Effects of Sitka Black-tailed Deer (*Odocoileus hemionus sitkensis*) on understory in old-growth forest on Haida Gwaii (Queen Charlotte Islands), British Columbia

By

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Abstract

In the early 1900's, the Game Commission of British Columbia introduced Sitka Black-tailed Deer (*Odocoileus hemionus sitkensis*) to the offshore archipelago of Haida Gwaii (Queen Charlotte Islands). In the absence of predators and competing herbivores, the deer population erupted. Deer remain abundant throughout Haida Gwaii today, and concerns have been raised about the effects of deer browsing on the regeneration of Western Redcedar *(Thuja plicata)*, which is important commercially and culturally on Haida Gwaii. There is also concern about the effects of deer on endemic plants and other components of the old-growth forest ecosystems. The objective of this study was to determine how varying levels of deer density affected understory composition and biomass in old-growth forests on Haida Gwaii. I used accumulated pellet groups to estimate relative deer density. I used regression equations to estimate aboveground, pre-browsed and utilized biomass of plant species considered to be important forage for deer, including: Red Huckleberry (*Vaccinium parvifolium)*, Blueberry (*V. ovalifolium / alaskaense)*, False Azalea (*Menziesia ferruginea)*, Deer Fern (*Blechnum spicant)* and Western Redcedar (Models had fits (r^2) ranging between 0.66 and 0.98). The study area extended from Ian Lake on Graham Island to the south end of Louise Island. All 110 sampling sites (1 ha) were located in old-growth stands. At each site, I counted pellet groups on three strip transects (1.66 m wide and 100 m long), estimated the shrub biomass on fifteen 4 m^2 plots and herbaceous biomass on thirty 1 m^2 plots. The estimated aboveground biomass of the selected forage species, varied from 0 to 2137 kg/ha, with a median of 82 kg/ha and a mean of 258 kg/ha (SD = 388). The estimated available biomass ranged from 0 to 93 kg/ha, with a median of 3 kg/ha and a mean of 7 kg/ha (SD = 14).

The estimated utilized biomass ranged from 0 to 22 kg/ha, with a median of 3 kg/ha and a mean of 4 kg/ha (SD = 4.4). The range of forage species was low, but their occurrence varied widely. I encountered *Vaccinium* spp. (*V. parvifolium*, *V. ovalifolium* and *V. alaskaense*), Salal (*Gaultheria shallon*), False Azalea, and Salmonberry (*Rubus spectabilis*) in 99%, 35%, 20% and 4% of the sites, respectively. Western Redcedar saplings were found in only one sampling site and seedlings in 34% of the sites, which corroborates concerns about the effect of deer on its regeneration. Red Huckleberry was the most common species measured, and contributed 86% of the aboveground biomass and 38 % of the available biomass. Salal (*Gaultheria shallon),* which was not measured in a comparable way to other shrubs, also contributed considerably to the aboveground biomass. Density of pellet groups (PG) varied from 0 to 1840 PG/ha, with a median of 300 PG/ha and a mean of 402 PG/ha (SD = 362). I found no correlations between relative deer density and aboveground biomass or available biomass, and a very weak, positive correlation between relative deer density and utilized biomass. I did not find the expected correlation between overstory canopy closure and aboveground biomass, which suggests that deer browsing is overwhelming other controlling environmental factors. Using a regression quantile method, I found that the upper limit of relative deer density was negatively correlated with aboveground biomass at 75%, 90% and 95% regression p 50
quartiles. The upper limit of relative deer density was positively correlated with utilized p 48,50,51
biomass at 75%, 90%, and 95% regression quartiles. However, the upper limit of relative deer density was not correlated with available biomass. Relative deer density, p 52
aboveground biomass, available biomass, and utilized biomass did not differ between stands considered as important winter range and other stands. These same parameters did

not vary with distance from settlements either. However, on Moresby Island, relative deer density and aboveground biomass estimates were lower in remote areas compared to easily accessed areas. Deer have dramatically reduced the understory vegetation and deer carrying capacity in old-growth forests over much of Haida Gwaii. Today, relatively few deer are able to keep the sparse understory from recovering - a situation that is unlikely to change in the absence of density-independent mortality (e.g. weather). In addition to altering the character of the understory, deer will also have profound affects on the overstory by eliminating recruitment of Western Redcedar. Effects on other flora and fauna that historically occupied Haida Gwaii are perhaps less studied, but no less important.

Examiners:

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1. Introduction.

1.1. Background

The ecological interactions of large herbivores with their environment have been studied in North American temperate zone ecosystems since the 1940's, e.g., Cowan (1945). On the west coast of North America, Black-tailed Deer (*Odocoileus hemionus sitkensis* and *O. h. columbianus*)[1] have been studied throughout most of their range, primarily because of the conflict between timber harvesting and the habitat needs of deer. In British Columbia, Columbian Black-tailed Deer (*O. h. columbianus*) have been studied most intensively on Vancouver Island. Many aspects of their ecology have been examined, including use of seral stages (Gates 1968), impact of hunting pressure (Smith 1968), habitat use and selection (Cowan 1945; Wilms 1971; Jones 1975; Harestad 1979; Bunnell et al. 1985), impact of wolf predation (Jones and Mason 1983; Hatter 1988), nutrition (Bunnell et al. 1978; Rochelle 1980; Ellis 1984), use of arboreal lichens in winter (Stevenson 1985) and seasonal movements (McNay 1995). In Alaska, many ecological aspects of the Sitka Black-tailed Deer (*O. h. sitkensis*) have been studied, including seasonal movements (Schoen et al. 1985), fitness (Klein and Olson 1960; Parker et al. 1993; Kirchhoff and Larsen 1998), predation (Ballenberghe and Hanley 1982), habitat use (Bloom 1978; Wallmo and Schoen 1980; Kirchhoff et al. 1983; Kirchhoff and Schoen 1987; Schoen and Kirchhoff 1990; Yeo and Peek 1992) and nutrition (Parker et al. 1999). Importance of winter ranges to the survival of deer populations was recognized already in the 1930's (Hosley and Ziebarth 1935), and winter ranges have been studied on

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[1] Names of plants follow Pojar and MacKinnon (1994), and names of mammals follow Nagorsen (1990).

Vancouver Island (Harestad 1979; Nyberg, Bunnell, Janz, and Ellis 1986; Bunnell 1990; McNay 1995) as well as in Alaska (Klein 1965; Bloom 1978).

Prior to man's active intervention, the faunal composition of Haida Gwaii was shaped largely by the last ice-age and the isolation of the islands (Byun et al. 1999). Knowledge of the distribution of refugia on the northwest coast of North America and consequent impacts on biodiversity is limited (Byun 1998). Since the most recent ice age, changes have occurred in the climax forests on Haida Gwaii, but pollen counts from lake sediment cores suggest that the present forest type has been dominant over the last 5500 years (Warner 1984). However, once Haida Gwaii became isolated from the mainland, some plant and animal species likely went extinct. Although some new species were able to colonize Haida Gwaii from the mainland (carried by birds, or on flotsam), the rate of colonization likely did not equal the rate of extinction (MacArthur and Wilson 1967). Pojar and Banner (1982) observed a substantial reduction in floral and faunal diversity relative to the mainland, and they attributed this to the remote location.

It is well known that large herbivores can affect the species composition of plant communities (Augustine and McNaughton 1998). After introduction of Sitka Black-tailed Deer in the early 1900s to Haida Gwaii (Cowan 1984), their populations erupted, probably because of the presence of an unexploited niche and the absence of natural predators such as Cougar (*Felis concolor*) and Wolves (*Canis lupus*). Unfortunately, only anecdotal information exists of the successful introduction of deer, but by 1940, large herds of Sitka Back-tailed Deer could be seen (Price 1998).

With the successful introduction of deer, the understory in the old-growth forests changed dramatically (Pojar et al. 1980; Pojar et al. 1980). The original understory was described as a jungle "composed of such plants as Red Huckleberry, Tall Bilberry [now called Oval-leaved Blueberry], Thimbleberry, Salmonberry, Salal and Devil's Club growing eight or ten feet in height, not to mention young Sitka spruce and hemlock springing up densely all around" (Hopkinson 1931: 29). When the understory was surveyed on the islands approximately 50 years later, a "dramatic reduction" in vigour and abundance of the shrubs and herbs was discovered (Pojar et al. 1980; Pojar and Banner 1982; Banner et al. 1984), but, until then, only anecdotal evidence existed to suggest a causal relationship between depleted understory and deer browsing (Banner et al. 1984).

The depletion of the understory is hardly surprising because most of the species described by Hopkinson (1931) constitute important deer foods (Pojar et al. 1980; Kirchhoff and Larsen 1998; Parker et al. 1999). In the 1980's, three deer-proof exclosures were built at Sewell Inlet, Moresby Island. Vegetation monitoring inside as well as outside the deer exclosures showed a dramatic difference (Bennet 1996). In the fall of 1997, the Research Group on Introduced Species (RGIS) and Parks Canada initiated a deer cull on Reef Island and Skung Gwaii, two remote islands off Moresby Island, to investigate re-establishment of the understory after eliminating browsing pressure. Within three years, the understory showed a marked difference in composition and vigour that left little doubt that browsing suppressed the understory (J.-L. Martin, pers. comm. 2000).

Deer browsing pressure was also interfering with the establishment and recruitment of new *Thuja plicata* (a commercially important tree species) on Haida Gwaii. In most areas, *Thuja plicata* seedlings are viable only when physically protected from browsing by deer (Brian Saunders, pers. com. 1999). Natural regeneration of *Thuja plicata* varies throughout the islands, and unprotected *Thuja plicata* saplings established more successfully in accessible areas (Daufresne and Martin 1997; Baltzinger and Martin 1998). These authors explained this observation by assuming that hunting resulted in a lower deer density in easily accessible areas that consequently resulted in lower browse pressure.

Sitka Black-tailed Deer also consume many different shrubs and herbs. On Channel Island, Southeast Alaska, the diet consisted of more than 70 different plant species (Parker et al. 1999), with the bulk being shrubs and conifer (Kirchhoff and Larsen 1998; Parker et al. 1999). Lichen and fern rhizomes could at times constitute up to 30 % of the winter diet (Parker et al. 1999). No detailed studies exist on the diet of Sitka Black-tailed Deer on Haida Gwaii, but Pojar et al. (1980) recorded 12 species eaten by deer.

This appetite by deer for many different plant species has caused conservation concerns about the reduction of the overall habitat diversity (Daufresne and Martin 1997; Martin and Daufresne 1999) and the threat to endemic native plant species, especially in sub-alpine and coastal areas (Pojar et al. 1980). The Haida First Nations are also concerned because they are loosing culturally important species such as *Thuja plicata* and medicinal species such as Devil's Club (*Oplopanax horridus*).

In June of 1997, a Research Group on Introduced Species (RGIS) was launched to study the impacts of introduced species on native flora and fauna on Haida Gwaii. The four general objectives of RGIS were: 1) To understand the impact of Sitka Black-tailed Deer on vegetation regeneration and tree recruitment; 2) To predict vegetation recovery potential if deer are controlled; 3) To understand the role of spatial and temporal movements by Sitka Black-tailed Deer among islands and between habitats; and 4) To understand the individual impacts of deer (through habitat modification) and Red Squirrel (*Tamiasciurus hudsonicus*) on the ecology of forest birds on these islands. My study was part of RGIS.

1.2. Objectives and hypotheses.

My study had three objectives. The first objective was to evaluate the effects of deer on understory vegetation in old-growth forests on Haida Gwaii. I focused on old-growth forests because these are important for deer survival during severe winters. The old-growth forests intercept snow, resulting in higher food availability (Kirchhoff and Schoen 1987) and providing thermal cover (Bunnell 1990). If deer forage optimally in the old-growth forests during the winter, it could be expected that they seek areas with the highest amounts of food. I also choose old-growth forests because they were the original forests on Haida Gwaii, and knowledge about them can help provide information for future preservation of native flora and fauna. The second objective was to establish correlations between three components of biomass (aboveground, pre-browsed and utilized) and relative deer density. From this I hoped to establish vegetation thresholds at which deer abandon forest stands. The third objective was to investigate whether or not relative deer density and therefore effects on vegetation depended on topography, habitat or distance from urbanized areas, for example to see if deer favoured south-facing slopes for winter ranges, as documented on Vancouver Island and southeast Alaska (Harestad 1979; Bunnell 1990; Schoen and Kirchhoff 1990).

These objectives can be re-stated as the following hypotheses:

1. Relative deer densities are positively correlated with aboveground and available biomass in old-growth stands.

    Task 1: Estimate relative deer density

    Task 2: Estimate aboveground and available biomass

2. Relative deer densities are negatively correlated with utilized biomass in old-growth forest stands.

    Task 3: Estimate utilized biomass

3. Relative deer densities vary with respect to hunter access, aspect, slope and winter range.

2. Study Area.

2.1. General features.

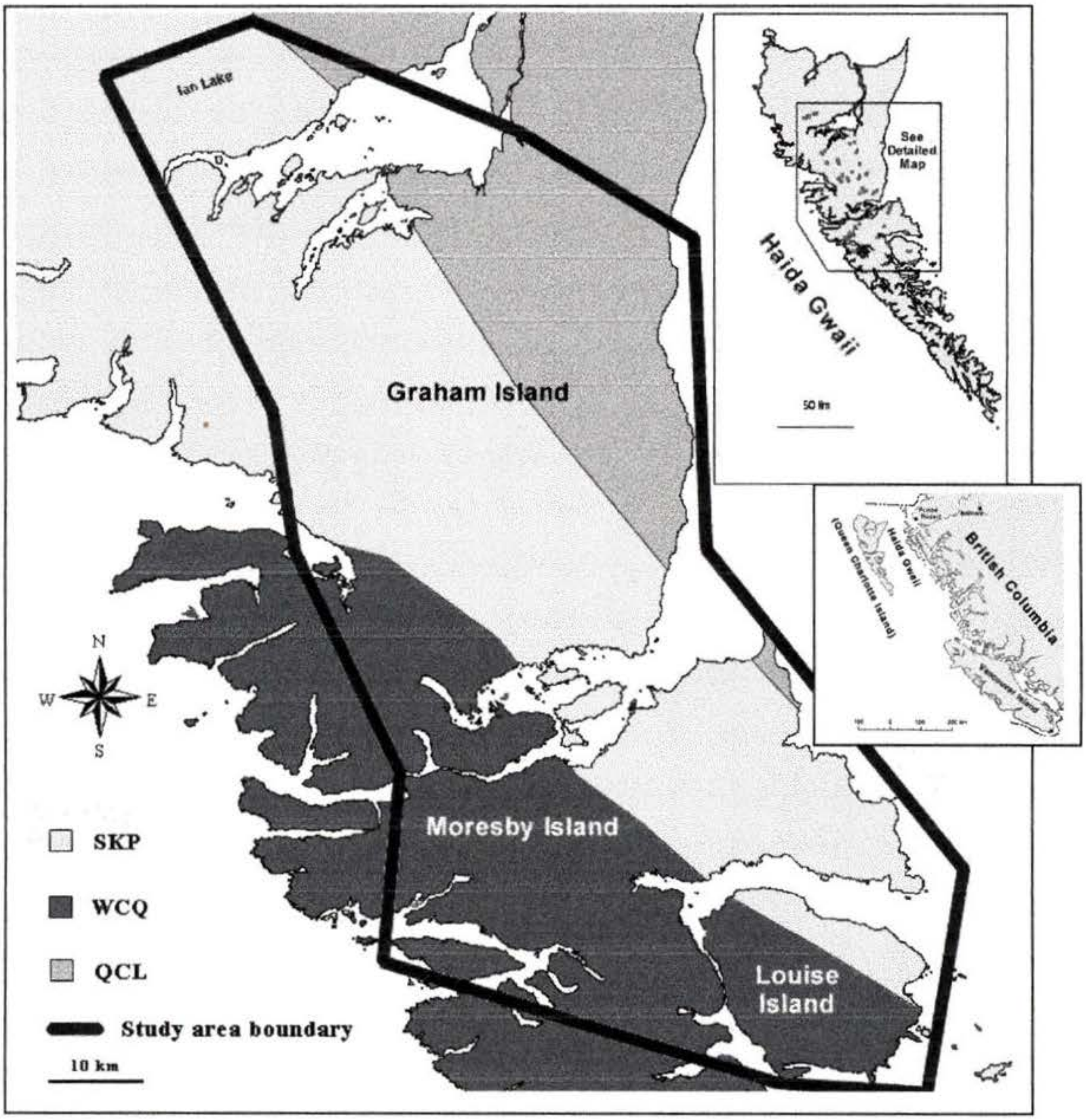
The Haida Gwaii archipelago is located off the mainland coast of British Columbia (53° 15' N, 132 ° 00' W), with its closest point about 50 km from the mainland. Haida Gwaii is comprised of approximately 150 islands that cover 9360 km^2 (Pojar et al. 1980). The island group is almost 300 km long, and Graham and Moresby Islands account for more than 90% of the land mass (Figure 1). Precipitation averages 1281 mm/yr on Haida Gwaii with the largest amounts on the west coast; amounts vary greatly throughout the islands. The average temperatures range from 0 - 17.6 C, depending on season (Hartman et al. 1997).

