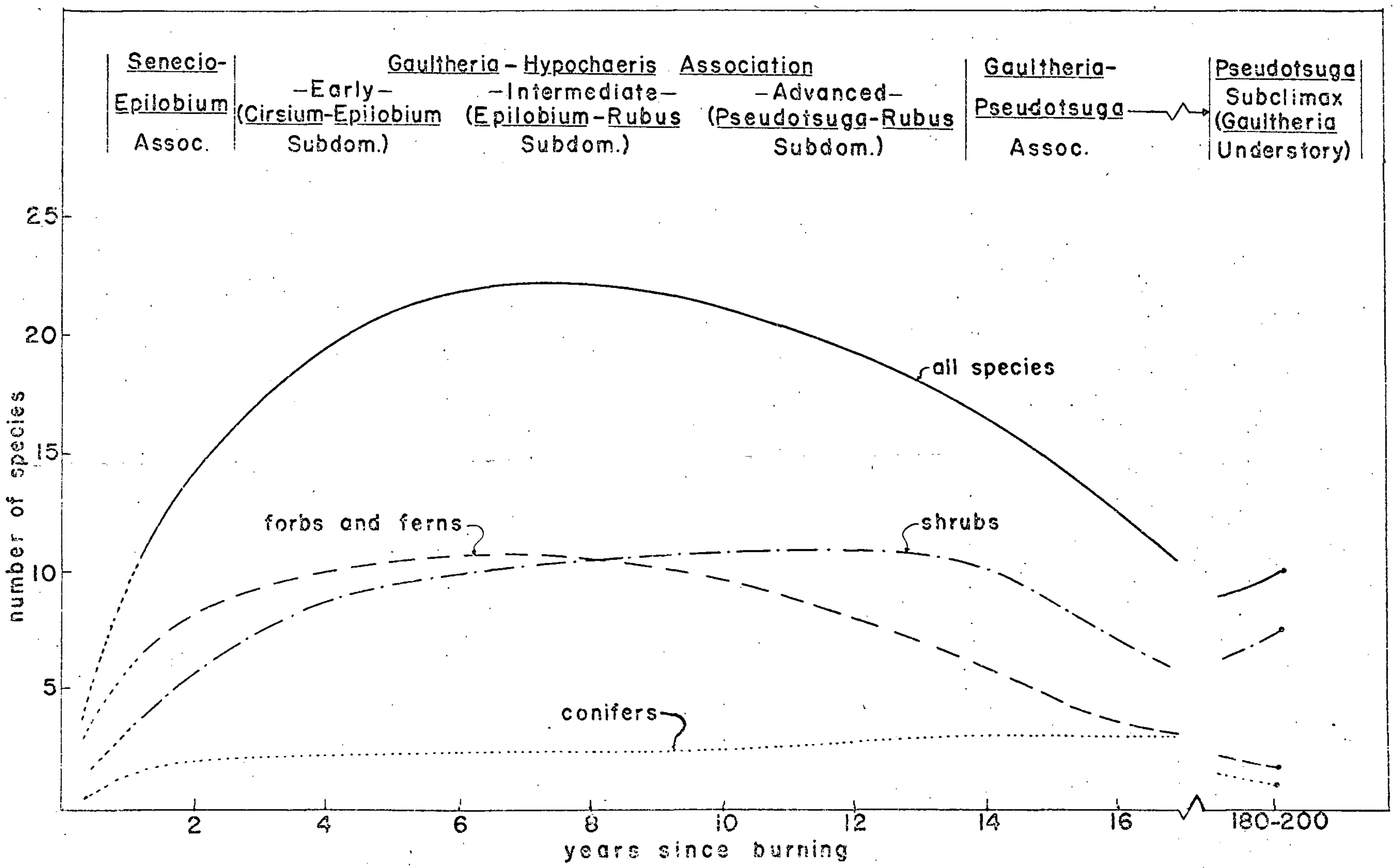
Species Variety in Seral Communities

The variety of palatable species present in any unit of regenerating range is probably as important as the total production of food. That deer consume many different foods at all seasons is clearly demonstrated by the results of rumen analyses presented earlier, and by food habit studies reported by other workers (Cowan 1945, Chatelain 1947, Rieck 1952, Brown 1961).

Species variety, as it is related to seral succession at Northwest Bay, is shown graphically in Fig. 9. The data from which the curves were derived are given in Appendix C. Only those species recorded in greater than trace quantities during the range survey, and known to contribute significantly to the diet (see food habits results above, and Cowan 1945), are included as "palatable" deer foods in this analysis. Since grasses and sedges were not identified to species, they are not included.

Peak variety occurred in the intermediate Gaultheria-Hypochaeris association six to eight years after burning. At this time the number of species of shrubs and the number of herbaceous plants important to deer were approximately equal. Thus, it was at this time that the greatest "diversity index" (Odum, 1960) occurred, and, if variety of foods is indeed important, the greatest attractiveness to deer could

Fig. 9. Trends in the variety of palatable deer foods present after logging and slash-burning.



be expected.

Eleven herbaceous plants, eleven shrubs, and three conifers were the maximum numbers of palatable species recorded, but each form reached maximum variety at a different time. Forbs invaded quickly, with many becoming established in the first growing season. Following maximum diversity in the intermediate Gaultheria-Hypochaeris association (6 to 8 years after burning) a gradual decline in forb variety occurred, and in the fifteenth season only four palatable forbs were recorded. Under the mature timber this number had decreased to two.

The browse plants invaded at a slower rate than forbs, not reaching maximum variety until development of the late Gaultheria-Hypochaeris and early Gaultheria-Pseudotsuga associations. Subsequently, there was indication of a significant decline in browse variety probably owing to the continued encroachment of salal and Douglas fir.

The three palatable coniferous trees, Douglas fir, western red cedar, and balsam fir, were not consistently present in regenerating areas until the fourteenth to fifteenth year (Fig. 9). Red cedar was the only conifer found within reach of deer under the mature subclimax forest.

Range Productivity

The production of deer foods in forest communities varies greatly with site, seral structure, past land use, and fire history (Halls and Crawford 1960, Ehrenreich and Murphy 1962). Generally, after destruction of subclimax and climax sites, food production increases for a period varying with the biotic area, and then decreases to a relatively low level as the community approaches climax conditions. In the study area, estimates of the amount of palatable new growth available, and of the percent of the surface covered by palatable plants appear to follow this trend (Table 5). The former figures were derived from the browse clipping investigation, the latter by subtracting cover-percentages for non-palatable plants from the total cover-percentages given in Appendix C. Estimates of the amount of palatable browse in December (Table 6) cannot be expected to follow the same trend because they include only the available evergreen foods, and do not account for total annual production.

No measure was obtained of the amount of browse which had already been consumed by deer at the time the samples were collected. Therefore, the estimates represent the standing crop in July and August (near the end of the growing season), and in December. During the clipping program relatively little food was noted to have already been

Table 5 Annual production of deer food in various post-fire seral stages, expressed as pounds per acre wet-weight. The numbers in parentheses express palatable food production as a percentage of total new-growth production.

Years since burning	4	10	12	14	Mature Timber
Forbs and grasses	151	125	13	97	T
Ferns	15	69	140	166	2
Shrubs	782	847	791	744	423
Conifers	T	249	28	105	5
Total	948 (93.5)	1290 (93.0)	972 (63.9)	1114 (79.5)	430 (95.5)
Percent of ground covered by palatable species[1]	39.3	61.8	47.0	43.4	67.1

[1]Figures extrapolated from range survey data.

Table 6 Winter availability of deer foods in various post-fire seral stages, expressed as pounds per acre wet-weight. The numbers in parentheses express food availability during winter as a percentage of total available new-growth.