Haida Gwaii is inhabited by 19 terrestrial mammal species and of these, 12 are indigenous (including 4 bat species, *Vespertilionidae*; (Cowan 1984)). Over 50% of the indigenous species represent endemic subspecies (Foster 1984), and one of these, the Caribou (*Rangifer tarandus dawsoni*) is recently extinct (COSEWIC 2000). Eight terrestrial mammals were introduced to the islands, including Sitka Black-tailed Deer (Cowan 1984), and Red Deer (*Cervus elaphus*) were poached to extinction (Cowan 1984; Foster 1984). Unofficially, the Sitka Black-tailed Deer was introduced to Haida Gwaii in the late 19th century, but the first official introduction occurred between 1911 and 1913 (Pojar et al. 1980; Cowan 1984). Compared with other areas in the Sitka Black-tailed Deer's range, the situation is unique on Haida Gwaii because of the maritime climate and the lack of typical predators such as Wolves (*Canis lupus*) and Cougars (*Felis concolor*).

The Black Bear (*Ursus americanus carlottae*) is the only natural predator, and it particularly preys on fawns (Pojar et al. 1980). Nobody has studied what regulates the population on Haida Gwaii, but it is widely believed that a major factor is limited forage. This is partly supported by anecdotal evidence, which suggests that severe winters cause a decline in the population (G. Martin, pers. com. 2000). In areas close to settlements, hunting pressure is also thought to help regulate the current deer population. The Sitka Black-tailed Deer is the only widespread large herbivore found on Haida Gwaii. A small herd (<100) of introduced Elk (*Cervus elaphus*), is present in the Tlell River watershed. Unlike the rest of coastal western North America, where Black-tailed Deer have been well studied, little is known about ecology of deer on Haida Gwaii.

My study area covered approximately 36 % (3350 km^2) of the islands (Figure 1). The primary study area was the Skidegate Plateau (Figure 1) because of its adequate availability of old-growth forest stands with sufficient variation in topography, and good access. Also, the Black-tailed Deer population was thought to occur in different densities in this area. The study area's north boundary was the forest stands immediately north of Ian Lake on Graham Island, and the south boundary was the south end of Louise Island.

Figure 1: Study area indicating Skidegate Plateau (SKP), West Coast Queen Charlotte Island (WCQ) and Queen Charlotte Lowlands (QCL) ecosection zones on Haida Gwaii.



2.2. Ecosections on Haida Gwaii.

The biota in British Columbia has been classified into ecosections by the Ministry of Environment, and on Haida Gwaii, the landscapes can be divided into three ecosections (Demarchi 1995) (Figure 1). The West Coast Queen Charlotte Island Ecosection is mountainous, reaching a maximum elevation of 1148 m. Western Hemlock (*Tsuga heterophylla*) and Western Redcedar dominate the forest at lower elevations and Mountain Hemlock (*Tsuga mertensiana*) and Yellow Cedar (*Chamaecyparis nootkatensis*) dominate the forest at higher elevations. The Skidegate Plateau consists of mountains ≤ 500 m, with forests dominated by Western Hemlock, Sitka Spruce (*Picea sitchensis*), Western Redcedar and Yellow Cedar. The Queen Charlotte Lowland Ecosection is found in the northeastern part of Haida Gwaii, and is an area of low relief, slow drainage, and extensive muskegs and wetlands. The main tree species here are the Shore Pine (*Pinus contorta*), Western Redcedar and Mountain Hemlock.

As noted above, the study area was located on mainly on the Skidegate Plateau, with a few sites on the Queens Charlotte Lowlands and a few on the West Coast Queen Charlotte Ecosection.

2.3. Biogeoclimatic classification on Haida Gwaii.

British Columbia has also been classified according to the biogeoclimatic classification system (Pojar et al. 1987; Meidinger and Pojar 1991). This system is hierarchical, starting with classifying landscapes into biogeoclimatic zones and ending up classifying forests, stands and patches into subzones, variants, and site series. Three biogeoclimatic zones occur on Haida Gwaii, but the non-forested Alpine Tundra zone and the Mountain

Hemlock zone were not included in this study, because they are at elevations > 500 m. The Coastal Western Hemlock zone is the rainiest biogeoclimatic zone in British Columbia, and is divided into subzones by continentality and precipitation (Meidinger and Pojar 1991). Western Hemlock dominates the forest, but Western Redcedar and Sitka Spruce are also common.

The study area was situated in the Coastal Western Hemlock biogeoclimatic zone, specifically in the Submontane Wet Hypermaritime (CWHwh1) (0-350 m), the Montane Very Wet Hypermaritime (CWHvh) and the Wet Hypermaritime (CWHwh) (250-600 m) variants. The plant species characteristic of these variants differ slightly, but they all included *Vaccinium parvifolium, V. ovalifolium, V. alaskaense, Menziesia ferruginea, Gaultheria shallon, Blechnum spicant, Coptis asplenifolia* (Fern-leaved Goldthread), *Picea sitchensis* and *Scapania bolanderi* (Yellow-ladle Liverwort).

3. Methods

3.1. Estimating plant biomass and utilized biomass.

Biomass can be estimated in several ways. Sampling is either destructive (Yarie and Mead 1989) or non-destructive. Destructive methods include clipping and weighing all the plants in a certain area or plot. This method is accurate but time consuming. The non-destructive method utilizes the regression approach, and has been widely used to estimate the biomass of ungulate browse and other woody plants (Telfer 1969; Lyon 1970; Peek et al. 1971; Jensen and Scotter 1977; Harestad 1979; Potvin and Hout 1983; Alaback 1986; Alaback and Sidle 1986; Schwab and Pitt 1987; Yarie and Mead 1989; Smith and Clark 1990; Marshall et al. 1990; Messier and Kimmins 1991; Smith and McLeod 1992; MacCracken and Ballenberghe 1993; Araujo et al. 1996; Chai 1997; Dyck and Shay 1999). These methods trade-off accuracy for ease of measurement in the field and subsequent processing.

Several authors have attempted to find the best biomass estimator by conducting regression analyses with variables such as basal diameter, height, form and stature of plants (Brown 1976; Alaback 1986; MacCracken and Ballenberghe 1993). In each case, the single most important variable was the basal diameter (Whittaker and Woodwell 1968; Brown 1976; Stanke and State 1983; Nyberg 1985; Alaback 1986; MacCracken and Ballenberghe 1993). The best estimates were from equations that were habitat specific, but reasonably accurate estimates produced from models derived from sampling in a multitude of habitats (Peek et al. 1971; Ruyle et al. 1983; Roundy et al. 1989). Due to the variation in growth on different sites, Alaback (1986) found that it was important to develop the estimation functions from samples that represent all the sites where estimates are required. Because the data used to generate these regressions are not normally distributed, the general approach has been to transform the data logarithmically (Brown 1976; Jensen and Scotter 1977), correct for retransforming biases (Baskerville 1972; Sprugle 1983), and test for heteroscedasticity (Glejser 1969).

Regarding the use of plant biomass by herbivores, two fundamentally different ways have been used to estimate consumption (Rutherford 1979). One approach studies the animal and records parameters such as browsing times, fecal or rumen content (Wilms et al. 1976) and number of mouthsful per time unit (Guy 1976). The other approach studies the plant and records parameters such as amount of browse present and amount removed (Telfer 1969; Lyon 1970; Jensen and Scotter 1977; Marshall et al. 1990). I used the plant-based approach utilizing regression models because it allows me to estimate understory biomass during a single visit to a forest stand, the method was logistically feasible, it had less of an impact on vegetation, and it provided reliable estimates.

Browse is most commonly regarded as the current annual growth (Blair 1971), but when hungry, deer will consume more than this amount. Under these circumstances, a more realistic definition of browse considers the biomass beyond some twig diameter determined by actual point of browsing (Peek et al. 1971). Available browse is a subset of total biomass and it represents the portion of the total biomass that is available as food. It is generally restricted by some height aboveground and by some maximum twig diameter (Blair 1971). Snow load on shrub branches can weigh them down making browse temporarily available (Harestad 1979; McNay et al. 1988).

Alaback (1986) used vigorously growing plants to develop regressions to estimate biomass, but I collected specimens with varying vigour on 19 sites because I wanted the equations to apply to the growth forms, vigour and habitats for which estimates were needed. I used a stratified random approach to ensure that the appropriate range of stem diameters was sampled. I developed functions to estimate aboveground ($n = 142$), pre-browsed ($n = 309$) and utilized ($n = 352$) biomass for *Vaccinium* spp. (*Vaccinium parvifolium*, *V. ovalifolium / alaskaense*), *Menziesia ferruginea*, *Thuja plicata*, and *Blechnum spicant* (Table 1).

During sampling (March – April, 2000), the stems and twigs were identified to species, measured *in situ* using an electronic calliper with a precision of 0.01 mm, clipped, placed in labelled plastic bags and brought back to the laboratory. In the laboratory, samples were transferred into numbered paper bags, and later dried in a mechanical convection oven (Precision STM80 or 130DM) at 70 C for 24 hours (Alaback 1986). The weights were determined with a precision of 0.001 g on an electronic scale (Ohaus GT480). This electronic scale was outfitted with a cover over the sample tray to prevent air currents from interfering with measurements. Because the samples could not always fit under the cover, measurements were taken without closing the cover. A paired t-test of thirty samples showed no difference between measurements made covered and uncovered (t =

0.9948, p = 0.33). The same equipment and procedure were used to determine dry-weight of all other plant samples discussed below.

Table 1: Functions for estimating aboveground, available and utilized biomass for selected forage species in old-growth forests on Haida Gwaii.

Species	r^2 adj.	Equation [a,b]	Diameter range (mm)	*n*[c]	No. sites
Aboveground biomass					
Blechnum spicant [d]	0.90	$0.0972D^{2.9122}$	0.28-2.63	133	9
Vaccinium spp.[e]	0.94	$0.0739D^{2.6308}$	1.10-20.50	87	15
Menziesia ferruginea	0.98	$0.0309D^{2.902}$	0.86-30.96	27	9
Thuja plicata	0.90	$0.1438D^{2.3215}$	1.48-15.11	11	3
Available Biomass					
Vaccinium spp. [d]	0.66	$0.0759d^{2.5963}$	0.45-3.14	257	15
Utilized biomass					
Vaccinium spp. [d]	0.64	$0.0691x^{2.3871}$	0.38-3.07	323	15
Menziesia ferruginea	0.94	$0.0304x^{3.1563}$	0.71-2.61	7	29

[a] All functions were significant ($p<.001$).

[b] D = the basal stem diameter (mm), d = basal twig diameter (mm), x = point-of-browse (mm).

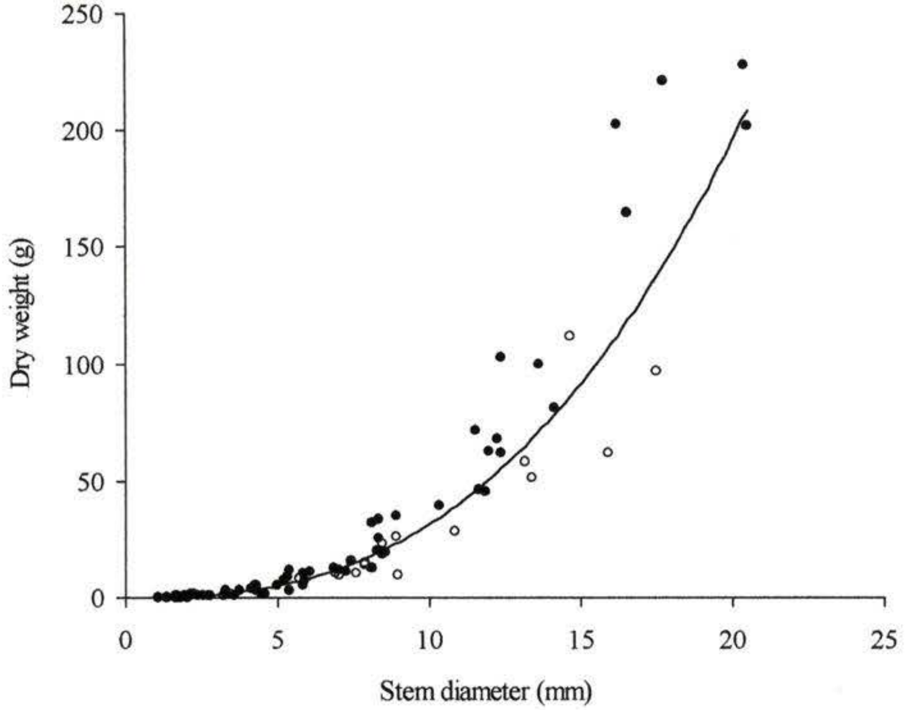
[c] *n* indicates the sample size.

[d] Aboveground and available biomass models are the same.

[e] *Vaccinium* spp. = *V. parvifolium* and *V. ovalifolium / alaskaense* combined.

I used the power functions to estimate amount of aboveground biomass because they had good fits (Figure 2, Table 1), and because they always yielded positive values for all diameter measurements. I compared estimates from my power equations to traditional log-log transformation procedures and found that they were similar (ANOVA, $F_{3,9352}$ = 0.7273, p = 0.5355).

Figure 2: An example of the relationship between basal stem diameter and dry-weight, using combined data from *Vaccinium parvifolium* (solid circle, n= 66) and *Vaccinium ovalifolium / alaskaense* (open circle, n=21[a]) to generate the plot and power function [b].

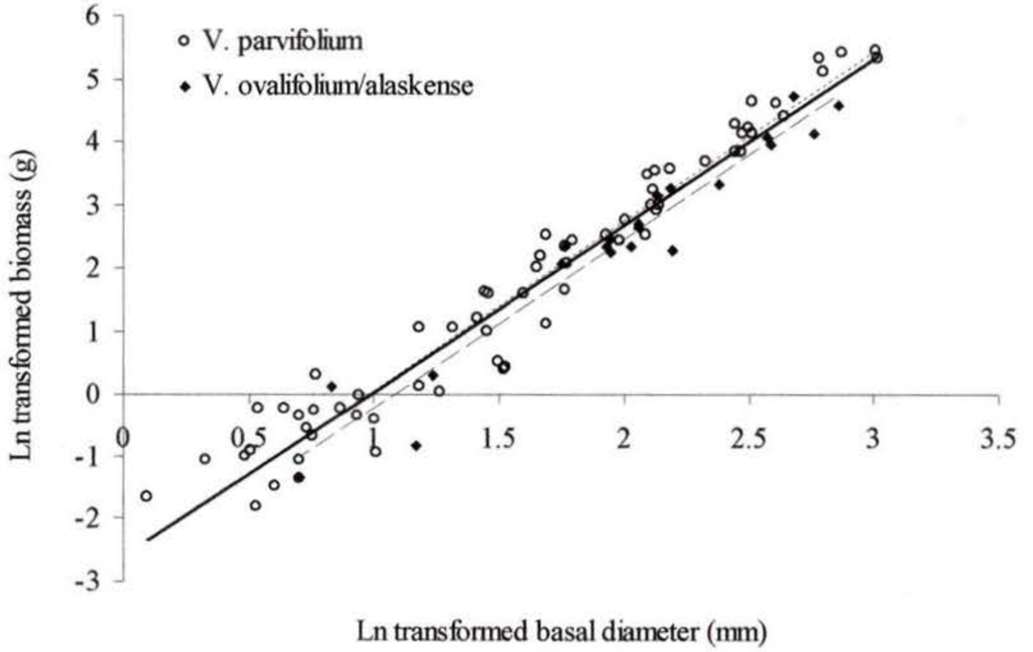


[a] Some of the open circles are not visible because they fell in the 1.1 –5.8 mm range.
[b] Dry weight = 0.0739 x Diameter$^{2.6308}$, $r^2 = 0.95$.

Vaccinium can be hard to identify to species during the winter, so I tried to develop estimation models that combined *Vaccinium parvifolium, V. ovalifolium* and *V. alaskaense.* Also I examined the possibility of developing only one function to estimate pre-browsed biomass and utilized biomass. I tested the relevant regression models for similarities in slope and y-intercept (Zar 1984). If both slope and y-intercept were found to be statistically similar, I used a model based on combined data. These analyses showed that aboveground biomass models for *Vaccinium parvifolium* and *Vaccinium ovalifolium*

/ *alaskaense* (Figure 3) could be combined ($t_{\text{slope}} = -0.03968$, $DF_{\text{slope}} = 83$, $p_{\text{slope}} > 0.5$, $t_{\text{y-intercept}} = -0.6883$, $DF_{\text{y-intercept}} = 84$, $p_{\text{y-intercept}} > 0.2$). The same was the case for pre-browsed ($t_{\text{slope}} = 1.491$, $DF_{\text{slope}} = 253$, $p_{\text{slope}} > 0.1$, $t_{\text{y-intercept}} = 1.179$, $DF_{\text{y-intercept}} = 254$, $p_{\text{y-intercept}} > 0.2$) and utilized biomass ($t_{\text{slope}} = -1.033$, $DF_{\text{slope}} = 321$, $p_{\text{slope}} > 0.2$, $t_{\text{y-intercept}} = 0.431$, $DF_{\text{y-intercept}} = 322$, $p_{\text{y-intercept}} > 0.5$). It was not possible to combine pre-browsed and utilized biomass because the y-intercept in the two linearized equations were statistically different ($t_{\text{slope}} = -2.392$, $DF_{\text{slope}} = 492$, $p_{\text{slope}} < 0.02$, $t_{\text{y-intercept}} = 5.64$, $DF_{\text{slope}} = 492$, $p < 0.05$).

Figure 3: Comparison of natural logarithmic transformed models to estimate aboveground biomass for *Vaccinium parvifolium* (small dashes), *V. ovalifolium / alaskaense* (large dashes) and combined (solid). (Samples were collected on Haida Gwaii, in March – April, 2000).



Models have also been developed for herbaceous plants. Several authors have developed models to estimate *Blechnum spicant* biomass using parameters such as frond length (Alaback 1986), length and width of frond (Smith and McLeod 1992) and percent cover (Yarie and Mead 1989). The fit (r^2) of these models varied between 0.78 and 0.97. Because deer often eat the tip of the frond, length of frond was not a feasible measurement. I developed a regression using the stem diameter below the first set of leaves as an independent variable to estimate biomass of *Blechnum spicant*

Because growth of shrubs varies with habitat (Peek et al. 1971; Nyberg 1985; Alaback 1986; MacCracken and Ballenberghe 1993), I tested the influence of different site series, elevations and aspects on models for estimating available biomass. I chose data from pre-browsed biomass of *Vaccinium parvifolium* to ensure reasonable sample sizes in each category. When testing the models for the two different site series (SM, n = 131; RS, n = 47), I did not find any difference in slope ($t_{\text{slope}} = -1.2136$, $DF_{\text{slope}} = 174$, $p_{\text{slope}} > 0.1$) and y-intercept ($t_{\text{y-intercept}} = 0.2328$, $DF_{\text{y-intercept}} = 175$, $p_{\text{y-intercept}} > 0.5$). The resulting equations from data split by north-south aspect or elevation (above and below 100 m) were identical, and no difference was found between these either ($t_{\text{slope}} = -0.4211$, $DF_{\text{slope}} = 174$, $p_{\text{slope}} > 0.5$; and $t_{\text{y-intercept}} = 0.1049$, $DF_{\text{y-intercept}} = 175$, $p_{\text{y-intercept}} > 0.2$). Based on these analyses, I did not need separate equations for different site series, aspect or elevation.

3.2. Estimating relative deer density.

There is no simple way to determine deer density, but methods such as spotlight counts at night, and pellet group counts have been used to gain information about relative abundance (Resource Inventory Committee 1998). It is possible to conduct total counts in small areas; and in areas with high deer density, transect counts can be used to estimate numbers (Daufresne and Martin 1997). The spotlight count method requires road access, suitable weather, and appropriately aged clear cuts, which makes this method inappropriate in old-growth forest stands. I selected the pellet group method because pellet group counts during the spring on winter ranges provide an opportunity to investigate use by deer during the previous winter. As well, this technique was the most feasible, given constraints of time and money, and it was well suited for sampling many areas in a short time period.

Pellet group counts were first used to monitor the relative abundance of deer in the late 1930's (Bennet et al. 1940), and were later used to estimate big game trends, numbers and distribution (Neff 1968; Rowland et al. 1984; Stordeur 1984). Interpretation of pellet group counts must consider inherent problems such as counting biases, pellet deterioration, defecation rates and animal habits (Neff 1968). For example, defecation rates were found to be higher for animals in transit and resting than for grazing animals (Collins and Urness 1981). On Vancouver Island, persistence of pellets varied depending on habitat and moisture: fecal pellets on moist sites deteriorated approximately twice as fast as those on dry sites (Harestad and Bunnell 1987).

3.3. Site selection.

I selected sampling sites in two ways. Initially, I targeted old-growth forest stands greater than 20 ha with similar site series and sampling sites more than 300 m apart. I wanted to stay within the same site series to control for variables such as nutrient and moisture regimes in the stand. I chose the most common site series (sm, dominated by Western Hemlock, Sitka Spruce, and Lanky moss (*Rhytidiadelphus loreus*)) in the following biogeoclimatic variants CWHvh1, and CWHwh1 and 2 (Green and Klinka 1994). I realized relatively early in the field season that old-growth forests in this site type were not as common as initial investigations had led me to believe because many had been logged. Subsequently, I also sampled in other biogeoclimatic variants with an emphasis on distributing sampling sites geographically within the study area. These sites were selected on maps (see below) and field crews were then sent to the sites. I distributed sampling effort across a wide range of aspects and slopes below 450m elevation. Most sampling took place in areas with road access, but some sampling took place in remote areas with no road access.

Local forestry companies provided forestry and terrestrial ecosystem maps (1:50 000) for site selection, and the Ministry of Environment, Lands and Parks provided TRIM maps (1:20,000).

3.4. Sampling design.

3.4.1. Sampling design terminology.

Because there are different levels of sampling, I have standardized the use of the sampling terminology and used it throughout this document (Table 2).

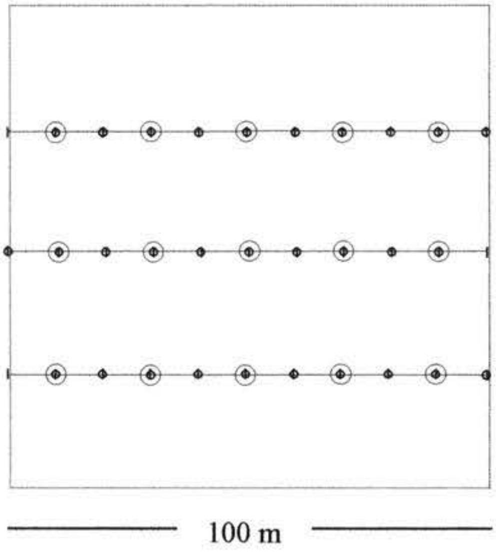
Table 2: Sampling design terminology.

Term	Description and purpose
Sampling site	*Description*: The 1 ha area chosen to be sampled. *Purpose*: The basic sampling unit, used in statistical comparisons.
Pellet group transect	*Description*: Straight line transects, 100 m long and 1.66 m wide, and divided into 10 m subplots. *Purpose*: Measuring pellet group density.
Herb plot	*Description*: Circular plots, each with an area of 1 m^2. *Purpose*: Measuring biomass of selected ferns, herbs, shrubs and tree seedlings.
Shrub plot	*Description*: Circular plots, each with an area of 4 m^2. *Purpose*: Measuring biomass of selected shrubs and young trees.

3.4.2. General design.

Sampling layout was designed to estimate the relative deer density and the amounts of aboveground, available and utilized biomass. The sampling sites were one hectare (ha) square areas (Figure 4). I sampled pellet groups by counting them along transects, and sampled herbs (including ferns) and shrubs by centering circular plots along these transects (Figure 4).

Figure 4: Sampling design. Pellet group counts transects (solid line), shrub plots (large circles), and herbaceous plots (small circles).



The three parallel pellet group count transects were 30 m apart (Figure 4) and parallel to contours. The width was 1.66 m, which resulted in sampling 5 % of the site. The pellet group counts were recorded every 10 m. Each section was measured with a drag chain that also marked the center of the transect. The observer carried a measuring stick to verify whether pellet groups were inside or outside the transect. A pellet group was counted if the center of the group was within the transect. A pellet group consisted of 10 or more individual pellets (Resource Inventory Committee 1998), and adjacent pellet groups of similar age had to be clearly separated to be recorded as different groups. To minimize counter biases (Neff 1968), each crew had a trained pellet group counter who did all counts. I attempted to divide pellet groups into three age categories: recent, medium-aged, and old. A recent group had to be shiny black or green, have a smooth surface, and be situated on top of forest floor debris and vegetation. The surfaces of a medium-aged pellet had lost its shininess and had gained a rougher surface, but were still on top of forest floor plants and debris. The individual pellets in an old pellet group had a rough granular surface or pellets had lost their shape, and appeared to have "melted" into the forest floor.

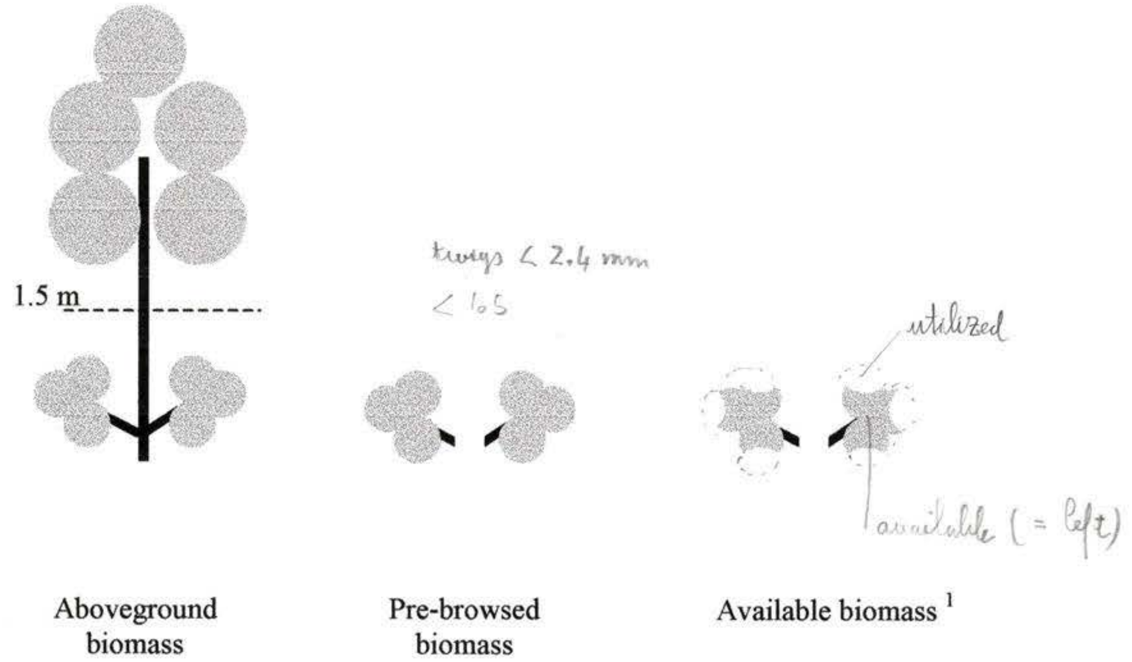
I converted pellet group estimates to equivalent deer densities, so that I could compare my results with deer densities reported elsewhere. To make this conversion I assumed that the deterioration period was 240 days (Schoen and Kirchhoff 1983) and defecation rate was 12.6 PG/day per deer (Kirchhoff 1990). These values come from studies in old-growth forest in southeast Alaska, and I assumed similar values for Haida Gwaii. For example, to convert an estimate of 300 PG/ha to deer/km^2, I divided the PG estimate by 240 days multiplied and by 12.6 PG/day to get 0.099 deer/ha. The area was then converted to deer/km^2 by multiplying by 100 resulting in 10 deer/km^2.

Alaback (1986) investigated the effect of plot size on biomass estimates in old-growth forests of coastal southeast Alaska, and he found that precision of shrub biomass estimates did not improve much beyond 8 – 10 plots. He also determined that the most cost efficient plots had an area of 4 m^2 (Alaback 1986). To estimate mossy and herbaceous biomass, Alaback (1986) found that 30 - 40 plots each with an area of 1 m^2 were efficient and resulted in reasonable precision (he did not specify this precision level). Because of the proximity and similarities between the forests of southeast Alaska and the forests of Haida Gwaii, I adopted Alaback's guidelines.

To ensure clear definition of the different types of biomass calculated, I have described each below (Figure 5). The aboveground biomass includes all stems, twigs and foliage of the understory species that I studied. In order to estimate currently available biomass, I first estimated the pre-browsed biomass that included only the part of twigs smaller than 2.4 mm in diameter and foliage below 1.5 m height aboveground. Then I estimated the utilized biomass, which consisted of the cumulative biomass removed by deer. Finally, to estimate the currently available biomass, I subtracted the utilized biomass from the pre-browsed biomass. Because each of these estimates used slightly different functions, some estimates of utilized biomass (especially at small diameters) were slightly larger than the available biomass resulting in negative available biomass. In these cases, I changed negative values to zero.

I estimated the biomass of *Blechnum spicant* (Deer Fern) and *Cornus canadensis* (Bunchberry). To estimate biomass of *Blechnum spicant,* I counted number of stems, and then measured four average *Blechnum spicant* stem diameters below the first set of leaves. Pre-browsed biomass of *Blechnum spicant* was determined by applying the regression equation developed for the study area (Table 1). Biomass was estimated by multiplying the average biomass for the measured plants by the number of stems counted. Using the pre-browsed biomass estimates from the plots, I estimated the biomass in the entire site. To estimate utilized biomass of these species, I estimated the percentage of browsing on the fronds. I multiplied the pre-browsed biomass by the percent utilized to determine the available biomass. For *Cornus canadensis* I counted the number of stems in each plot. By converting the stem count of *Cornus canadensis* to percent cover (see below) I was able to estimate biomass using the equation developed by Alaback (1986). I identified and estimated the percent ground cover of other herbs and fern species I encountered, but did not attempt to estimate biomass for these.