Years since burning	4	9	14	Mature Timber[1]
Forbs and grasses	T	T	T	T
Ferns	T	6	10	2
Shrubs	10	164	299	421
Conifers	45	59	34	5
Total	55 (82.4)	229 (87.7)	343 (97.4)	428 (98.1)

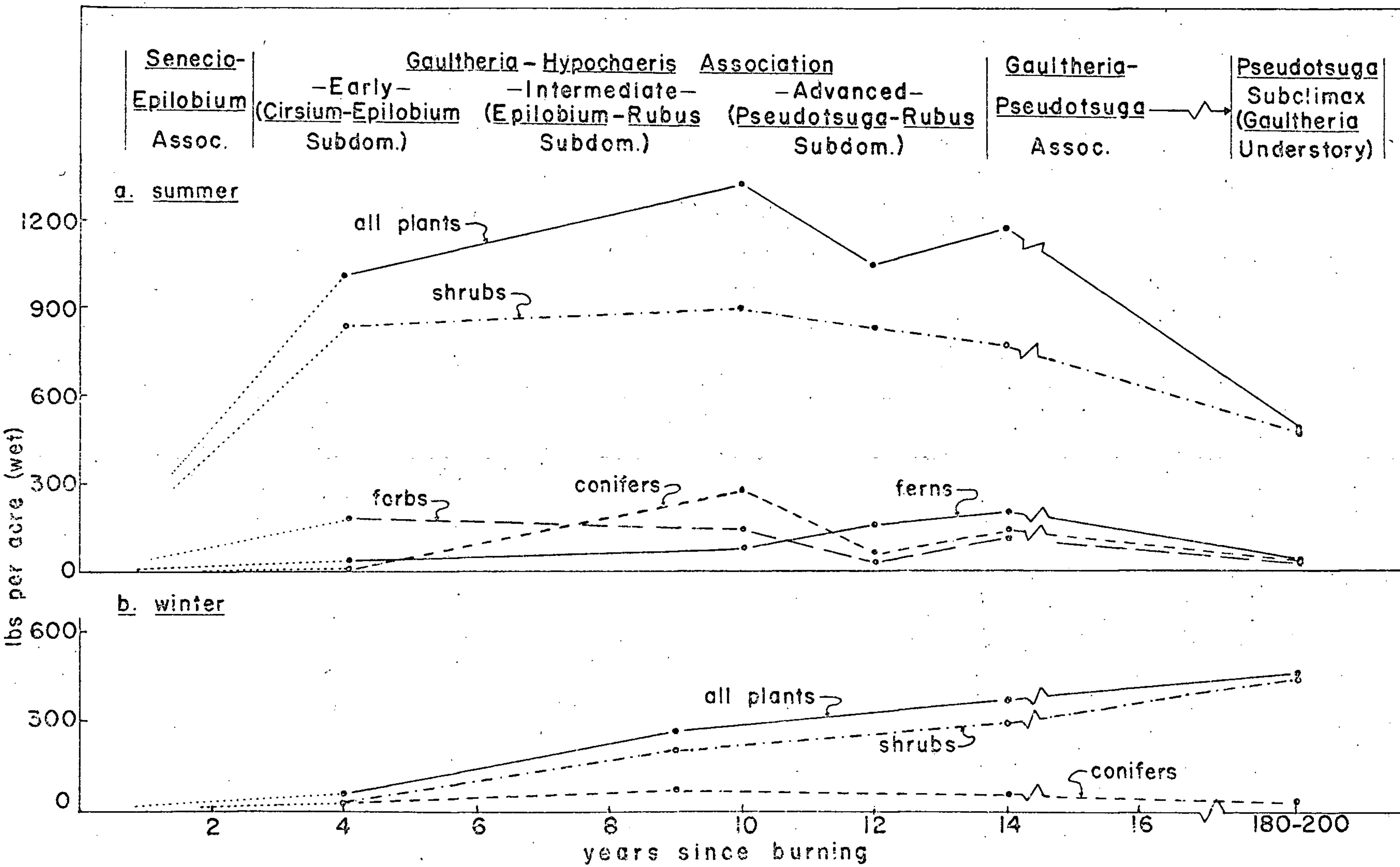
[1]Derived from summer estimates by including only the weights of evergreen plants.

consumed, so it would appear that estimates of the standing crop closely approximate the total crop.

Data for the summer indicate a rapid increase in total food production for the first ten years after a fire, followed by a slight decline for at least the next four years (Fig. 10A). This decline probably continues gradually through to the subclimax forest stage. As a group, forbs and grasses were produced in greatest quantities four years after burning, at which time approximately 151 pounds per acre were available. Their abundance tended to decline through subsequent years to trace quantities in the subclimax forest. Ferns showed an opposite trend, increasing in abundance from the fourth to the fourteenth year, when approximately 166 pounds per acre were available. As with the forbs and grasses, however, fern production under the mature timber was negligible. Shrub growth formed the bulk of the annual production in all age-classes, and was most abundant ten years after burning. Approximately 847 pounds of preferred browse were available on each acre at this time, but a progressive decline through to the subclimax stage was indicated.

Estimates of the annual production of coniferous foods do not compare favorably with the cover-percentage estimates shown in Fig. 6. They do not follow the expected

Fig. 10. The weight of deer food available in summer and winter in each of the major seral stages.



trend of a very gradual increase for the first 10 to 12 years followed by a more rapid increase at about 14 years. This is likely attributable to variable rates of conifer regeneration in different soil types as reported by Mueller-Dombois (1959). In two seral stages, however, the results do agree. Low annual production and negligible surface coverage by conifers were recorded in the early _Gaultheria-Hypochaeris_ association and under the _Pseudotsuga_ subclimax.

As shown in Fig. 10B, availability of preferred winter foods in December increased constantly with seral succession. Only 55 pounds per acre were available four years after burning, and most of this was Douglas fir. In the nine- and 14-year-old sites 229 pounds per acre and 343 pounds per acre respectively were available, with shrubs the dominant source. Under the mature timber, where availability was estimated by subtracting the weights of herbaceous and deciduous growth from the weight of all annual growth estimated in summer, approximately 428 pounds were available on each acre, 97 per cent of which was salal.

It is apparent from Table 6 that as secondary succession advanced, an increasing percentage of new growth available in December was important deer food. This can be accounted for by the gradual replacement of deciduous plants by palatable evergreens such as salal and Douglas fir, and points out the importance of the more advanced seral stages to wintering deer.

When the data in Tables 5 and 6 are related to the seral associations described earlier, the intermediate *Gaultheria-Hypochaeris* association is clearly most productive in terms of weight of food, and rates high in terms of palatable cover. Furthermore, its varied composition makes it capable of supplying food from spring to late autumn and early winter. The mature *Pseudotsuga* subclimax has a relatively high cover of palatable foods in both summer and winter, and is potentially the greatest producer of evergreen winter foods. But compared with the salal and catsear-dominated seral stages, it rates relatively low in total production of annual growth.

The early *Gaultheria-Hypochaeris* association produces only moderate amounts of food. Moreover, subtraction of the amounts produced by herbaceous plants and by plants not eaten in winter indicates that less than six per cent of the total is available as winter food. Therefore, foraging by deer in this association must be confined mainly to forbs and grasses available during the spring and summer.

The *Gaultheria-Pseudotsuga* association was considered by Cowan (1945) to be the most important food-producing community, particularly when supplemented by fringes of subclimax forest. The combined results of the rumen content analyses and of the range survey indicate that this association provides near optimum conditions for late summer, autumn and early winter feeding, but is less than ideal during the spring and summer when various succulent forbs are preferred. Along with other early seral stages it is of limited value when food availability is restricted by deep snow.

Chemical Composition of Deer Forage Species

The purposes of obtaining data on the nutrient content of various food species were to test the hypothesis that forage quality decreases with advancing succession (Cowan *et al.* 1950), and to measure seasonal and species differences in nutrient levels. Work by Einarsen (1946) and Dietz *et al.* (1958) suggests that each of these factors may be important in influencing range selection by deer. Generally, the results presented below indicate that the average nutrient composition of selected groups of important food species did not change significantly from the fourth to the fourteenth year of succession. However, seasonal changes and differences between species were generally significant.

The effect of seral succession on forage nutrients - Table 7 summarizes the results of a series of four analysis of variance tests designed to show the influence of advancing regeneration on forage quality. For most species, means

Table 7 Results of a series of four analysis of variance tests designed to determine the effect of seral succession on the nutrient content of important deer forage species. The values tested are given in Appendix E, Tables 1-4.

Test 1: Five-year-old vs 14-year-old communities; nine species sampled in March.

		Values of F				
Source	df	Crude Protein	Crude Fat	Ash	Crude Fibre	N.F.E.
Between Species	8	6.18**	7.58**	3.84*	79.66**	28.27**
Between Ages	1	1.07	.82	.26	.02	1.73
Error	8					
Total	17					

Test 2: Four-year-old vs nine-year-old communities; four species sampled in December.

		Values of F				
Source	df	Crude Protein	Crude Fat	Ash	Crude Fibre	N.F.E.
Between Species	3	14.72*	12.28*	10.74*	75.60**	20.13*
Between Ages	1	.07	2.72	.73	.63	.02
Error	3					
Total	7					

Test 3: Nine-year-old vs 14-year-old communities; three species sampled in December.