Figure 5: Diagram illustrating the different components of biomass estimated.



[1] Utilized biomass is here shown as the missing parts of the pre-browsed biomass

For species, such as *Thuja plicata* seedlings (plants less than 10 cm high) and *Cornus canadensis* plants, where the entire plant can be consumed in a single bite, it is almost very time consuming and almost impossible to estimate utilized biomass. Attempts to assess this issue failed, so utilized biomass may be underestimated.

The shrub plots covered 4 m^2, and were centered every 20 meters along the pellet group transects (Figure 4). I determined the edge of the plots by using a measuring tape. I counted the number of stems emerging from the ground for each species and measured the basal stem diameter of a sub-sample. I divided the total number of stems (x) in a plot and divided them with a number (y) such that I got an integer (z) between 5 and 10 (Kirchhoff 1994). Every z stem was sampled, starting with the stem closest to the center and counting in a clockwise direction. I estimated the aboveground biomass in each shrub plot, using regression equations with basal stem diameter as the independent variable (Table 1). I found the average of the plant biomass of the sampled stems, and multiplied this average by the number of stems in a plot. Using the result from the plots, I estimated the biomass of the individual species for each sample site.

To estimate pre-browsed biomass, I counted all the twigs smaller than 2.4 mm in diameter below the height of 1.5 m, on those plants selected for measuring basal stem diameter, and measured 3 average twig diameters. I estimated the biomass of these measured twigs by applying a regression function, averaged the biomass and multiplied this mean by the number of stems found in each plot. This allowed me to calculated the total pre-browsed biomass for each plant species and site.

Utilized biomass was defined as the cumulative amount removed from the time the plant was first browsed. I estimated utilized biomass for each species and site by counting points-of-browse on the shrubs selected for basal stem diameter measurement. Three mean points-of-browse were measured. Using regression functions developed for the study, I estimated utilized biomass for the measured twigs. Then I calculated an average utilized biomass per twig and multiplied this with the number of points-of-browse counted. Finally, I calculated the utilized biomass of the different shrub species and the entire sampling site.

For *Rubus spectabilis*, I used an equation developed by Alaback (1986). Small stem diameters resulted in negative biomass, which I changed to zero. I did not include 3 stem measurements that fell outside the lower range (2-25 mm) of Alaback's equations. Because these stems had very low biomass, their omission had a negligible effect on the estimated *Rubus spectabilis* biomass. I calculated total biomass by adding together annual growth ($-3.7189 + 2.8406\ln x$), woody stems ($-2.5536 + 2.5467\ln x$) and foliage ($-2.0270 + 1.8840\ln x$) biomass estimates (Alaback 1986).

I surveyed *Gaultheria shallon* (Salal) differently from other shrubs because it was thought to be too time consuming to estimate by a regression model. Ground cover was estimated in each of the pellet group transects (166 m^2) for all sites surveyed. Using the total biomass function (Biomass (kg/ha) = 11.534 x % ground cover) developed by Yarie and Mead (1989), I was able to estimate total biomass of the top ten cm of the plants for all transects. I used this estimate as an index for salal biomass. Starting at plot number 50, I also estimated percent ground cover using the same equations as mention above and estimated percent utilization of Salal in each shrub plot. I roughly estimated the crown closure above each shrub plot, by looking through a circle made by the index finger and thumb placed on the eyebrow.

Aspects of the sampling sites were determined with a compass (Suunto MC-1), and slopes were derived using the built-in clinometers in these compasses. I used UTM (Universal Transverse Mercator) coordinates to locate the sampling sites, and the UTM coordinates were found on TRIM maps (1:20 000). Stand volume was provided by D. Trim, Weyerhaeuser, using digital forest cover data.

3.4.3. Combining species and biomass.

To eliminate identification mistakes of *Vaccinium* species encountered on the sampling sites, I used an estimation function that included all three species. Estimates derived using these combined functions produce slightly lower estimates than species-specific functions. Because I did not develop species-specific functions to estimate utilized biomass of *Vaccinium ovalifolium* and *Vaccinium alaskaense* biomass estimates, all *Vaccinium* spp. estimates are based on combined data.

The estimates of aboveground, utilized and available biomass did not compensate for the change in growth form and shape that browsing of the plants caused. These estimates were a "snap-shot" of the amounts present during the survey period, and provided no information about amounts of biomass the sites could have produced without browsing. Because biomass estimation regressions were developed from plants that did not experience browsing, this difference in growth form and shape most likely created errors when estimating the present biomass. The short period of field work (March – April) prevented the coming of spring from significantly influencing the biomass estimates. I also moved surveys around in the study area to reduce the effect of the progression of spring.

I did not develop a model to estimate biomass of *Cornus canadensis*. Instead, I used a model developed by Alaback (1986) that allowed me to estimate the biomass (g) per m^2 from plant cover. First, I converted the stem counts to a percent ground cover, assuming that each individual plant covered $0.008 m^2$. I used different equations to estimate biomass, depending on the percent cover. When cover measurements fell into the 1-3 % range, I used $0.218 + 0.0440 x^2$ ($r^2=0.52$, MSE=0.024). When cover measurements fell into the 3-60 % range, I used $-0.6950 + 0.5360x$ ($r^2=0.95$, MSE=0.032) (Alaback 1986).

3.4.4. Spatial analysis.

To explore the data spatially, I created three dimensional bar plots. These 3D plots were created using the Universal Transverse Mercator (UTM) coordinates with the northing on the x-axis, the easting on the z-axis and the other variables on the y-axis. Because the locations fell in two UTM zones (8 and 9), I transformed all sampling site coordinates in zone 9 to zone 8 coordinates, using topographical maps that had both zones outlined. Because the bars hid information, I plotted the data so both sides of the plot could be seen, by rotating the x-axis 180 degrees.

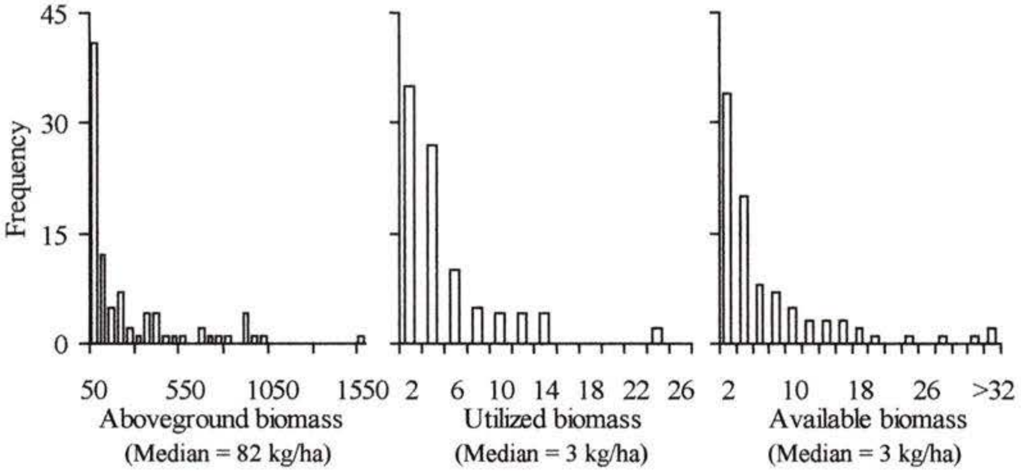
3.5. Statistical analyses.

The median was often supplied together with the average measurement, because the median is a better measure of central tendency than the mean when data are skewed and contain outliers (Zar 1984). The median expresses different information than the mean because it does not take the values of measurements into account, but extreme data points affect the median less than the mean (Zar 1984).

Correlation analysis assumes that the variables are derived from a bivariate normal distribution. This assumption is not important when there is only a slight correlation in the population, but it is important if the populations are substantially correlated (Zar 1984). I used the Box-Cox procedure to establish the best transformation for data with non-normal distribution (Krebs 1999), or trial and error when the Box-Cox procedure produce lambdas equal to zero. If no satisfactory transformation could be determined, non-parametric tests were employed.

The pellet group estimates, and the aboveground, available, utilized biomass data were all positively skewed, (Figure 6, Figure 7) and the Box-Cox lambda was zero in all four cases. A square root transformation visually normalized the pellet group density estimates and available biomass data sets, but statistically the transformed data sets were not normally distributed (pellet group densities, Shapiro-Wilk's $W = 0.9592$, $p = 0.0126$; available biomass, Shapiro-Wilk's $W = 0.8466$, $p = 0.0001$). A natural log plus one transformation visually normalized the aboveground and utilized biomass estimate data, but statistically the transformed data sets were not normally distributed (aboveground biomass: Shapiro-Wilk's W = 0.9386, p<0.0001; utilized biomass, Shapiro-Wilk's W = 0.9525, p = 0.0077). Because of the non-normal distributions, only non-parametric tests were used when these data sets were involved in analysis.

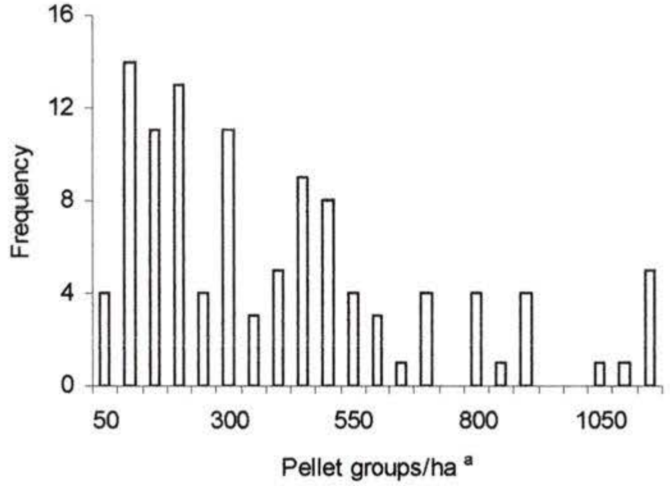
Figure 6: Frequency distribution of aboveground, utilized and available biomass estimates (kg/ha) in sampling sites on Haida Gwaii (n = 91).



To conduct statistical analyses, I used SPSS (version 7.5 for Windows), S-Plus 4.5 (student edition) or JMPin (version 3). When conducting Mann-Whitney tests, I followed Zar's (1984) method of calculating normal approximation statistics when sample size exceeded 20. These normal approximation statistics are reliable for α =0.05 (Zar 1984). I used an α level of 0.05 unless otherwise stated.

The basic ecological concept of limiting factors and spatial structure are in conflict with conventional correlation analysis (Thomson et al. 1996). In bivariate scatter-plots, data often show a factor-ceiling distribution with widely varied data-points below an upper limit. This variation is presumably caused by factors not measured. From methods developed in economy, Cade et al. (1999) devised an objective statistical procedure to determine these biological limits. This regression quantile procedure had no assumption about error distribution, so transformation was not necessary. I used regression quantiles to estimate these limits using least absolute deviation (LAD) regression. The LAD regression derives the median function whereas the ordinary least squares regression derives the average function. This makes the LAD regression less influenced by outliers and it divides the data into two portions with the same number of data points above and below the regression line (Cade et al. 1999). The goal of using the regression quantile is to derive lines with a certain percentage of the data below them that depict trends at the limits. This method is best used when one variable is clearly the independent variable or if it is biologically reasonable to treat one as independent (Cade et al 1999). I treated pellet group estimates as the independent and biomass estimates as dependent variables. It is important to keep in mind that the upper regression quantile may not apply to all situations, but should provide an approximation for the data set. I used a rank-score test to generate an asymptotic p-value approximation with a Chi-square test (Cade and Richards 2000). Regression quantile calculations with associated p-value were done with Blossom, Version W2001.02b, developed by Midcontinent Ecological Science Center, U.S. Geological Survey (Cade and Richards 2000).

Figure 7: Frequency distribution of pellet groups density estimates in sampling sites in old-growth forests on Haida Gwaii.



[a] Each category is 50 wide and the number on the x-axis indicate the highest number.

4. Results.

The fieldwork took place in March and April 2000, on Graham, Moresby and Louise Islands. I surveyed 110 sampling sites with 72 sites on Graham Island, 28 sites on Moresby Island and 10 on Louise Island (Figure 8). It was impossible to conduct surveys on 1% of the plots and transects because of snow patches (in the beginning of March), rock outcrops and creeks. Data from all sites are presented in Appendix 1.

4.1. Plant diversity in early spring.

Plant species diversity in early spring in the understory of old-growth forests was limited, but I did record the 12 species noted by Pojar et al. (1980) as deer foods (Table 3). *Vaccinium parvifolium* was the most widely occurring shrub species. It grew in 98 % of the sites (Table 3), but on most sites it was rather sparse and rarely the "jungle" described by Hopkinson (1931). *Vaccinium* spp. grew in 99% of the sites. *V. ovalifolium/alaskaense* grew in 20 % of the sites, and *Gaultheria shallon* grew 34% of the sites. The most common fern species was *Blechnum spicant* that grew in 95 % of the sites. Most of these plants grew as very small rosettes that had escaped browsing by growing very close to the ground, often under forest floor debris. The most common herb species was *Coptis asplenifolia* that grew on 45 % of the sites. This species was not an important component of the deer diet in southeast Alaska (Kirchhoff and Larsen 1998). *Cornus canadensis*, which grew on 38 % of the sites, was found in 29 % of fecal pellets in Alaska (Kirchhoff and Larsen 1998). This species was not mentioned by Pojar et al. (1980) to be eaten by deer on Haida Gwaii. The ground cover estimated for herbaceous plants rarely

Figure 8: Location of sampling sites.

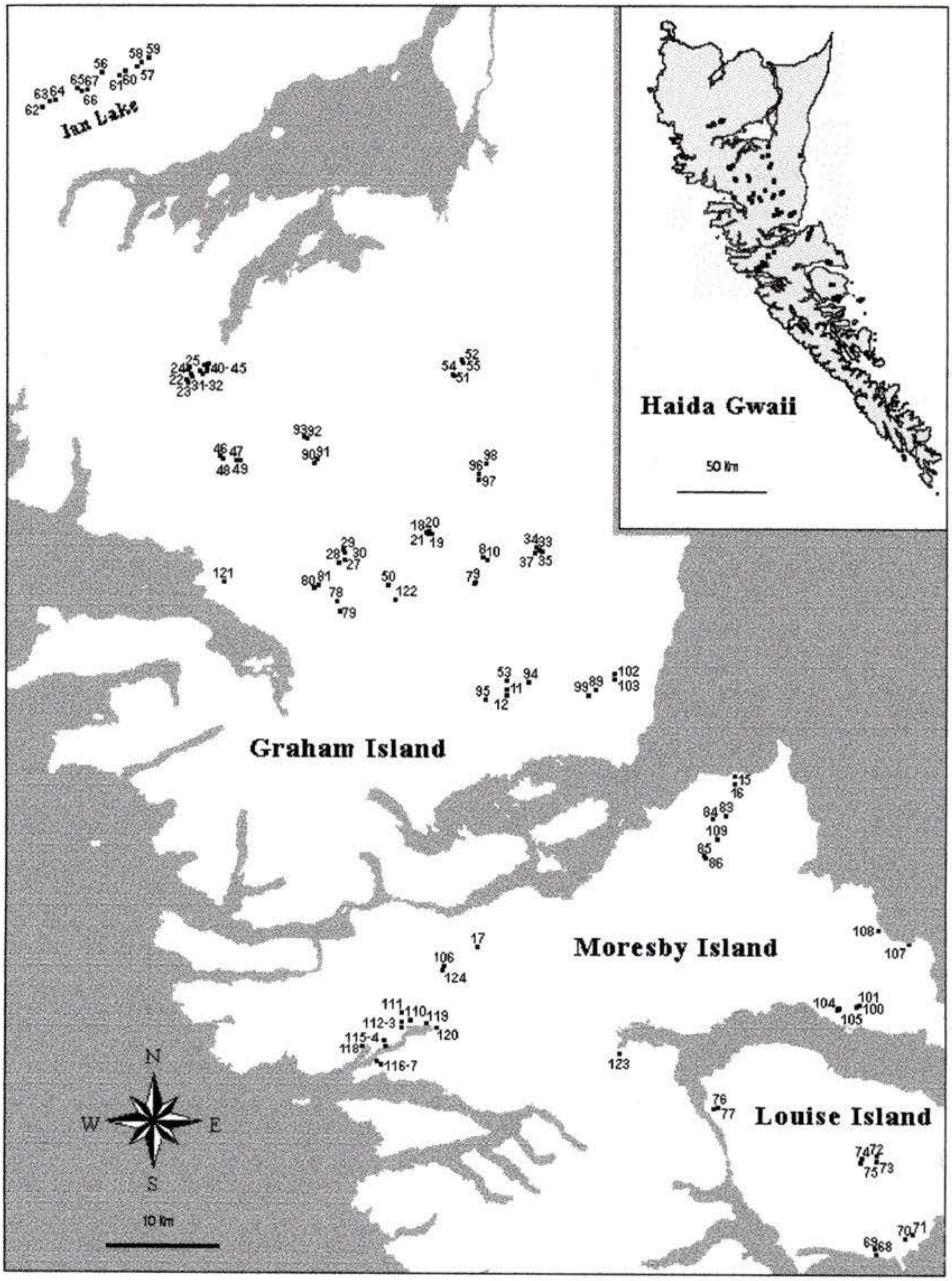


Table 3: Frequency and importance as browse of understory plant species in old-growth forests on Haida Gwaii (n=110).