		Values of F				
Source	df	Crude Protein	Crude Fat	Ash	Crude Fibre	N.F.E.
Between species	2	23.13*	16.40	2.05	43.72*	663.67**
Between ages	1	5.25	.40	.33	.01	130.37**
Error	2					
Total	5					

* $p < 0.05$
** $p < 0.01$

Test 4: Four-year-old vs nine-year-old vs 14-year-old communities; four species collected in June.

		Values of F				
Source	df	Crude Protein	Crude Fat	Ash	Crude Fibre	N.F.E.
Between species	3	68.48**	4.03	15.19**	40.66**	59.85**
Between ages	2	.57	.07	.30	.65	.09
Error	6					
Total	11					

* $p < 0.05$
** $p < 0.01$

derived from samples collected in two or more sites of equal successional age were used in the analysis. However, for some species only a single sample was obtained for a given age-class and consequently the interaction factor could not be determined in the analysis of variance. The species involved in each test and their nutrient values are given in Appendix E.

In only one test were there significant differences attributable to age-of-site; December nitrogen-free extract (N.F.E.) levels in Douglas fir, trailing blackberry and willow, when treated as a group, were higher fourteen years after burning than nine years after burning (Test 3). A similar result was reported by Cowan et al. (1950) for three coniferous species in central British Columbia, but no physiological explanation can be offered for the increase. The levels of other nutrients in groups of plants collected in December, March, and June were not altered by seral succession.

In general, these results do not support those of Cowan et al. (op cit.), who concluded that food quality declines as forests regenerate toward climax conditions. As will be discussed later, however, significant changes might have been recorded in the present investigation if samples had been analysed from regenerating areas younger than four years of age and older than 14 years.

The effect of season on forage nutrients - On the basis of the above results it was possible to use values obtained from all age-classes to derive average seasonal nutrient levels for each species (Table 8). These data then provided a means of testing for differences attributable to seasons. Values for six of the most important browse species, sampled in summer (July), early winter (December), and late winter (March), were extracted from Table 8, pooled, tested with an analysis of variance, and where applicable, with a range test. The six species were Douglas fir, western red cedar, salal, trailing blackberry, red alder, and willow. Results of these tests are shown in Tables 9 and 10.

Table 8 The average seasonal composition of some important deer forage species at Northwest Bay, Vancouver Island.

Browse Species		% Moisture	Percent of dry weight: Crude Protein	Ether Extract	Ash	Fibre	N.F.E.
Douglas Fir	July	63.5	6.32	16.43	2.36	20.20	54.67
	Dec.	59.6	10.17	12.69	3.97	20.31	52.84
	Mar.	53.9	7.63	13.76	2.60	18.96	57.03
Western Red Cedar	July	61.0	4.68	18.04	4.22	25.34	47.71
	Dec.	58.5	7.38	18.02	4.48	27.02	43.09
	Mar.	51.6	4.75	9.65	3.40	21.10	61.10
Salal	June	78.4	9.68	14.16	3.83	18.26	54.07
	July	71.4	7.97	13.63	4.46	22.93	51.56
	Aug.	57.6	3.70	7.20	3.85	26.05	59.10
	Dec.	58.5	6.40	10.42	5.23	24.48	53.45
	Mar.	55.9	5.03	10.20	4.66	19.60	60.50
Trailing Blackberry	July	66.3	15.04	12.64	6.22	13.13	52.96
	Aug.	61.2	9.30	8.10	5.60	15.40	61.60
	Dec.	63.0	13.23	12.70	6.57	13.92	53.56
	Mar.	57.4	8.55	8.00	5.40	11.40	66.20
Red Alder	July	56.5	17.47	13.66	4.14	11.41	53.32
	Aug.	59.4	13.70	10.60	3.30	16.50	55.90
	Dec.	46.5	11.16	14.16	3.00	23.47	47.47
	Mar.	53.6	7.90	17.17	2.50	21.17	51.23
Willow	June	69.1	14.46	12.69	6.30	15.78	50.77
	July	62.9	12.35	14.27	6.46	16.26	50.63
	Aug.	-	5.40	4.60	5.70	22.90	61.40
	Dec.	50.4	9.46	8.30	3.92	29.54	48.76
	Mar.	50.5	6.25	10.50	3.40	24.00	56.10

Table 8 (cont)

Browse Species		% Moisture	Percent of dry weight: Crude Protein	Ether Extract	Ash	Fibre	N.F.E.
Oregon grape	Aug.	50.8	4.40	4.40	3.25	36.90	51.05
	Dec.	50.2	10.72	7.61	2.87	33.10	45.70
	Mar.	50.4	7.53	5.30	2.57	29.53	55.07
Black Raspberry	June	75.9	18.38	12.17	6.92	13.79	48.74
	July	-	15.04	12.57	6.96	17.22	48.21
	Aug.	53.0	8.30	3.20	5.50	22.00	61.00
	Dec.	61.5	6.24	8.07	4.50	35.59	45.59
	Mar.	41.6	6.90	3.95	3.15	31.25	54.75
Salmonberry	June	69.1	17.10	12.50	5.50	13.32	51.58
	July	-	12.35	13.31	5.41	13.31	55.62
	Aug.	57.0	7.00	7.40	6.30	23.30	56.00
	Dec.	51.1	7.37	6.86	3.72	23.33	56.72
Arbutus	Aug.	56.0	4.70	7.20	3.60	13.30	71.20
	Mar.	55.1	5.93	4.53	2.97	9.37	77.20
Rose	July	56.3	11.45	15.15	6.32	18.07	49.01
	Aug.	49.6	4.10	6.20	6.20	26.90	56.60
	Mar.	43.9	4.13	4.37	6.10	34.10	51.30
Red Huckleberry	Mar.	84.4	5.50	8.65	5.00	26.45	54.40
Thimble-berry	Aug.	65.6	11.70	15.40	7.36	15.39	50.15

Table 8 (Cont)

		% Moisture	Percent of dry weight: Crude Protein	Ether Extract	Ash	Fibre	N.F.E.
Herbaceous Species							
Catsear	June	84.4	15.50	16.97	8.67	14.90	43.95
	July	80.5	13.42	16.83	8.37	17.45	44.93
	Aug.	-	4.10	5.30	8.20	29.10	53.30
Fireweed	June	75.8	14.85	13.42	6.89	8.77	56.12
	July	76.8	13.17	14.18	5.74	8.81	58.10
Pearly Everlasting	July	76.2	10.86	14.02	9.79	18.63	46.60
	Aug.	-	5.00	5.20	5.80	28.90	51.10
Thistle	June	81.6	11.28	12.55	10.81	16.73	48.63
	July	82.0	12.58	15.53	10.36	26.84	34.69
	Aug.	-	4.10	7.80	5.40	35.30	47.40
Lettuce	July	77.0	12.22	9.29	6.72	19.98	47.15
	Aug.	-	3.00	5.00	6.40	35.20	50.40
White Hawkweed	Aug.	-	3.40	5.90	3.70	36.00	51.00
Ferns and Grasses							
Bracken	June	85.6	33.24	15.25	8.22	9.73	35.55
	July	60.6	11.90	14.75	7.15	22.77	43.42
	Aug.	59.3	6.65	5.00	8.75	21.25	57.35
Swordfern	Dec.	61.9	12.48	10.84	4.56	28.79	43.32
Grasses	July	53.0	8.10	9.84	5.30	43.56	33.20
	Aug.	-	3.10	4.80	6.30	31.40	54.40

Crude protein levels were found to be significantly higher (p .05) in summer than late winter, but not significantly different between summer and early winter. The two coniferous species included in the test (Douglas fir and western red cedar) showed seasonal trends in protein opposite to those of the other four species, both having highest levels in December and lowest levels in July (Table 8). These two species were apparently enough to offset a general July to December decline in protein indicated by each of the other four plants.

Average N.F.E. levels for the six species were higher in late winter than in either summer (p 0.05) or early winter (p 0.01). Dietz (1965) reported that N.F.E. content of shrubs and trees generally increases as phenology advances toward winter dormancy, thus contributing significantly to the winter maintenance ration of ungulates. The only species in the group which was not consistent with this trend was red alder, in which highest N.F.E. levels were recorded in July and August. It is perhaps significant that only in late August and September was current browsing on this plant noted.

Differences in the seasonal levels of the remaining nutrients bordered on significance (all p 0.14). The general relationships and conclusions which can be

Table 9 Analysis of variance for differences in nutrient composition of six important deer forage species[1] collected in July, December and March. Values of F are shown.[2]

Source	df	Crude Protein	Crude Fat	Ash	Crude Fibre	N.F.E.
Between species	5	4.39*	1.78	5.94**	4.21	1.85
Between seasons	2	4.65*	2.31	2.67	3.11	9.97**
Error	10					
Total	17					

[1]Douglas fir, western red cedar, salal, trailing blackberry, red alder and willow.

[2]Interactions were not separable from error mean squares because replicate samples were not available for all species.

*Differences significant at $p < 0.05$
**Differences significant at $p < 0.01$

Table 10 Results of Duncan's new multiple range test applied to the seasonal means for crude protein and nitrogen free extract derived for the analysis of variance shown in Table 9. Any two means not underscored by the same line are significantly different at $p < 0.05$.

Mean percentage for:	Mar.	Dec.	July
Crude protein	6.63	9.63	10.46
Nitrogen-free extract	58.69	49.91	51.81

suggested, therefore, are that: ash (mineral) levels were highest during early winter in the evergreen plants and highest during summer in the deciduous plants; crude fiber levels were highest in early winter for all six species but had declined slightly by March; crude fiber levels during summer were lower in the deciduous plants than in the evergreens; crude fat (ether extractive) levels were high in both summer and winter but showed no consistent seasonal trend; moisture percentages were highest during the summer growing period and lowest during late winter.

Dietz et al. (1958) reported that Colorado mule deer "choose browse containing the highest amounts of important nutrients during each season, especially in the case of protein". A similar relationship is indicated at Northwest Bay. For example, June samples of bracken fern shoots, typically the portion eaten by deer, averaged 33.2 per cent crude protein (range 29.7 per cent to 35.6 per cent). One month later, when almost all plants had reached the open frond stage and were rarely browsed, average protein had decreased by almost two thirds to 11.9 per cent (range 11.6 per cent to 12.1 per cent). Moisture and ash content were also higher, and crude fibre lower in the preferred new shoots than in the mature fronds.

Another example was noted with red alder and thimbleberry. Among August samples, the highest protein and fat levels, and the lowest fiber levels were recorded in the leaves of these two species (Table 8). As noted above for red alder, both were browsed only in late summer and autumn, at a time when other plants sampled were of low nutritional quality.

Six evergreen species, including Douglas fir, western red cedar, salal, trailing blackberry, sword fern, and Oregon grape contained suprisingly high percentages of protein and fats in early winter. Although some of these were eaten in other seasons when their chemical compositions had changed, as a group they comprised about 60 per cent of the winter diet.

Finally, the crude protein, fat, and ash contents of pearly everlasting and catsear declined markedly between June and August, coincidental with a decrease of these foods in the rumen samples. A similar relationship was found with black raspberry and salmonberry. Although not abundant in the rumen samples, signs of current browsing on these latter two plants were observed only between spring and mid-summer - at a time when their nutrient contents were highest.

It can be concluded, therefore, that there is significant seasonal variation in the chemical composition of major plant groups as well as of individual species. Since floral composition differs in each seral stage, over-all seasonal changes in the nutritional status of each of these seral stages must also occur. The relationships between seasonal variation in nutrient levels and food habits tend to support the contention that deer not only select the most nutritious plants, but also the most nutritious seral association available at each season.

Deer Use of Seral Communities

Pellet group densities are a function of deer numbers and the time spent by the animals in a community. After equal time intervals, highest densities reflect the most heavily used or preferred communities (Harper, 1967). This criterion was used as the basis for determining preference by deer for (1) different-aged seral stages, and (2) differently treated seral stages of equal age. It is understood that the deer density indices used in this study are actually converted expressions of "deer-days of use" occurring over relatively short periods of time. The index "deer-days per square mile", or as used here, simply "deer per square mile", was chosen in preference to "deer-days per acre" to avoid confusion associated with the use of decimal numbers. Results are based upon data from 85 spring and autumn counts conducted in early seral units representing 17 age-classes and the adjacent mature timber.

Although it is shown later that slash-burning significantly enhances range selection by deer, the combined means for both burned and unburned areas given in Table 11 were used to describe trends in site selection. This provided a more realistic approach to the ecological relationships between deer and forest regeneration in the study area, since burned, partially burned, and unburned sites were closely associated.

Seasonal use in relation to seral succession - Trends in deer use for the summer period and for the autumn-spring period are shown graphically in Fig. 11. During the summer, exploitation of developing seral communities began soon after logging or burning and reached peak intensity in the early *Gaultheria-Hypochaeris* association, three to four years after disturbance. At that time, use-indices equivalent to 140 deer per square mile (4.5 acres per deer) were recorded. A marked decline through the next six years into the late *Gaultheria-Hypochaeris* association followed, by which time use equivalent to 55 deer per square mile (12 acres per deer) was recorded.

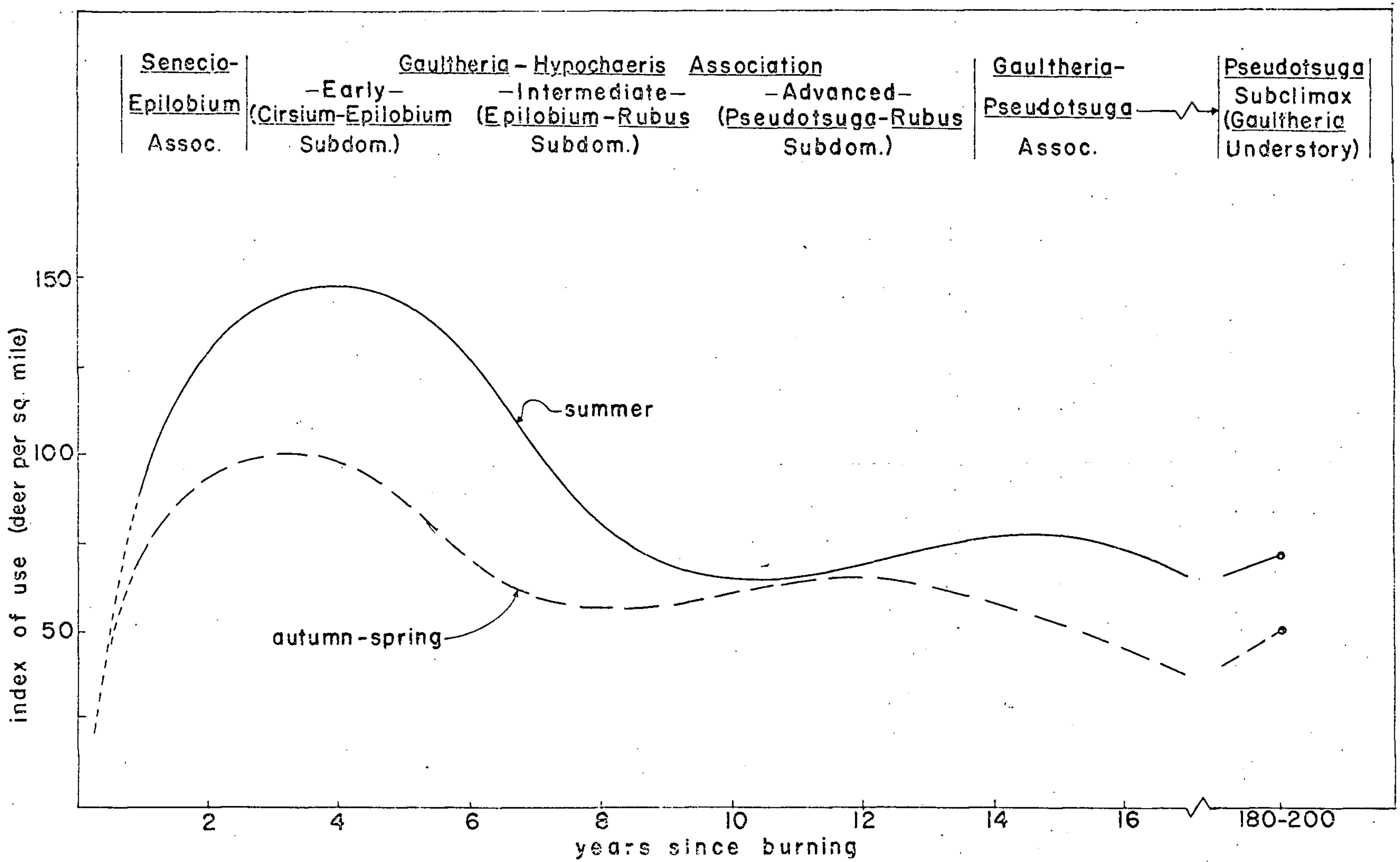
A slight upward trend beginning in the 12th year of succession may reflect a tendency of deer to take advantage of dense protective cover developing in the more advanced seral stages. It may also reflect greater use of the late *Gaultheria-Hypochaeris* association and the early *Gaultheria-*

Table 11 Mean indices of deer use in different-aged seral sites. Values were determined by pellet group counts and are expressed as deer per square mile.[1] The number of replicate samples obtained for each age-class is shown in parentheses.