Scientific name	Common name	Frequency (%)	Important[b] deer browse
	Shrubs		
Vaccinium parvifolium [a]	Red Huckleberry	98	√
Gaultheria shallon	Salal	35	√
Thuja plicata	Western Redcedar (seedling)	34	(√)
V. ovalifolium/alaskaense [a]	Oval-leaved/Alaskan Blueberry	22	√
Rubus pedatus	Five-leaved Bramble	21	
Menziesia ferruginea	False Azalea	20	√
Rubus spectabilis	Salmonberry	4	√
Thuja plicata	Western Redcedar (sapling)	1	√
	Ferns		
Blechnum spicant	Deer Fern	95	√
Dryopteris expansa	Spiny Wood Fern	25	√
Polystichum munitum	Sword Fern	12	√
Gymnocarpium dryopteris	Oak Fern	5	
Polypodium glycyrhiza	Licorice Fern	2	
Athyrium filix-femina	Lady Fern	1	√
	Herbs		
Coptis asplenifolia	Fern-leaved Goldthread	45	
Cornus canadensis	Bunchberry	38	√
Listera cordata	Heart-leaved Twayblade	38	
Moneses uniflora	Single Delight	38	
Tiarella trifoliate	Foamflower	28	
Lysichiton americanum	Skunk Cabbage	5	√
Claytonia sibirica	Siberian Miner's Lettuce	3	
Maianthemum dilatatum	False Lily-of-the-valley	3	
Galium spp.	Bedstraw	2	
Listera caurina	Northwestern Twayblade	2	
Linnaea borealis	Twinflower	1	
Veratrum virida	Indian Hellebore	1	
Stellaria spp.	Chickweed	1	

[a] When combining *Vaccinium parvifolium* and *V. ovalifolium/alaskaense* they grew in 99 % of the sites.

[b] Following Pojar et al. 1980.

exceeded 5% for any species. The ground cover estimates of *Coptis asplenifolia* fell between 5-10% ground cover in 0.4% of plots (12 plots). None of the other herb or fern species were found to have ground covers greater than 1 %. *Polystichum munitum* had between 15 and 20 fronds in three plots. *Claytonia sibirica* covered 8% in one plot. These data illustrate that the understory was sparse with limited species diversity.

4.2. Vegetation biomass.

I estimated the total aboveground, available and utilized biomass for *Vaccinium parvifolium*, *Vaccinium ovalifolium*, *Vaccinium* spp., *Menziesia ferruginea*, *Rubus spectabilis*, *Thuja plicata* and *Blechnum spicant*. I also calculated an index for *Gaultheria shallon* aboveground and utilized biomass.

4.2.1. Aboveground biomass.

The total amount of biomass (all species combined) in each sampling site varied from 0 to 2137 kg/ha, with a mean of 258 kg/ha (SD = 388) and a median was 82 kg/ha (Table 4). Relatively few sampling sites had large amounts of aboveground biomass (Figure 6). Recall that the aboveground biomass does not include *Gaultheria shallon*.

The aboveground biomass varied among individual species as well. The largest estimated amount of aboveground biomass in one site was 2137 kg/ha, and *Vaccinium parvifolium* contributed 2134 kg/ha of this amount. The maximum amount of biomass for *V. ovalifolium*/ *alaskaense* was 911 kg/ha; for *Menziesia ferruginea* 663 kg/ha; for

Blechnum spicant 76 kg/ha; and for *Cornus canadensis* 3 kg/ha. *Rubus spectabilis* was found in 4 sites, but biomass was estimated to be near zero in three of these sites. At site 124, *Rubus spectabilis* contributed 27 % of the overall biomass (Table 4). For *Rubus spectabilis* and *Thuja plicata*, the total plant height never reached above 1.5 m, so the biomasses of these two species are also included in the total available biomass.

Table 4: Summary of aboveground and available biomass (kg/ha) estimates in old-growth forest sampling sites (n=110) on Haida Gwaii, March and April, 2000.

	Aboveground					Available			
Species	*n*[a]	Avg[b]	SD[b]	Med[c]	Max[c]	Avg	SD	Med	Max
Vaccinium sp. [d]	109	242	385	75	2134	**3**[e]	**6**	**0**	**32**
Vaccinium parvifolium	108	227	396	59	2134	**4**	**7**	**1**	**45**
V. ovalifolium/alaskaense	24	19	99	0	911	-	-	-	-
Menziesia ferruginea	22	11	74	0	663	**1**	**10**	**0**	**92**
Thuja plicata (sapling)	1	-	-	0	1	-	-	0	1
Thuja plicata (seedling)	37	1	2	0	13	1	2	0	13
Rubus spectabilis	1	-	-	0	30	-	-	0	30
Cornus canadensis	42	0	1	0	3	0	1	0	3
Blechnum spicant	104	3	9	1	76	2	8	1	76
Total biomass	110	258	388	82	2137	**7**	**14**	**3**	**93**

[a] *n* = The number of sites where the plant grew.

[b] Avg = average in all sites, SD = standard deviation.

[c] Med = median, Max = maximum.

[d] *Vaccinium* sp. is *Vaccinium parvifolium* and *V. ovalifolium/alaskaense* combined.

[e] Bold indicate numbers based on 91 sampling sites, see text.

I did find a weak, but statistically significant, correlation between the aboveground biomass and available biomass and also between aboveground and utilized biomass (Table 5). Because *Vaccinium parvifolium* contributed the majority of the biomass, its aboveground biomass was, not surprisingly, strongly correlated with the total aboveground biomass (Table 5).

?

Table 5: Spearman's rank correlations between a variety of biomass estimates and other parameters.

Parameter 1	Parameter 2	r_s [a]	P [b]	*n* [c]
Aboveground biomass	*B. spicant* biomass	-0.096	0.316	110
	V. parvifolium biomass	0.901	**<0.001**	108
	Available biomass	0.493	**<0.001**	91
	Utilized biomass	0.502	**<0.001**	91
	Tree canopy closure (%)	-0.120	0.211	110
Available biomass	Utilized biomass	0.328	**0.002**	91
	Tree canopy closure (%)	-0.267	**0.010**	91
Utilized biomass	Tree canopy closure (%)	0.127	0.232	91
No. Points-of-browse / ha	Stem / ha	0.797	**<0.001**	110
Stand volume	Aboveground biomass	-0.040	0.720	81
	Available biomass	0.082	0.507	68
	Utilized biomass	-0.059	0.635	68
Slope	Aboveground biomass	0.092	0.351	106
	Available biomass	-0.099	0.358	88
	Utilized biomass	-0.037	0.730	88
G. shallon AG. T[c]	*G. shallon* AG.. S[d]	0.812	**<0.001**	71
	Aboveground biomass	0.013	0.890	110
	Utilized biomass	0.128	0.288	71
	Tree canopy closure (%)	-0.358	**<0.001**	110
	Stand volume	-0.468	**<0.001**	81
	Slope	-0.266	**0.006**	106

[a] Spearmans rank correlation coefficient.

[b] probability, and bold indicate significance at $\alpha = 0.05$.

[c] T shows that aboveground (AG) biomass index was derived from ground cover estimates in PG transects.

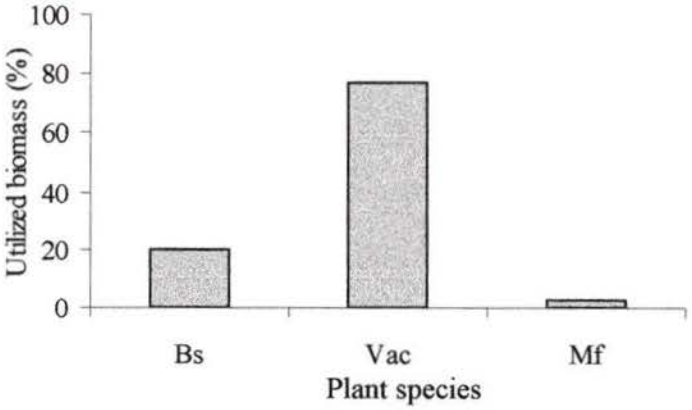
[d] S shows that aboveground (AG) biomass index was derived from ground cover estimates in shrub plots.

4.2.2. Utilized biomass.

Utilized biomass was estimated for the same plant species mentioned earlier, but one of the two crews was unable to identify a point-of-browse in the beginning of the survey period. Accordingly, data were not used from 19 sampling sites (Appendix 1), and estimates of utilized biomass were based on 91 sampling sites for the shrub species. This elimination of data had no impact on the geographical distribution of the sampling sites, or on biomass estimates of *Blechnum spicant* and *Cornus canadensis*. Utilized biomass was greater than zero kg/ha in all in 91 sites and ranged from 0.4 –22.5 kg/ha. The largest amount of utilized biomass was estimated at 22 kg/ha, but the mean was 4 kg/ha (SD = 4.4 kg/ha) and the median was 3 kg/ha. Utilized biomass averaged 0.2 % of the aboveground biomass.

For individual shrub species, aboveground biomass was not correlated with utilized biomass, most likely because shrubs that have escaped browsing grow new shoots out of reach of deer. Utilized biomass was correlated weakly but significantly with aboveground biomass (Table 5). The most utilized species was the *Vaccinium* spp., followed by *Blechnum spicant* (Figure 9, Table 4). Utilized biomass could not be calculated for *V. ovalifolium/alaskaense* because no regression equation was developed for this species combination, but based on my field observations deer prefer *Vaccinium parvifolium.*

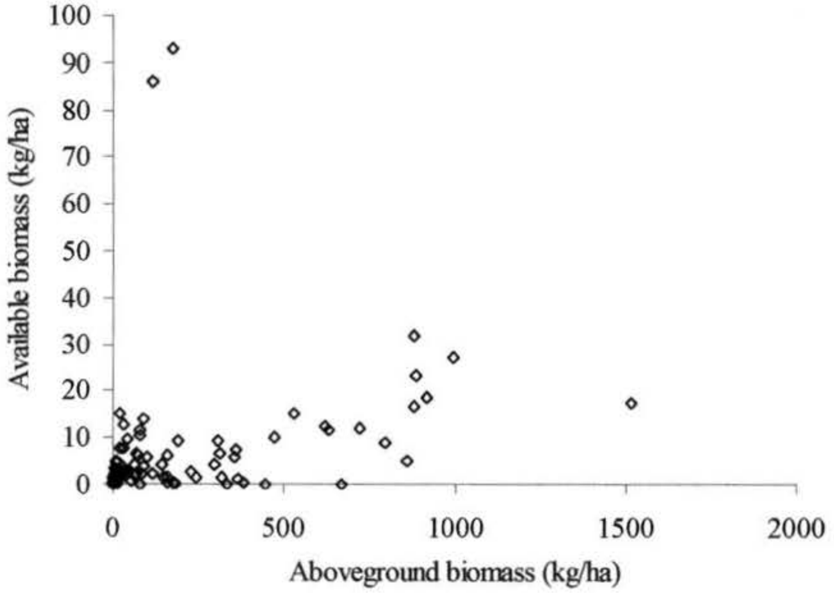
Figure 9: Percent of utilized biomass of *Blechnum spicant* (Bs), *Vaccinium* spp. (Vac) and *Menziesia ferruginea* (Mf) on Haida Gwaii.



4.2.3. Available biomass.

The average available biomass was 12 kg/ha (SD = 17 kg/ha), generally an order of magnitude smaller than aboveground biomass (Table 4). Available biomass was present in 80 sites, and the amounts ranged from 0.2-93.1 kg/ha (Figure 10). This range is skewed upwards by two outliers from the same valley on Moresby Island. If I exclude these sites, available biomass reached only 32 kg/ha. These two sampling sites differed from most others because the dominant species was not *Vaccinium parvifolium*. On site 124, *Rubus spectabilis* constituted 28% of available biomass and *Blechnum spicant,* 71%. On site 106, *Menziesia ferruginea* constituted more than 99% of the available biomass. The correlation between aboveground biomass and available biomass using all sites was weak but statistically significant (Table 5).

Figure 10: Available biomass versus aboveground biomass estimates for 91 sampling sites located on Haida Gwaii.

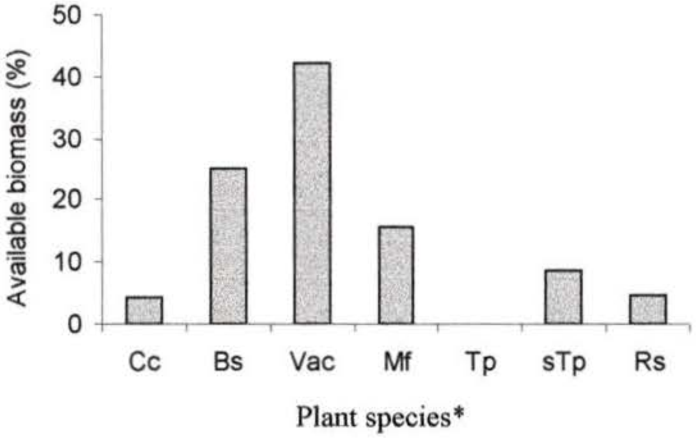


I estimated biomass for *Cornus canadensis* and *Blechnum spicant* in the 110 sampling sites because these two species were considered preferred deer forage. *Cornus canadensis* grew on 43 sampling sites with a total estimated biomass not exceeding 3 kg/ha (Table 4). *Blechnum spicant* grew on 104 sampling sites and estimated biomass reached 76 kg/ha on one site (Table 4). The medians for *Cornus canadensis* and *Blechnum spicant* were respectively, zero and 1 kg/ha, based on all 110 sites. When based only on sites where the two species were present, the medians were 0.43 kg/ha and 0.54 kg/ha, respectively.

Vaccinium parvifolium comprised 42% of all available biomass, and *Blechnum spicant* comprised 25%, *Menziesia ferruginea* 15%, and *Cornus canadensis* 4%. *Thuja plicata* constituted 4% of available biomass, as did *Rubus spectabilis*, even though it contributed biomass only on one site. Because a regression to predict utilized biomass was not developed for *V. ovalifolium / alaskaense*, it was not possible to calculate available biomass for this species combination, but from my field observation they dominated some sites.