Years since logging and burning	Summer Use-period			Autumn to Spring Use-period		
	Burned Sites	Unburned Sites	Pooled data	Burned sites	Unburned sites	Pooled data
2	106.6 (1)		106.6 (1)	110.4 (1)		110.4 (1)
3	118.8 (3)	99.3 (1)	113.9 (4)	111.7 (4)	79.3 (1)	103.2 (5)
4	181.2 (5)	113.4 (1)	169.9 (6)	-	-	-
5	152.8 (3)	166.2 (1)	156.1 (4)	44.2 (1)	71.8 (1)	58.0 (2)
6	58.5 (2)	85.5 (1)	52.2 (3)	60.5 (2)	-	60.5 (2)
7	97.0 (4)	37.8 (1)	85.2 (5)	69.4 (1)	25.0 (1)	47.2 (2)
8	35.4 (2)	111.5 (1)	61.8 (3)	-	95.2 (1)	95.2 (1)
9	126.6 (2)	70.9 (2)	98.8 (4)	68.7 (1)	64.7 (1)	66.7 (2)
10	99.6 (1)	63.2 (1)	81.4 (2)	-	-	-
11	24.8 (3)	86.4 (1)	40.2 (4)	29.4 (3)	-	29.4 (3)
12	50.1 (3)	-	50.1 (3)	-	-	-
13	75.1 (3)	43.1 (1)	67.4 (4)	57.4 (3)	48.4 (2)	53.7 (5)
14	61.4 (3)	54.1 (3)	57.8 (6)	-	45.9 (1)	45.9 (1)
15	-	86.1 (2)	86.1 (2)	-	-	-
16	44.2 (1)	-	44.2 (1)	3.3 (1)	-	3.3 (1)
17	47.5 (1)	-	47.5 (1)	-	-	-
Mat. timber	-	-	55.0 (5)	-	-	42.9 (2)

[1]See page 22 for method of converting pellet group densities to deer per square mile.

Fig. 11. The relative utilization by deer of early seral stages during the summer and the autumn-spring period.



Pseudotsuga association where, as shown above, preferred summer and autumn browse species are most abundant and varied. The shift to these associations likely occurs after herbaceous growth dries and becomes unpalatable.

From autumn to spring, deer use of the various seral stages was basically parallel to that of the summer months (Fig. 11), but in most age-classes was substantially lower in intensity. Early *Gaultheria-Hypochaeris* sites were most heavily used, supporting densities equivalent to 100 deer per square mile (six acres per deer) - about 26 per cent lower than peak densities recorded during summer. Similarly, the intermediate *Gaultheria-Hypochaeris* association, the *Gaultheria-Pseudotsuga* association, and the mature *Pseudotsuga* subclimax were used less intensively in the autumn-spring period than in summer. The late *Gaultheria-Hypochaeris* association, however, received equally intensive use during both sample periods. Evidence will be presented later indicating that fewer deer were present within the study area in the autumn-spring period than in summer. This being the case, it would appear that during autumn and winter, deer tend to concentrate in this late *Gaultheria-Hypochaeris* association in preference to other seral stages.

Age classification of the pellet groups counted in the spring of 1961 and 1962 (those used to derive the autumn-spring curve of Fig. 11) are summarized in Table 12. The

Table 12 Age classification of pellet groups encountered during the regular systematic May counts of 1961 and 1962.

Age of Site (years)	Fresh No.	(%)	Mod. Fresh No.	(%)	Aged No.	(%)
1 to 6	16	(4.9)	144	(43.7)	169	(51.4)
7 to Mature timber	7	(1.3)	128	(23.0)	421	(75.7

"fresh" and "moderately fresh" groups were considered to have been deposited within two months of the counting period - subsequent to the onset of spring growth. In age-classes one to six, 48.6 per cent of all groups counted were classified as "fresh" or "moderately fresh"; in the advanced seral stages only 24.3 per cent of the groups were placed in these categories. Therefore, approximately half the use of the very early seral stages (where spring foods were plentiful) occurred in the early spring. In the more advanced stages (where spring foods were not plentiful), only about one quarter of the use occurred in spring, the other 75 per cent occurring in autumn and winter. Thus, the autumn-spring curve of Fig. 11 can be considered a synthesis of two distinct seasonal patterns of deer-use: a spring pattern which increases rapidly soon after deforestation, reaches peak intensity in the third or fourth year, and declines relatively quickly after the sixth year; and an autumn-winter pattern which rises very gradually after deforestation, reaches a peak in the eleventh to thirteenth year, and, depending on the depth and duration of snowfall, declines relatively little through to the subclimax stage. The two seasonal peaks are apparent in Fig. 11.

The effects of slash-burning on range use - A comparison of the data for burned and unburned sites presented in Table 11 indicated that areas subjected to slash-burning were more intensively used by deer than unburned areas. A *t* Test of these data was executed, using only the age-classes for which samples from both treatments were available. The differences were significant for both the summer ($p < 0.01$) and the autumn-spring period ($p < 0.05$).

Isaac and Hopkins (1937) reported that an average of 29,000 cu ft of slash remains on each acre after clear-cut logging of coastal Douglas fir forests. They also concluded that even light slash-fires remove as much as 90 per cent of the smaller debris and 10 per cent of the larger wood. Therefore, the more intensive use by deer of burned sites probably reflects freer movement within the site. It may also reflect greater variety and availability of foods, and perhaps even higher nutrient levels in foods growing in burned than in unburned sites (Einarsen, 1966).

Figures 12 and 13 compare early seral conditions in two logged units, one in which the slash was thoroughly burned, the other in which burning was not attempted. Wood groundsel, lettuce, black raspberry and willowherb are abundant in the burned site; residual salal is the only plant available in quantity in the unburned site.

Estimated Number of Deer in the Study Area

The method of estimating numbers of deer within the study area, based on pellet group densities, is described on page 22. The first of the conditions upon which the accuracy of the method depends was fulfilled. Estimates of pellet group densities in each plot, when transformed with the square-root transformation and applied to Stein's two-stage sampling procedure (Steele and Torrie, 1960: 86), indicated that the desired sampling level of 70 per cent confidence with 10 per cent sampling error (Robinette et al. 1958) was obtained. The second assumption may not have been entirely fulfilled. For some age-classes of land, large differences between replicate estimates of deer use were noted. For most, however, the replicates were reasonably consistent, and the method can be expected to produce an acceptable approximation to the true population size.

The results of the calculations are presented in Table 13. In the winter of 1961-62 there were estimated to

Fig. 12 A Senecio-Epilobium association one year after logging and broadcast burning (Plot A). Deer use in this plot was intensive.

Fig. 13 An unburned area one year after logging. Productivity was limited to salal surviving from the mature timber stage. Access to, and movement through the area by deer was noticeably restricted.

Table 13 Estimates of the number of deer supported by each age-class of regenerating land, and the estimated deer population in the study area.