Less than 0.5 % of aboveground biomass in the understory was available as forage. This coincides with the common observations of plants whose terminal growth was beyond the reach of *Odocoileus hemionus sitkensis.* Pojar and Banner (1982) mentioned this growth form of plants as well. *Vaccinium* spp., made up 42 % of available biomass and *Blechnum spicant* accounted for 25% of it (Figure 11).

Figure 11: Plant species composition of available biomass for the understory vegetation in old-growth forests on Haida Gwaii.



* *Cornus canadensis* = Cc, *Blechnum spicant* =Bs, *Vaccinium* spp. = Vac, *Menziesia ferruginea* = Mf, *Thuja plicata* saplings = Tp, *Thuja plicata* seedlings = sTp, and *Rubus spectabilis* = Rs.

For *Vaccinium parvifolium,* the number of points-of-browse counted in each sample site correlated with pre-browsed biomass ($r_s^2 = 0.41$, $p < 0.001$, $n = 110$), and so was utilized biomass ($r_s^2 = 0.42$, $p<0.001$, $n = 91$). This is unexpected because utilized biomass was derived from the number of points-of-browse. Available biomass was significantly correlated with utilized biomass (Table 5). This could indicate that deer seek sites with higher available biomass.

4.2.4. Biomass and tree crown closure.

The relationship between crown closure and plant biomass was variable. Aboveground and utilized biomass was weakly and inversely related ($r_s = -0.12$) to the tree canopy closure, but available biomass was not related (Table 5). On a species basis, the two commonest taxa, *Vaccinium* spp. and *Menziesia ferruginea*, showed no clear patterns although highest biomass for the latter species occurred at the low categories of canopy closure (Table 6).

Table 6: Aboveground biomass of understory shrub species in relation to canopy closure in old-growth forests on Haida Gwaii.

Canopy closure categories (%)	Aboveground biomass ($g/4m^2$)							
	Vaccinium spp.				*Menziesia ferruginea*			
	Avg	Sd	n	Max	Avg	Sd	n	Max
<5	123	319	164	3058	689	1881	11	6294
5>=x<25	189	722	406	9508	523	2359	28	12484
25>=x<50	106	280	221	1817	90	175	14	540
50>=x<75	209	576	127	4213	67	89	9	271
>=75	183	428	82	2292	129	169	4	363

4.2.5. Biomass and topographical attributes.

Topographical attributes, such as slope, aspect and elevation, influence the phenological progression of plants in spring (Klein 1965). Aspect and slope affect initiation of growth in spring by up to two weeks in southeast Alaska (Klein 1965), and these site attributes presumably have similar effects on Haida Gwaii. However, slope was not significantly correlated with aboveground biomass for any species except for a weak negative correlation with *Cornus canadensis* ($r_s = -0.385$, $p < 0.001$, $n = 106$) and *Gaultheria shallon* ($r_s = -0.266$, $p = 0.006$, $n = 106$). Elevation and biomass were not correlated significantly for any species except *Gaultheria shallon* ($r_s = -0.208$, $p = 0.033$, $n = 105$). I found also a weak correlation between elevation and available biomass of *Vaccinium* spp. ($r_s = 0.277$, $p = 0.009$, $n = 88$). I did not find any statistical difference between the north-facing (270< deg <= 90) and south-facing (90> deg<= 270) aspects with respect to aboveground biomass, utilized biomass, and available biomass (Table 7).

Table 7: Effect of aspect on estimated biomass components of understory vegetation on north- and south-facing slopes.

Biomass component	Mann-Whitney Z approximation test	
	Z	p
Aboveground	1.1793	> 0.1
Utilized	0.5155	> 0.25
Available	0.4334	> 0.25

4.2.6. Salal biomass.

Gaultheria shallon was surveyed differently from other shrubs because it was initially thought to be too abundant and too time consuming to survey in the same way as other shrubs. Thus, the biomass index developed here could not be included in total biomass estimated from the sites. Throughout the field season, percent groundcover was estimated in each of the 10 m sections in all pellet group transects. When I was approximately half way through the field season, I began to estimate ground cover of *Gaultheria shallon* in the shrub plots and estimated the percentage of utilization as well. The estimates from the shrub plots and the pellet group transects were highly correlated and statistically significant (Table 5) suggesting that either index can be used. The transect biomass index was the only biomass estimate to show a weak but negative correlation with slope and stand volume (Table 5).

I found salal in 40 of 108 transects. The mean biomass index in these transects was 56 kg/ha (SD =160), and the median was 0 kg/ha. No correlation was found between aboveground biomass and the biomass index of *Gaultheria shallon* in the transects, or the utilized biomass and the index for utilized *Gaultheria shallon* (Table 5).

4.3. Relative deer density.

Before analysing the entire pellet group count data-set, I first checked for differences between counters, and for their ability to age pellets consistently. When comparing the results of the three pellet group counters in my field crews, I found no difference between them (Kruskal Wallis $\chi^2 = 3.804$, $p = 0.149$, $df = 2$). However, because I did find a difference between the recent pellet group counts (Kruskal Wallis $\chi^2 = 45$, $p < 0.001$, $df = 2$) and old pellet groups (Kruskal Wallis $\chi^2 = 6.251$, $p < 0.044$, $df = 2$), I decided to combine pellet groups, regardless of estimated age-classes: boundaries between the categories were not clear and one of the counters could not age the pellet groups consistently.

The mean pellet group density was 402 PG/ha (SD = 362 PG/ha), and the median estimate was 300 PG/ha. Expressed as equivalent deer densities, the mean deer density equivalent was 13.3 deer/km^2, and the median deer density was 10 deer/km^2. The maximum number of PG/ha for one sampling site was 1840 that converted to an equivalent deer density of 60.8 deer/km^2.

Pellet group densities were quite variable, even over short distances. In one case, 12 surveys conducted in an old-growth forest stand yielded estimates between zero and 800 PG/ha.

I found no correlation between PG/ha densities and sampling site attributes such as elevation, stand volume, and slope (Table 8). However, I did find a weak correlation between PG/ha and utilized biomass as well as with the number of points-of browse (Table 8). I did not find any statistical difference between the north-facing ($270 <$ deg $<= 90$) and south-facing ($90 >$ deg $<= 270$) aspects with respect to PG/ha (Mann-Whitney z-approximation test, $Z = 1.2982$, $p > 0.1$). If I selected sites that could be considered deer winter ranges (low, south-facing slopes), I found that only the median of the old pellet groups differed statistically between these two aspects ($U = 698$, $n_1 = 25$, $n_2 = 79$, $p < 0.05$).

Table 8: Spearman's rank correlations between pellet groups/ha and other parameters.

Parameter 1	Parameter 2	r_s [a]	p [b]	*n* [c]
Pellet groups / ha	Aboveground biomass	0.043	0.658	110
	Available biomass	-0.034	0.746	91
	Utilized biomass	0.234	**0.026**	91
	No. Points-of-browse / ha	0.260	**0.006**	110
	Stem / ha	0.097	0.313	110
	Stand volume (m^3/ha)	0.008	0.944	81
	Elevation (m)	0.053	0.590	105
	Slope (degrees)	0.069	0.480	106
	G. shallon AG. T [t]	0.060	0.535	110
	G. shallon Utilized S [s]	0.167	0.165	71

[a] Spearman's rank correlation coefficient.

[b] p = probability, and bold indicate significance at $\alpha = 0.05$.

[c] Sample size.

[t] T denotes that aboveground (AG) biomass index was derived form ground cover estimates in PG transect.

[s] S denotes that aboveground (AG) biomass index was derived form ground cover estimates in shrub plots.

Pellet group densities did not appear to differ among islands, ecosections and site series (Table 9). Pellet group densities on Graham, Moresby and Louise Islands did not differ (Kruskal Wallis $\chi^2 = 0.178$, $p = 0.915$, $df = 2$). As well, I found no difference between means of pellet groups / ha in the three different ecosections (Kruskal Wallis $\chi^2 = 2.641$, $p = 0.267$, $df = 2$). In individual biogeoclimatic site series, sample sizes were generally small, and the median was also generally smaller than the mean (Table 9). No statistical difference could be detected between pellet groups / ha in the sites series (Kruskal Wallis $\chi^2 = 4.905$, $p = 0.428$, $df = 5$).

4.4. Pellet group densities and biomass correlations.

In this section, I examine overall correlations between relative deer density (expressed as PG/ha) and estimated aboveground, available and utilized biomass; as well as the same relationships stratified by proximity to access, biogeoclimatic zones and site series, winter ranges and valleys.

4.4.1. Relative deer density and biomass relationships.

The estimated utilized biomass was the only biomass estimate that was weakly but significantly correlation ted with pellet groups densities (Table 8). The number of points-of-browse was also found to be weakly but significantly correlated utilized biomass, which was not surprising because utilized biomass was derived from these. The *Gaultheria shallon* indices were not correlated with pellet group counts (Table 8).

Table 9: Relative deer densities on different islands, ecosections, biogeoclimatic variants and site series on Haida Gwaii.

	Relative deer density (pellet groups/ha)				
	Median	Avg	Sd	N	Max
Surveyed islands					
Graham Island	310	377	313	72	1760
Moresby Island	310	482	498	28	1840
Louise Island	370	360	209	10	680
Ecosections					
Skidegate Plateau	120	429	383	81	1840
Queen Charlotte Lowland	340	328	492	5	1200
West Coast Queen Charlotte	270	327	243	24	880
Biogeoclimatic subzone and variant					
vh2	150	215	157	12	500
wh1	340	426	389	85	1840
wh2	300	420	262	13	900
Site series					
CWHvh2 hm	120	120	283	2	140
CWHvh2 hs	160	252	194	5	500
CWHvh2 rf	70	70	71	2	120
CWHvh2 sc				1	240
CWHwh1 hs	260	271	138	7	440
CWHwh1 rf	210	252	234	10	800
CWHwh1 rs	100	100	28	2	120
CWHwh1 sc	160	360	346	3	760
CWHwh1 sm	340	389	284	33	120
CWHwh1 yg	440	348	279	5	680
CWHwh2 hs	480	493	200	3	700
CWHwh2 sm	360	455	287	8	900
Total counts	300	402	362	110	1840

The large variation of aboveground biomass when plotted with pellet group densities appeared to show an upper limit that was explored with regression quantiles (Figure 12). For the 75%, 90% and 95% regression quantiles the slope was negative, which indicates that the factor ceiling slope declines with increasing deer density. In particular, it appeared that aboveground biomass estimates drastically dropped off at around 950 PG/ha (Figure 12).

The distribution of utilized biomass correlated weakly with pellet group densities (Table 8), and 75%, 90% and 95% quantiles all had positive correlations indicating that the upper limit of the scatter plot decrease with increased deer density (Figure 13).

Figure 12: The relationship between estimated aboveground biomass and pellet group densities (PG/ha) in old-growth forests on Haida Gwaii ($n = 91$).

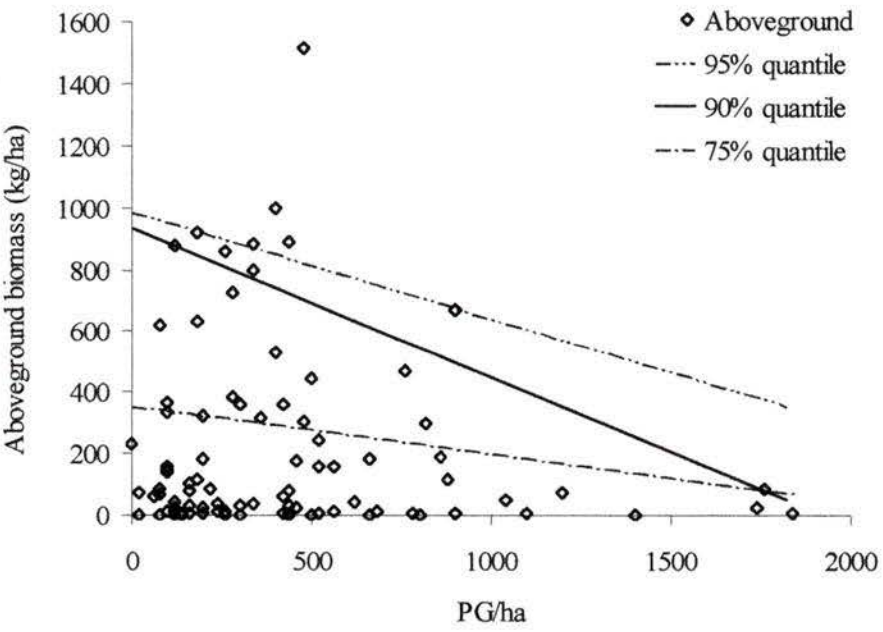
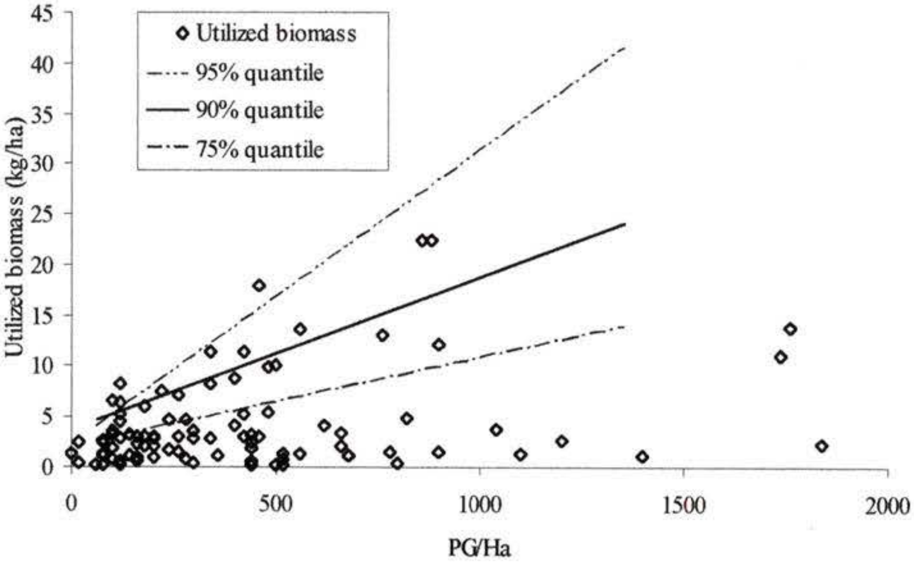


Figure 13: The relationship between utilized biomass and pellet group densities in old-growth forests on Haida Gwaii (*n* = 91).

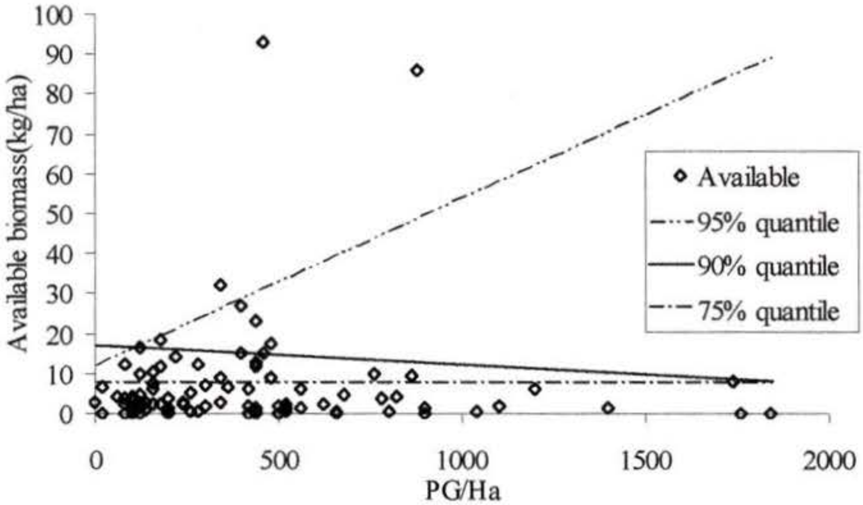


Finally, available biomass estimates also seemed to show an upper limit (Figure 14). The 75% and 90% and 95% regression quantiles did not provide similar slope, so it is not possible to suggest an upper limit. The two outliers influenced the quantile regressions with respect to slope. When I experimentally omitted the two outliers, the 95% quantile assume a negative slope and the 90% quantile a positive slope, the opposite trend to when outliers were included.