Years since logging or burning	Autumn-Spring 1961-62			Summer 1962		
	Total area (sq mi) (C)	Use index (deer/sq mi) (D)	No. deer in age-class (CD)	Total area (sq mi) (A)	Use index (deer/sq mi) (B)	No. deer in age-class (AB)
0	.22	-	-	.02	-	-
1	.19	63	12.0	.22	63	13.9
2	.16	98	15.7	.19	120	22.8
3	.29	102	29.6	.16	140	22.4
4	.14	92	12.9	.29	140	40.6
5	.28	76	21.3	.14	130	18.2
6	.04	63	2.5	.28	114	31.9
7	.12	53	6.4	.04	86	3.4
8	.32	49	15.7	.12	79	9.4
9	.61	49	29.9	.32	65	20.8
10	.27	51	13.8	.61	56	34.1
11	.78	53	41.3	.27	53	14.3
12	.25	54	13.5	.78	54	42.1
13	2.26	48	108.5	.25	60	15.0
14	.42	38	16.0	2.26	64	144.6
15	-	-	-	.42	65	27.3
16	.16	9	1.4	-	-	-
17	-	-	-	.16	40	6.4
Timber	3.64	43	156.5	3.62	55	199.1
Totals	10.15		497	10.15		666

be 497 deer in the ten square miles - an average of one deer for every 13 acres. In the summer of 1962, numbers had increased by approximately 34 per cent to an estimated 666 animals - slightly less than one deer for every ten acres. The increase is believed to be due partly to birth in June and partly to immigration from adjacent winter ranges. Smith (1968) concluded that recruitment through birth in the Northwest Bay herd may be as high as 35 per cent immediately after fawning and as low as 18.9 per cent by August. The average recruitment to August probably lies somewhere between these two extremes, perhaps in the order of 20 to 25 per cent. If so, a balance of 10 to 14 per cent of the total 34 per cent increase noted above would be attributable to immigration. No specific data were gathered to support this latter assumption, but limited observations and returns of deer tagged as fawns in the study area (Smith, op.cit.) indicate that at least some individuals which summer in the study area spend the winter months at lower elevations just outside the north and east boundaries. A significant winter movement into the lower, peripheral areas is probable because climatic conditions are less rigorous there and winter food production in the advanced second-growth stands adjacent to the Englishman River appears to be high. Thus, a 34 per cent increase in deer numbers from winter to summer is considered entirely reasonable.

Also considered reasonable is a 26 per cent reduction in numbers between the summer of 1962 and the winter of 1962-63. This represents the theoretical return of the population to the same level estimated for the winter of 1961-62. Smith (op.cit.) concluded that in each of the years 1960 to 1962, annual hunting mortality accounted for as much as 20 per cent of the Northwest Bay herd, and miscellaneous mortality, excluding summer fawn deaths, for an additional 10 per cent. Therefore, the differences between winter and summer population sizes indicated by pellet group densities are consistent with independent studies of the herd.

DISCUSSION

This investigation was designed to describe vegetative changes occurring in seral communities, and to determine the role of these changes in influencing range selection by deer. The results have demonstrated that, for four of the five factors investigated, a close relationship exists between stage of seral succession and deer use. Changes occurring in floral composition, food variety, food production, and in the seasonal nutrient content of available foods are closely associated with seasonal range selection. However, significant and consistent trends in the nutrient content of important forage species were not found to occur with advancing seral succession, and therefore could not be implicated as influencing range selection.

Limitations of the data

Certain limitations in the data, due mainly to the methods used, should be recognized as influencing the results. The range survey, for example, may not have estimated with equal accuracy the cover percentages of plants displaying different growth forms. Only the uppermost plant at each transect point was recorded, and since tall broad-leaved shrubs are inherently more likely to be "hit" than either single leader forbs or ground-level species, plants such as catsear, fireweed, pearly everlasting, grasses and sedges may have been proportionately underrated as components of the community. Conversely, the shrubs may have been overrated. Such an error would tend to be most prevalent in the more advanced seral stages where shrubs dominate. It is potentially serious if cover estimates are used as a measure of forage availability. This was not the case here, however, as a separate clipping investigation was undertaken to estimate food production. Thus, this error is restricted to estimates of cover composition only.

Stocking density, whether natural or artificial, was not measured separately in this investigation. Cover estimates tend to overcome the need for such measurements if most species are normally distributed and if sizes (diameters) of individuals within each species are relatively uniform. However, where variability occurs (as it usually does in a regenerating shrub-conifer community), stocking density may be important in modifying the chronology, the sequence, or even the number of seral stages developing. A high natural stocking rate of salal or Douglas fir, for example, may prevent the development of some of the catsear-dominated associations described above. As pointed out earlier, artificial stocking was limited to Douglas fir seedlings, and was negligible in the sites selected for study. Thus, any differences in species density or in cover composition between equal-aged sites was due entirely to natural factors.

The proportion of the annual crop already taken by deer at the time of measurement was mentioned earlier as a factor preventing accurate estimation of total food production. Naturally the differences between standing crop and total production would be greatest in seral stages which at any given season are most heavily used by deer. For example, figures estimating the standing crop of herbaceous plants in early Gaultheria-Hypochaeris sites are probably substantially lower than total productivity, and disproportionately so when compared with those for other seral stages. It was in these sites that highest spring-summer deer use was exhibited (Fig. 11), and in the spring and summer months that herbaceous plants dominated the diet (Fig. 4). Therefore, the greatest discrepancy would probably occur in estimates of the key foods pearly everlasting and catsear.

Taber and Dasmann (1958) discussed other factors which produce errors in estimating available foods. Not all new-growth on palatable plants is potential food because of certain behavioural characteristics shown by deer. Innate habits such as the tendency to avoid dense thickets and central portions of large open areas (see also Harper, 1967), and the utilization of only the lower sides of shrubs and trees growing on hillsides (see also Cowan, 1945) must be considered. If not, over-estimates of food production result. Although a few impenetrable thickets do exist in localized unburned sites, the gentle topography, patch-logging methods, and extensive slash-burning program at Northwest Bay tend to minimize the effect of behaviour on food availability.

Food availability may also depend to some extent upon the variety of plants present. Seral associations dominated by a single palatable species (such as salal) may appear to be highly productive. In reality, however, actual and potential utilization of this food may be low because of the lack of variety. Therefore, production estimates for the dense second growth Douglas fir stands and for salal-dominated associations are recognized as being higher than the actual consumption of food by deer would ever be..

Results of the proximate analyses do not completely preclude the possibility that succession is an important factor causing regression of forage nutrient levels. Immediately after slash-burning, soils are rich in calcium, potassium, nitrogen, and possibly other growth elements (Isaac and Hopkins, 1937). In the initial two or three years of succession, soil concentrations decline rapidly through erosion, leaching, and storage in perennial or slowly decaying plant tissues (see also Taber and Dasmann, 1958). For this reason, the age-classes of land sampled in the present study may have been unsuitable for testing the effects of succession on nutrient availability. Major changes may already have taken place when samples from the youngest (four-year-old) communities were obtained. The age of the individual shrubs and trees from which samples were collected may also have been important in masking nutrient trends (Cowan et al. 1950, Cook and Harris 1950, Swank 1956). But since each sample analysed was pooled from many individual plants, this type of error is considered minimal.

Finally, deer defecation rates have been reported to vary with differences in seasonal food habits. Daily rates ranging from a mid-winter low of 10 groups per deer to a high in early spring of 17 groups per deer have been recorded (Dasmann and Taber 1955, Rogers et al. 1958). Since all calculations in this study were based on a daily average of 13 groups per deer (Eberhardt and Van Etten 1956), it is recognized that use-indices derived for the summer period may be slightly high. Those for the autumn to spring period, however, are probably reasonably accurate because, as discussed above, almost half the use of early seral stages exhibited during the autumn-spring period appeared to have occurred in early spring. If so, high spring defecation rates would tend to balance low winter defecation rates, with the average being close to 13 groups per deer.

The relationship between food and the selection of spring and summer range

Pellet group densities indicated that the seral stage preferred during the late spring and summer was the early Gaultheria-Hypochaeris association, a stage developing after three to five years of regeneration. In these sites the intensity of deer use was equivalent to 140 animals per square mile. There is little doubt that quality and quantity of food are the primary factors stimulating such heavy use of this association, particularly when other environmental requirements such as protective cover are not readily available here.

Food habits, in conjunction with the other results, support this argument. Herbaceous plants were shown to dominate the spring-summer diet of Northwest Bay deer. Measurements of changes in range composition, as succession advanced, indicated that these same herbaceous species were: most abundant in terms of ground cover three years after logging and burning; most available on a weight basis four years after logging and burning; present in the greatest variety of species five to six years after logging and burning. Furthermore, seasonal trends in nutrient composition indicated that the quality of spring-summer herbaceous foods was generally high when compared to other foods not eaten at this time of the year. Although forage samples were not analysed at the beginning of the growing season, it is likely that nutrient levels were maximal then and had declined slightly when June samples were collected (Dietz, 1965). Nevertheless, not all individual plants are at the same phenological stage at any given time. If deer tend to select the youngest and therefore most nutritious plants available, as suggested by Taber and Dasmann (1958), it can be concluded that foods taken during this period were not only nutritionally adequate, but also superior to others available.

In terms of availability, variety, and nutritional quality of food, therefore, the early _Gaultheria_-_Hypochaeris_ association appeared to provide ideal spring-summer conditions. During the growing season, conversion of solar energy into available deer food is considered to be greatest in this early developing seral stage.