4.4.2. Proximity to access.

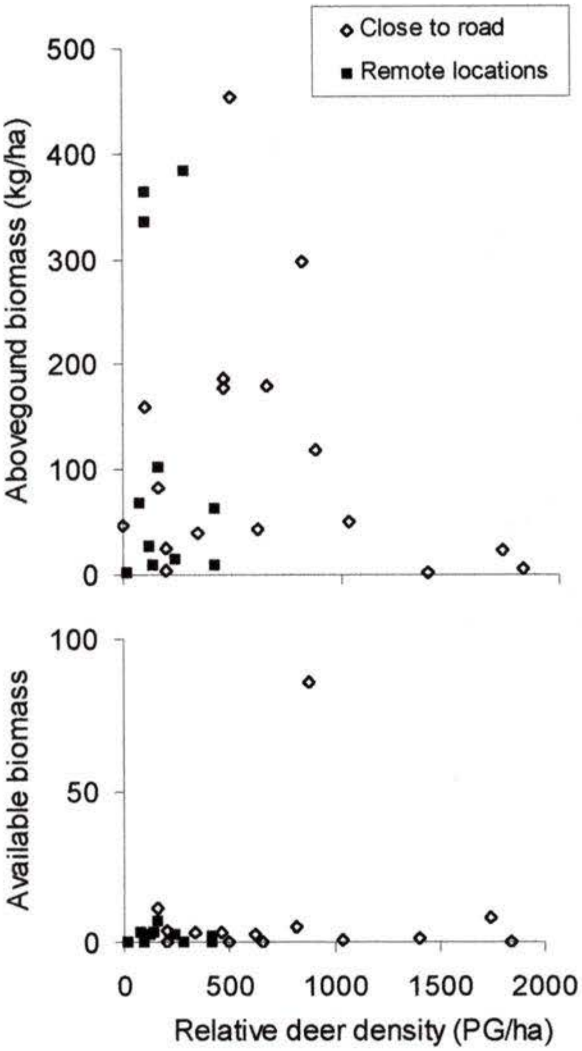
Proximity to roads influences pellet group densities and aboveground biomass (Figure 15). All sampling sites on Graham Island (n = 72), Louise Island (n = 10) and 18 of 28 sampling sites on Moresby were situated within walking distance (< 1 km) from logging roads. Ten sampling sites on Moresby were located in a sheltered but remote area on the west coast with no logging or roads.

Figure 14: The relationship between available biomass and pellet group densities in old-growth forests on Haida Gwaii ($n = 91$).



Sampling sites in remote locations on Moresby Island generally had fewer PG/ha and less aboveground biomass than locations closer to roads (Figure 15). The three sampling sites in the remote area with high aboveground biomass (>334 kg/ha) had less than 1.1 kg/ha available (Figure 15 A, B). These sites were south-facing slopes on the lee side of the inlet.

Figure 15: The relationship between aboveground (A) and available (B) biomass estimates and pellet group densities on remote locations (n=10) and with road access (n=18), in old growth forests on Moresby Island (n=28).



4.4.3. Ecosection and biogeoclimatic zones.

I divided the data according to ecosections and biogeoclimatic zones to investigate whether pellet group and biomass relationships differed. As noted above, I found weak but significant correlations between aboveground biomass and available biomass, aboveground and utilized biomass, and available and utilized biomass (Table 5). I expected that these correlations would increase in strength when looking at sampling site within the same ecosection, but this generally did not occur (Table 10). Only the correlation between aboveground biomass and available biomass on Skidegate Plateau and Queen Charlotte Lowlands increased. The latter had a perfect fit, and considering the variation everywhere else and the small sample size; this must be dismissed as a stochastic event.

When comparing the medians for the three ecosections, I found no difference between the pellet groups / ha (Kruskal Wallis $\chi^2 = 2.641$, $p = 0.267$, $df = 2$), utilized biomass (Kruskal Wallis $\chi^2 = 4.447$, $p = 0.108$, $df = 2$), and available biomass (Kruskal Wallis $\chi^2 = 3.970$, $p = 0.137$, $df = 2$). I did find a difference between the aboveground biomass in the three ecosections (Kruskal Wallis $\chi^2 = 9.373$, $p = 0.009$, $df = 2$). If I relaxed α to 0.10 and compared medians in only Skidegate Plateau and West Coast Queen Charlotte Island ecosections, the medians differed (available biomass: $U = 555$, $p = 0.056$, $n = 87$; aboveground biomass: $U = 580$, $p = 0.003$, $n = 105$; and utilized biomass $U = 881$, $p = 0.097$, $n = 87$). I conclude that the aboveground biomass mean of 147 kg/ha on Skidegate Plateau was statistically different from the 12 kg/ha on West Coast Queen Charlotte ecosection.

Table 10: Spearman's rank correlations between biomass estimates and pellet group densities in three ecosections on Haida Gwaii.

Parameter 1	Parameter 2	r_s[a]	p[b]	*n*[c]
	Skidegate Plateau			
Aboveground biomass	Available biomass	0.546	**<0.001**	63
	Utilized biomass	0.497	**<0.001**	63
	Pellet groups/ha	-0.002	0.986	81
	West Coast Queen Charlotte Island			
Aboveground biomass	Available biomass	0.344	0.100	24
	Utilized biomass	0.451	**0.027**	24
	Pellet groups/ha	0.084	0.698	24
	Queen Charlotte Lowlands			
Aboveground biomass	Available biomass	-1.000	**<0.001**	4
	Utilized biomass	0.800	**0.200**	4
	Pellet groups/ha	0.300	0.624	5

a: r_s = Spearman's rank correlation coefficient.
b: p = probability, and bold indicate significance at $\alpha = 0.05$.
c: *n* = sample size.

I examined the relationships between biomass components and different ecosystems, based on biogeoclimatic subzones and sites series. Because these ecosystems differ in soil nutrient and moisture content, I expected to find differences at least in aboveground biomass. At the subzone level, only available biomass differed statistically (Kruskal Wallis $\chi^2 = 6.163$, $p = 0.046$, $df = 2$).

To examine relationships between site series, two initial steps were necessary: allocating sampling sites to site series, and amalgamating similar site series to achieve adequate sample sizes. I allocated my sampling sites to site series based on a 1999 Terrestrial

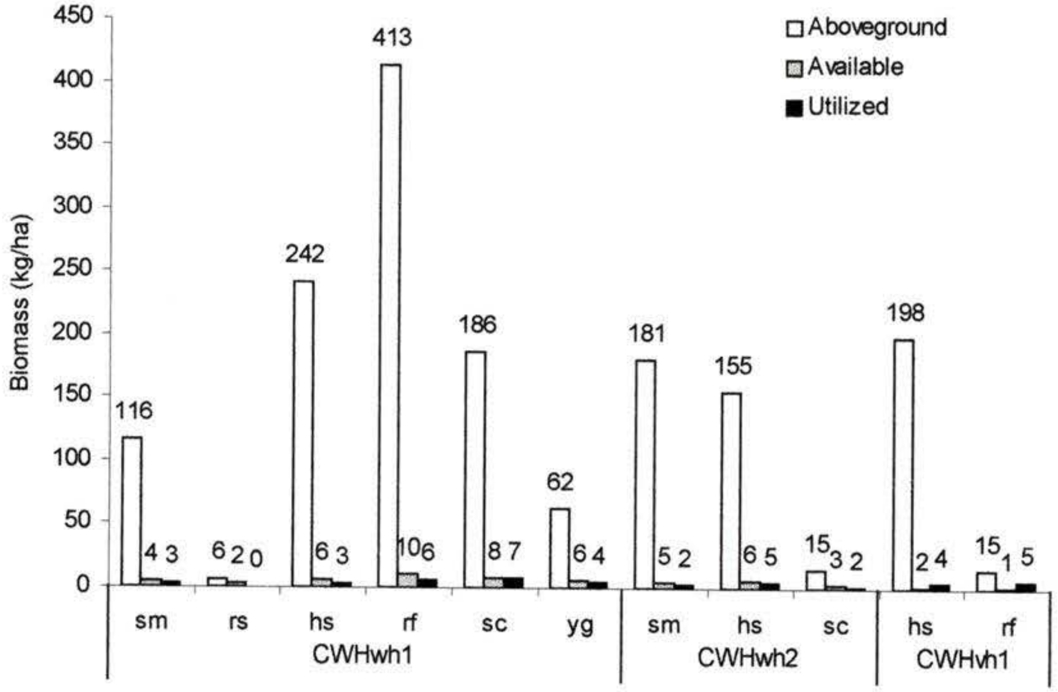
Ecosystem Map (TEM), by locating my sampling locations in labelled polygons on these TEM's. Then I combined the 11 site series of my sampling sites into four categories as shown in Table 11.

Table 11: Site series combinations based on soil nutrient and moisture regimes for sites on Haida Gwaii.

			Soil Nutrient Regime	
			V. poor- medium	Rich – v. rich
		BEC-subzone	Site series	Site series
Soil moisture	Fairly dry - dry	CWHwh1	sm, rs	
		CWHwh2	sm	
		CWHvh1		rf
	Moist – v. moist	CWHwh1	hs, yg	rf, sc
		CWHwh2	hs	sc
		CWHvh1	Hs	

No statistically significant differences were found between the four categories of site series combinations for the medians of aboveground biomass (Kruskal Wallis $\chi^2 = 3.030$, $p = 0.387$, $df = 3$), available biomass (Kruskal Wallis $\chi^2 = 2.723$, $p = 0.436$, $df = 3$), utilized biomass (Kruskal Wallis $\chi^2 = 0.1.731$, $p = 0.630$, $df = 3$), and pellet groups / ha (Kruskal Wallis $\chi^2 = 6.263$, $p = 0.099$, $df = 3$). It appears that no real difference exist between the sites series categories, although biomass estimates and sampling effort varied widely among and within site series (Figure 16).

Figure 16: Estimated aboveground, available and utilized biomass in the Coastal Western Hemlock biogeoclimatic (CWH) subzones (wh and vh), variants (1 and 2) and site series (letter code) derived from Terrestrial Ecosystem Maps. (Standard Ministry of Forests codes).



No. sites	25	2	5	7	3	5	8	2	1	7	2

Standard deviations associated with means in graph

Aboveground	168	8	431	355	248	55	309	215		179	17
Available	5	3	12	10	5	4	5	5		2.5	2
Utilized	4	0.0	2	5	6	7	2	7		4	4

4.4.4. Winter range.

I examined the data for differences between sampling sites that were located in areas that could be considered winter ranges with those that could not. The 3 criteria normally used to identify a winter range are: 1) large crown, 2) 65 - 70% canopy closure that allows understory to grow, and 3) multiple canopy layers (Bunnell 1990). I did not follow these criteria because the forest stands on Haida Gwaii did not have multiple layers, and only one sampling site fell in the range between 60 and 75 % canopy closure. Instead, I defined deer winter ranges as south-facing areas on lower slopes: I surveyed 25 sites with these attributes. The winter ranges were located on Graham (n = 18), Moresby (n = 3) and Louise Islands (n = 4) and in 11 different valleys. The variation of aboveground biomass decreased with increased number of pellet groups per hectare, and I found the same trend for available biomass (Figure 17). The 3 sampling sites (52, 101 and 105) with unusually high densities of pellet groups were all located close to areas where the forage supply had been augmented by branches from recently felled trees. In these situations this additional forage likely attracted deer because aboveground and available biomasses were low. The estimated low biomass present suggests either that the browsing has been heavy over many years or that these sites are not good growing sites.

When aboveground and available biomasses were plotted with relative deer density, it appeared that a ceiling factor could be determined (Figure 17). The regression quantiles used to investigate this upper limit were not statistically significant but showed a general trend. *Blechnum spicant* showed a similar factor ceiling (Figure 18).

Figure 17: Aboveground biomass and available biomass versus pellet groups per hectare in deer winter ranges on Haida Gwaii.

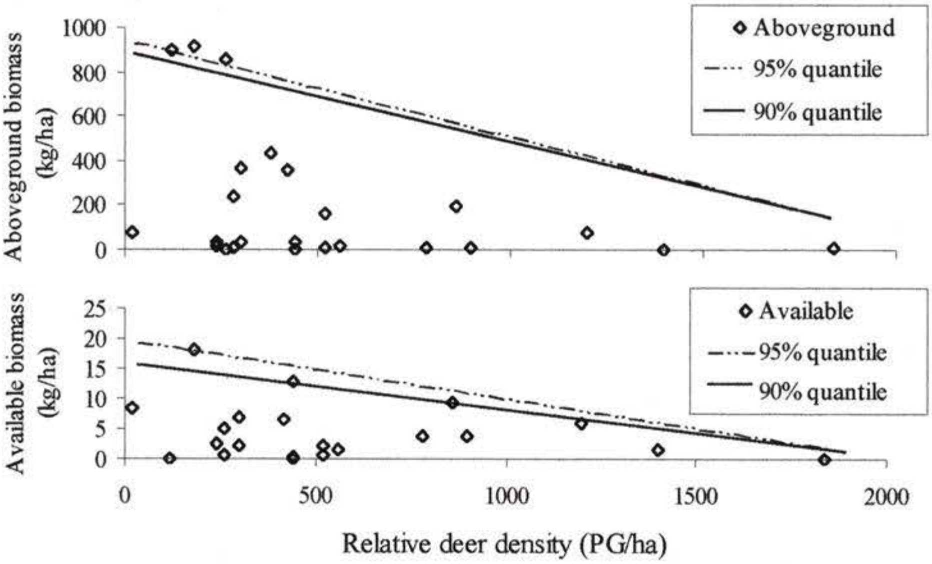
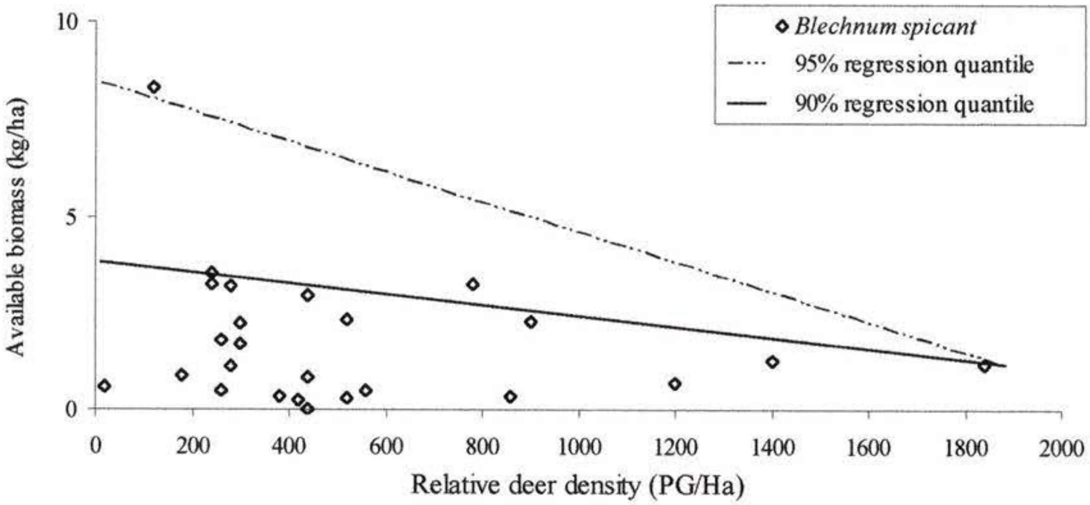


Figure 18: The relation between *Blechnum spicant* biomass and pellet group densities (PG/ha) in deer winter ranges on Haida Gwaii.