In an average summer, intensive exploitation of early _Gaultheria_-_Hypochaeris_ associations cannot continue beyond the period of active plant growth. Most of the herbaceous plants dominating this community become unpalatable as they approach maturity. Thus, with advancing phenology, deer are forced to feed more frequently in browse-dominated seral stages, particularly the advanced Gaultheria-Hypochaeris and Gaultheria-Pseudotsuga associations. This shift in range preference was reflected by an increased intensity of use noted in the 12- to 14-year age-classes (Fig. 11). Availability of various late summer and autumn foods, especially salal berries, is likely an important factor stimulating this increased exploitation. Abundance of salal in terms of ground cover and new growth production was highest at this time, and the nutritive quality of the preferred portions may have been higher here than under mature timber (Cowan 1945). This latter possibility could not be tested with the data available.

Not all activity contributing to the second upward trend in the use of seral stages during summer (Fig. 11) can be associated with feeding. Brown (1961) reported a corresponding trend after estimating pellet group densities in logged areas of western Washington. He attributed it to use associated with bedding and protective cover. The situation is undoubtedly similar at Northwest Bay. Although advanced seral stages provide very little in the way of spring and early summer food, they are nevertheless heavily used in those seasons and form an important part of the animals' habitat.

The intensity to which deer utilize the mature timber in summer (equivalent to approximately 55 deer per square mile) was surprisingly high, and must be interpreted as being representative only of mature timber stands within the study area. Cowan (1945) estimated that, because of low food production, undisturbed tracts of coast forest may support as few as one deer per square mile. The heavy use of timber at Northwest Bay is a direct result of the interspersion of small stands of mature trees within the patch-logged environment. Some late summer feeding on salal berries and mushrooms accounts for part of the activity, but most of it must be attributed to bedding and protection.

The relationship between food and the selection of autumn and winter ranges

Pellet groups accumulating between autumn and early spring were most numerous in the two- to four-year-old stages. However, results of three other aspects of this investigation indicate that most deer activity in these young stages occurred in spring rather than in autumn or winter. First, production and variety of autumn-winter foods were shown to be low in the early seral stages, the principal items such as salal, western red cedar, and arboreal lichens being most abundant in the *Gaultheria*-*Pseudotsuga* association and under the subclimax forest. Second, important autumn-winter foods were not found to be nutritionally better in the young than in the old seral stages. If they had been, the scant production of annual growth in the young stages would probably be insufficient to override the benefits of a higher nutrient content. Third, little protection from inclement winter weather is available in the regenerating coast forest until at least the development of the Gaultheria-Pseudotsuga association. Presumably, therefore, specific measurements of pellet group accumulations in autumn and winter would have revealed the highest intensities of use in the advanced, shrub- and conifer-dominated seral stages, and the lowest intensities of use in the early, forb-dominated seral stages. Data concerning the age of pellet groups recorded in spring counts support this reasoning. So does the analysis of population estimates derived from pellet group densities, which revealed an apparent shift of animals in autumn and winter into the more advanced and complex associations.

Thus, on the basis of food availability, comfort, and protection, the 12- to 15-year-old salal-catsear and salal-Douglas fir sites are considered to be the preferred autumn and winter ranges. Conversion of solar energy into available food appears to be most efficient in these sites.

CONCLUSIONS

This study indicates that quality and quantity of food are the primary factors governing range selection by blacktailed deer, with protective cover secondary.

In spring and summer, deer prefer seral stages which produce the greatest variety and quantity of herbaceous foods. Generally, these are sites which have undergone three to five years of regeneration. From late summer to late winter, deer prefer seral stages which produce the greatest variety and quantity of shrubs (particularly salal) and conifers. Generally, these are sites which have undergone twelve to fifteen years of regeneration. When snowfall reduces food availability in the regenerating areas, the subclimax forest becomes an important producer of deer forage. It follows then that food quantity affects range selection.

The nutritional quality of food changes with season and perhaps with seral succession. Furthermore, deer appear to select the most nutritious foods available in each season. Considering statements in the previous paragraph, it is established then that food quality also affects range selection.

The original hypothesis is supported: the numbers of deer within a regenerating unit of coast forest are affected by the efficiency at which radiant energy is converted into suitable and available food. Largest populations within the whole logged community can be expected when the number of ideal food-producing units for each season is at a maximum.

These conclusions lead to a further hypothesis: that sustained deer populations in the coast forest can be realized only if the area of land succeeding to subclimax and climax conditions equals the area being stimulated into regeneration through logging, burning or some other form of forest destruction. Since the rate of regeneration to maturity is frequently slower than current harvest rates, a balance between habitat creation and habitat deterioration never occurs. Patch-logging operations approach the ideal more closely than clear-cut, broadcast operations, but even here, a population decline is inevitable because of eventual regression in the food-producing capabilities of the land.

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Appendix A Temperature and precipitation records taken at the Nanaimo Airport, and averages for the four-year study period.

Mean Daily Temp. °F.	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
1959	36.6	38.2	41.0	46.1	52.0	57.8	65.2	60.8	56.0	48.9	39.9	38.0
1960	35.6	38.4	40.5	47.1	50.7	57.3	65.3	60.9	55.7	50.6	40.9	37.7
1961	38.8	41.8	42.5	47.2	53.2	60.8	66.3	66.2	55.4	47.2	39.0	36.4
1962	36.4	39.3	38.6	47.1	50.5	57.2	61.9	60.4	57.0	50.2	43.6	39.9
Average	36.4	39.4	43.1	46.8	51.6	58.3	64.7	62.1	56.0	49.2	40.8	38.0

Pre-cip-ita-tion (ins)	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Annual Pptn. (ins.)
1959	5.84	2.96	4.23	1.40	1.98	2.56	.25	.66	2.85	2.02	4.53	3.40	32.68
1960	7.62	5.10	3.56	3.05	2.25	.58	.07	1.35	.56	3.05	8.67	4.47	40.33
1961	9.76	9.93	6.76	1.94	2.88	.39	.83	.95	1.95	4.09	5.14	7.76	52.38
1962	3.32	2.43	3.78	3.57	1.99	1.35	.72	2.62	2.71	5.03	10.44	6.94	44.90
Avge.	6.64	5.10	4.58	2.49	2.29	1.22	.47	1.40	2.02	3.55	7.20	5.64	42.57

Appendix B Seasonal diets of blacktailed deer at Northwest Bay, based on analyses of rumen samples from female deer.

Species	Spring-summer Transition[1] Volume %	Spring-summer Transition[1] Frequency %	Autumn[2] Volume %	Autumn[2] Frequency %	Winter[3] Volume %	Winter[3] Frequency %
Salal	5.4	71	55.9	100	30.3	94
Red cedar	1.9	57	2.3	9	20.9	94
Arboreal lichens	7.3	29	T	9	13.2	49
Pearly everlasting	46.0	79				
Grasses and sedges	15.1	57	2.4	27	8.2	68
Trailing blackberry	4.6	54	7.3	91	3.7	73
Catsear	8.1	42	1.5	36	3.9	38
Mushrooms	T	8	7.0	73	2.8	38
Douglas fir	2.3	54	3.9	64	4.0	81
Bearberry	2.7	50	1.1	9	5.1	32
Red Alder	T	12	7.2	36	0.7	5
Vanilla leaf	4.4	17				
Hardhack					2.5	27
Liverwort					1.3	32
Willow	T	8	1.3	36		
Lichen	T	12			0.9	41
Equisetum	T	4	1.0	9		
Rose			0.8	9		
Fireweed			T	27		
Moss	T	4	T	27	T	16
Sword fern	T	4			T	11
Oregon grape					T	22
Unidentified	T	17	8.0	72.7	1.0	35

[1] Twenty-four samples, May 5 to June 15

[2] Eleven samples, Oct. 2 to Nov. 27

[3] Thirty-seven samples, Dec. 10 to March 25

Appendix C Average cover-percentages for the major categories of vegetation, the rank of dominant species, and the mean number of palatable species recorded in burned sites of increasing successional age.

Cover type	Years since slash-burning 1	2	3	4	5	6
Herbaceous plants	2.8	7.1	16.6	11.1	11.9	14.6
Shrubs and deciduous trees	0.5	12.0	14.7	27.0	49.9	38.6
Coniferous trees	0.1	0.7	0.4	0.4	0.9	1.6
All plants	3.5	24.8	31.6	33.5	62.7	54.8
Bare soil	60.9	44.2	18.2	11.7	5.7	4.3
Dominant species:	Wood groundsel Lettuce *Epilobium* spp Thistle Salal	Salal *Epilobium* spp Thistle Wood groundsel Catsear	Salal Catsear Thistle *Epilobium* spp Trailing blackberry	Salal Catsear Trailing blackberry Pearly everlasting Willow	Salal Catsear Raspberry Trailing blackberry Pearly everlasting	Salal Catsear Raspberry Trailing blackberry Lettuce
Mean number of Palatable Species:						
Forbs and ferns	7.0	7.0	9.0	9.0	8.0	11.0
Shrubs	4.0	4.0	6.5	7.5	9.0	10.0
Coniferous trees	2.0	1.5	1.5	1.5	2.0	2.0
Total	13.0	12.5	17.0	18.0	19.0	23.0

Appendix C (cont)

Cover type	Years since slash-burning 8	9	10	12	13	14	15
Herbaceous plants	7.2	14.1	5.5	10.5	6.3	7.0	1.3
Shrubs and deciduous trees	53.5	23.4	59.6	36.3	43.4	30.1	25.7
Coniferous trees	4.8	4.9	2.8	5.0	1.8	14.4	9.2
All plants	65.5	42.2	66.3	51.7	51.5	51.6	36.2
Bare soil	1.6	2.0	1.4	1.8	3.1	1.7	4.8
Dominant species:	Salal Catsear Douglas fir Western hemlock Trailing blackberry	Salal Trailing blackberry Catsear Vanilla leaf Black raspberry	Salal Catsear Trailing blackberry Douglas fir Western hemlock	Salal Catsear Douglas fir Western hemlock Willow	Salal Catsear Trailing blackberry Willow Oregon grape	Salal Douglas fir Western hemlock Catsear Trailing blackberry	Salal Douglas fir Oregon grape Red Alder Catsear
Mean number of Palatable Species:							
Forbs and ferns	11.0	6.0	7.5	8.0	8.0	8.0	4.0
Shrubs	10.0	9.0	9.5	9.0	11.0	9.0	7.0
Coniferous trees	2.0	2.0	2.0	2.5	2.0	3.0	3.0
Total	23.0	17.0	19.0	19.5	21.0	20.0	14.0

Appendix C (Cont)

Cover Type	Years since slash-burning Mature Timber
Herbaceous plants	0.6
Shrubs and deciduous trees	67.1
Coniferous trees	1.8
All plants	69.5
Bare soil	1.3
Dominant species:	Salal Western hemlock Dwarf rose Twin flower Western red cedar
Mean number of Palatable Species:	
Forbs and ferns	2.0
Shrubs	8.0
Coniferous trees	1.0
Total	11.0

Appendix D Average cover-percentages for the major categories of vegetation, and the rank of dominant species, recorded in unburned sites of increasing successional age.

Cover type	Years since logging					
	2	5	6	8	12	13
Herbaceous plants	12.6	2.8	4.6	8.0	2.9	7.0
Shrubs and deciduous trees	34.3	66.1	68.5	44.7	71.4	41.3
Coniferous trees	0.5	0.5	2.0	3.3	4.2	4.8
All plants	47.4	69.4	75.2	56.1	78.4	53.4
Bare soil	17.0	2.2	1.0	8.5	1.9	2.5
Dominant species:	Salal Trailing blackberry Bedstraw Bracken Vanilla leaf	Salal Catsear Grasses Twinflower Douglas fir	Salal Trailing blackberry Catsear Lettuce Dwarf rose	Salal Trailing blackberry Catsear Douglas fir Willow	Salal Western hemlock Douglas fir Catsear Trailing blackberry	Salal Catsear Douglas fir Trailing blackberry Willow

Appendix E Nutrient values of four groups of forage species sampled in different-aged sites and at different seasons. The analyses of variance for these data are given in Table 7.

Species	Age of Site (yrs.)	Percent Dry Weight: Crude Protein	Ether Extract	Ash	Crude Fibre	N.F.E.
Test 1: Five-year-old vs 14-year-old sites in March						
Willow	5	5.80	7.50	3.00	25.00	58.70
	14	6.70	13.50	3.80	22.50	53.50
Red Alder	5	7.60	17.50	1.50	20.50	52.90
	14	8.05	17.00	3.00	21.50	50.45
Red cedar	5	4.40	9.80	4.30	20.50	61.00
	14	5.10	9.50	2.50	21.70	61.20
Black raspberry	5	7.60	4.60	3.50	30.60	53.70
	14	6.20	3.30	2.80	31.90	55.80
Arbutus	5	5.60	3.30	2.80	10.40	77.90
	14	6.10	5.15	3.05	8.85	76.85
Rose	5	3.10	6.30	8.00	32.90	49.70
	14	4.65	3.40	5.15	34.70	52.10
Oregon grape	5	8.30	3.40	2.60	28.30	57.40
	14	7.15	6.25	2.55	30.15	53.90
Salal	5	5.30	11.30	4.50	19.30	59.60
	14	4.90	9.65	4.75	19.75	60.95
Douglas fir	5	6.30	9.80	2.80	20.10	61.00
	14	8.30	15.75	2.50	18.40	55.05
Test 2: Four-year-old vs nine-year-old sites in December						
Willow	4	8.79	9.32	3.89	28.51	49.49
	9	9.80	7.73	3.67	30.76	48.05
Douglas fir	4	12.09	12.24	2.87	21.19	51.61
	9	10.24	13.18	4.44	19.40	52.72
Black raspberry	4	6.85	8.69	4.21	35.54	44.71
	9	5.64	7.45	4.79	35.64	46.48
Trailing	4	12.69	13.98	7.65	11.87	53.81
blackberry	9	14.18	11.26	7.14	14.56	52.86

Appendix E (Cont)

Species	Age of Site (yrs.)	Percent Dry Weight: Crude Protein	Ether Extract	Ash	Crude Fibre	N.F.E.
Test 3: Nine-year-old vs 14-year-old sites in December						
Douglas fir	9	10.24	13.18	4.44	19.40	52.72
	14	8.13	12.18	4.14	21.24	54.31
Trailing	9	14.18	11.26	7.14	14.56	52.86
blackberry	14	12.82	12.88	4.93	15.34	54.03
Willow	9	9.80	7.73	3.67	30.76	48.05
	14	9.48	8.42	4.47	28.16	49.47
Test 4: Four-year-old vs nine-year-old vs 14-year-old sites in June						
Willow	4	15.72	11.66	6.28	15.50	50.84
	9	13.52	12.90	5.86	15.36	52.36
	14	13.51	14.03	6.78	16.60	49.08
Catsear	4	14.50	17.94	8.62	15.28	43.67
	9	16.86	16.76	8.86	15.24	42.28
	14	14.78	15.47	8.38	13.50	47.87
Fireweed	4	15.39	12.23	6.89	9.07	56.42
	9	12.11	15.46	6.88	9.54	56.01
	14	16.79	13.16	6.74	7.54	55.78
Bracken	4	34.13	14.05	8.58	8.69	34.55
	9	32.28	12.25	8.82	10.12	36.53
	14	33.79	13.85	7.44	9.86	35.06

Fig. 14a. A Senecio-Epilobium association two years after logging and slash-burning (Plot B). Wood groundsel and willowherb dominate, with catsear and thistle the principal associates. Salal dominates in unburned spots (upper left).

Fig. 14b. The same plot six years after slash-burning. The area has developed into an intermediate Gaultheria-Hypochaeris association, with salal and catsear replacing the groundsel and willowherb.

Fig. 15a. An early *Gaultheria-Hypochaeris* association five years after slash-burning (Plot G). Thistles, fireweed and trailing blackberry are subdominants to the salal and catsear.

Fig. 15b. The same plot as an advanced *Gaultheria-Hypochaeris* association nine years after burning. Trailing blackberry and natural Douglas fir seedlings are the principal associates.

Fig. 16a. An advanced Gaultheria-Hypochaeris association nine years after logging and spot burning (Plot I). Trailing blackberry is subdominant and forb cover is light. Note the debris.

Fig. 16b. The same plot as an early Gaultheria-Pseudotsuga association 13 years after deforestation. Red alder, trailing blackberry and willow are now the principal associates.

Fig. 17a. An advanced Gaultheria-Hypochaeris association 12 years after logging and spot burning (Plot K). Fireweed is abundant in the foreground.

Fig. 17b. Plot K as a Gaultheria-Pseudotsuga association 16 years after logging and burning. Douglas fir has encroached sufficiently to replace most herbaceous species.