When I tested the median of the sampling sites located in winter ranges with those not located in winter ranges, I found no statistically significant difference. The aboveground biomass ($U = 804.5$, $p > 0.05$, $n_1 = 25$, $n_2 = 85$), available biomass ($U = 729$,$p > 0.05$, $n_1 = 22$, $n_2 = 69$), utilized biomass ($U = 641.5$, $p > 0.05$, $n_1 = 22$, $n_2 = 70$), and Salal aboveground ($U = 402$, $p > 0.05$, $n_1 = 19$, $n_2 = 52$) and utilized ($U = 393.5$, $p > 0.05$, $n_1 = 19$, $n_2 = 52$) biomass indices all suggest that there were no differences. I did find statistical significantly differences for PG/ha ($U = 765$, $p < 0.05$, $n_1 = 25$, $n_2 = 85$), *Vaccinium parvifolium* aboveground biomass ($U = 684.5$, $p < 0.05$, $n_1 = 25$, $n_2 = 85$), and *Vaccinium parvifolium* utilized biomass ($U = 555$, $p < 0.05$, $n_1 = 22$, $n_2 = 70$).

4.4.5. Valleys.

Because sampling intensity in different valleys varied, and because these clumped samples might be pseudoreplication when considering the entire study area, I investigated the data variation among valleys. I used a non-parametric test because of the large variance and because data were non-normal ($W = 0.7505$, $p = 0.0394$). When I compared all 25 valleys, the medians differed for relative deer density (Kruskal Wallis $\chi^2 = 41.629$, $p = 0.014$, $df = 24$), aboveground biomass (Kruskal Wallis $\chi^2 = 74.254$, $p < 0.001$, $df = 24$), available biomass (Kruskal Wallis $\chi^2 = 50.840$, $p = 0.001$, $df = 24$), and utilized biomass (Kruskal Wallis $\chi^2 = 54.747$, $p < 0.001$, $df = 24$). The large variance within valleys leads me to believe that these differences were not necessarily biological differences but mostly likely caused by uneven sample sizes. For example, in one valley with 12 surveys, pellet groups density estimates varied from 0 to 800 PG/ha.

4.5. Spatial analysis.

To further investigate possible spatial trends and correlations in the data set, 3D plots were used to display the data. The graphs were visually inspected. I indicated the location of Graham, Moresby and Louise Islands on the graphs to help interpretation (Figure 19, Figure 20, Figure 21, Figure 22).

Pellet group densities were highest on the east side of Moresby Island and the south end of Graham Island (Figure 19). This is contrary to the commonly held belief on the islands that deer density increases proportionally with distance from settlements. The site (94) with the highest pellet group counts was situated only 10 km north of Queen Charlotte City (the largest settlement on the islands). Also, good access existed to the sites on Moresby Island with the highest pellet group densities encountered in the study. The Ian Lake area is not easily accessed but the pellet group densities were low. The same was the case on the remote inlet on the west coast of Moresby Island. The most likely explanation for the high pellet group density on the Moresby Island sites was that recent cutting of a road allowance had left cedar branches on the roadway that were accessible for browsing by deer.

The spatial distribution of aboveground biomass shows the largest amounts on Graham Island (Figure 20) and very little on Louise Island. Available biomass amounts peaked in the southwest side of Graham Island (Figure 21). As expected, the areas with the highest pellet group densities on Moresby Island provided very little aboveground and available biomass (compare Figure 19 with Figure 20 and Figure 21).

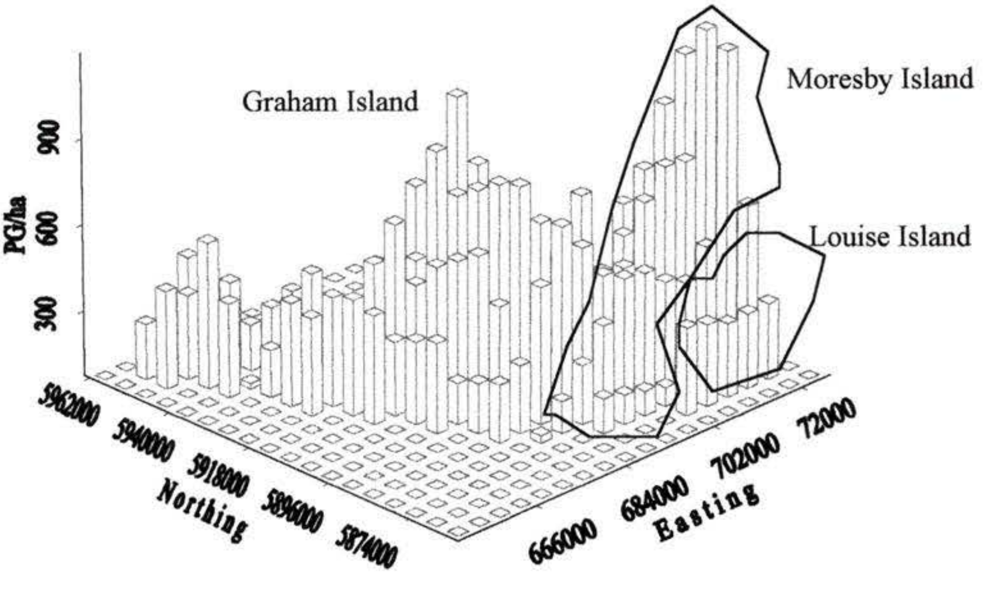
The amount of estimated utilized biomass was also the largest on Graham Island, and the least amounts occurred on the west coast of Moresby Island and around Ian Lake (Figure 22). From a visual inspection, it appears that there was a reasonable spatial correlation between the pellet group densities and the utilized biomass on Graham Island.

4.6. The influence of hunting pressure on deer density.

Daufresne and Martin (1997) assumed that hunter accessibility influenced browsing pressure on Haida Gwaii. To test this assumption, I divided the data into the following two groups: inaccessible (hunters needed to take a private boat to reach the location), and accessible (locations could be reached by car from any of the villages). I was not able to detect any difference between the mean number of PG/ha in these two areas groups ($U = 1137.5$, $p = 0.467$, $df = 1$, $n = 110$). When I divided the data into three groups with those sites that were closer than 10 km to any village, between 10 and 20 km and more than 20 km, I did not find any difference in pellet groups per ha either ($U = 1.092$, $p = 0.579$, $df = 2$, $n = 110$). It appears that hunter accessibility did not influence relative deer density.

Figure 19: Spatial variation of pellet group densities (PG/ha) in old-growth forests on Haida Gwaii, positioned using UTM coordinates in 3-D bar plots.

A: Data shown with x-axis on 225 deg.



B: Data shown with x-axis on 45 deg.

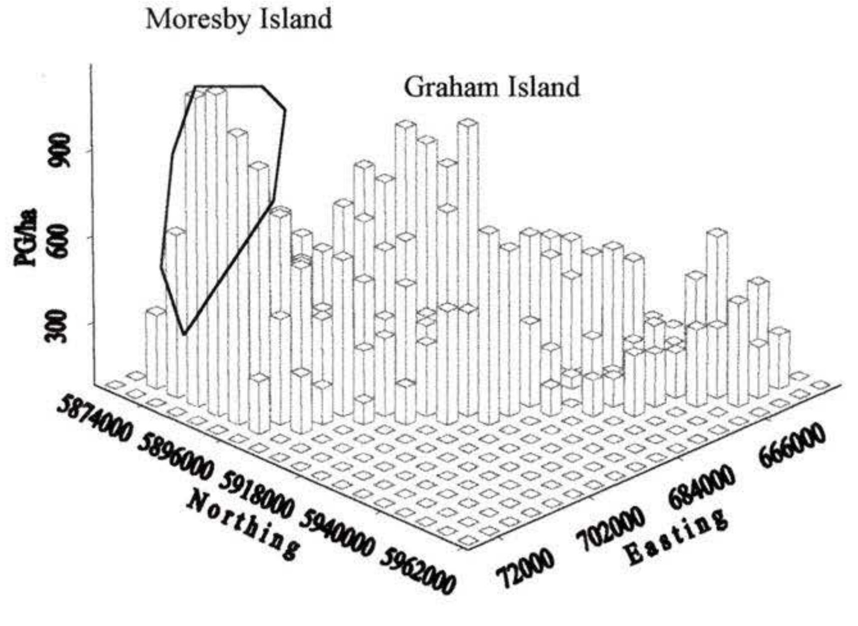
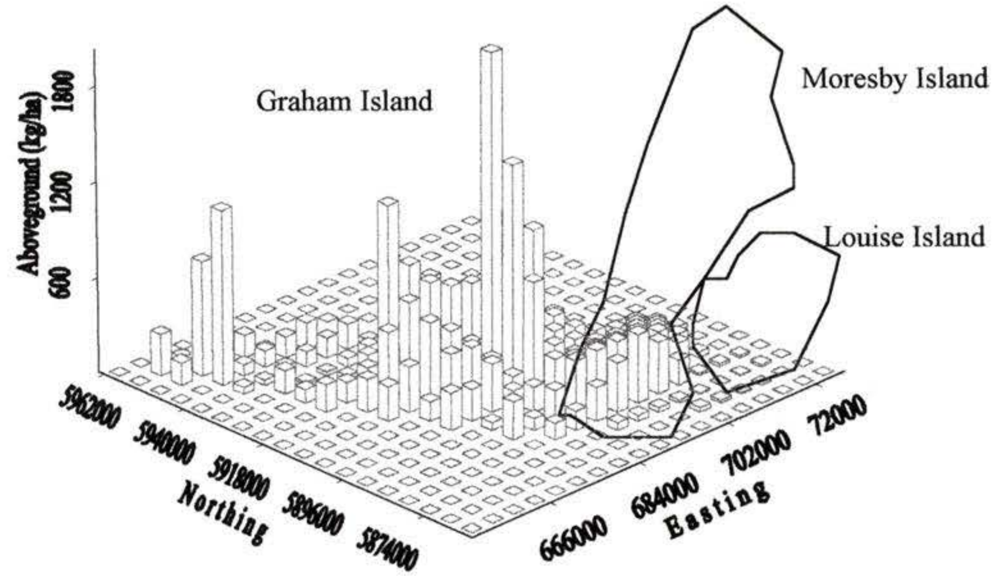


Figure 20: Spatial variation of aboveground biomass in old-growth forests on Haida Gwaii, positioned using UTM coordinates in 3-D bar plots.

A: Data shown with x-axis on 225 deg.



B: Data shown with x-axis on 45 deg.

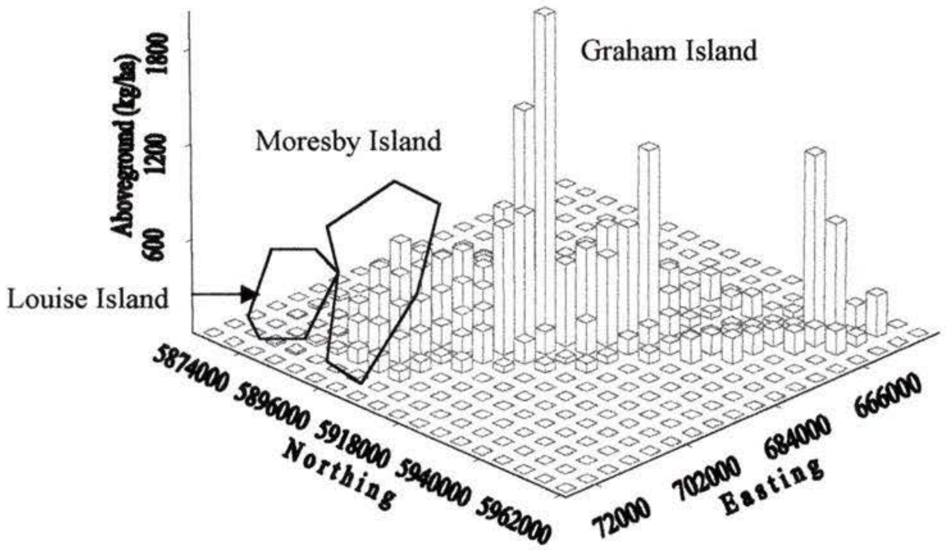
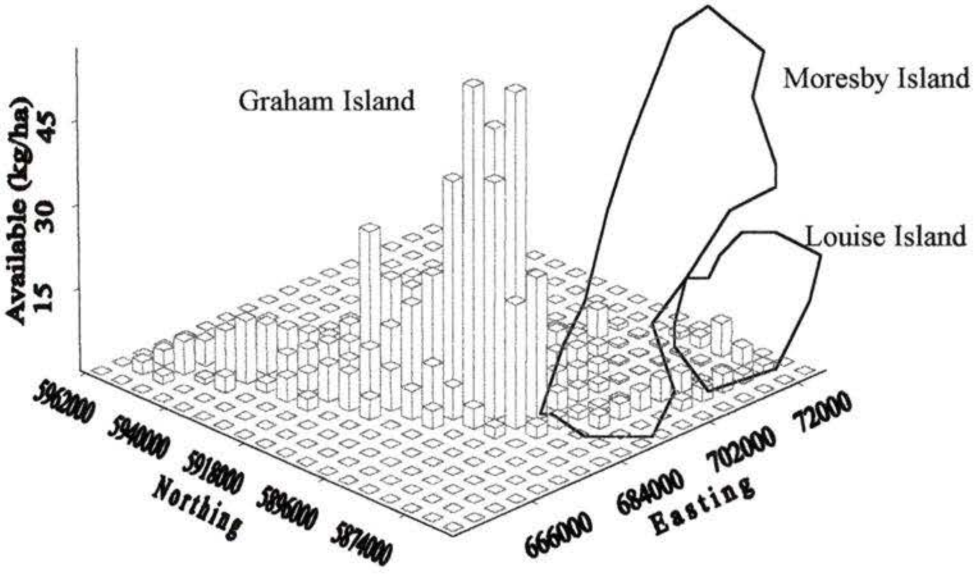


Figure 21: Spatial variation of available biomass in old-growth forests on Haida Gwaii, positioned using UTM coordinates in 3-D bar plots.

A: Data shown with x-axis on 225 deg.



B: Data shown with x-axis on 45 deg.

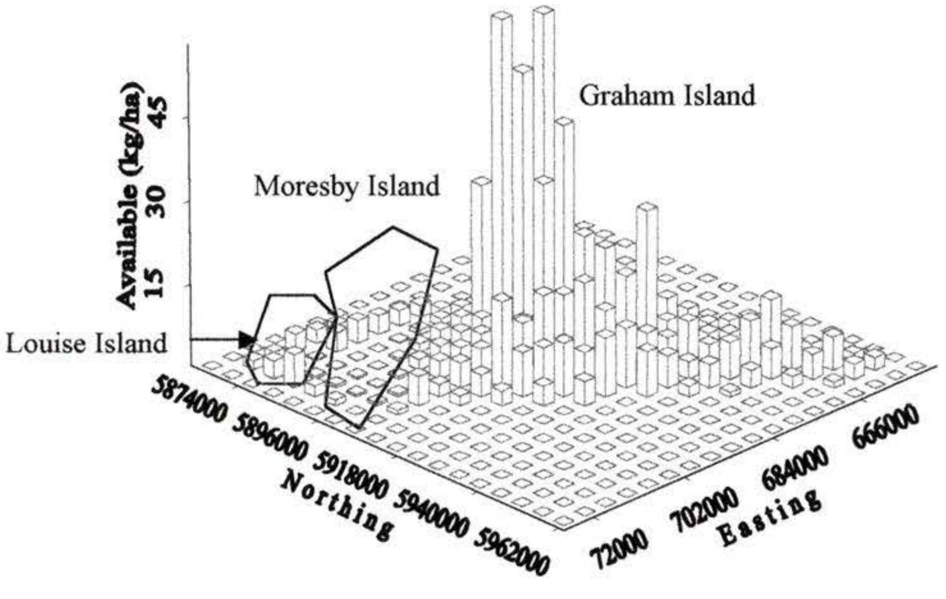
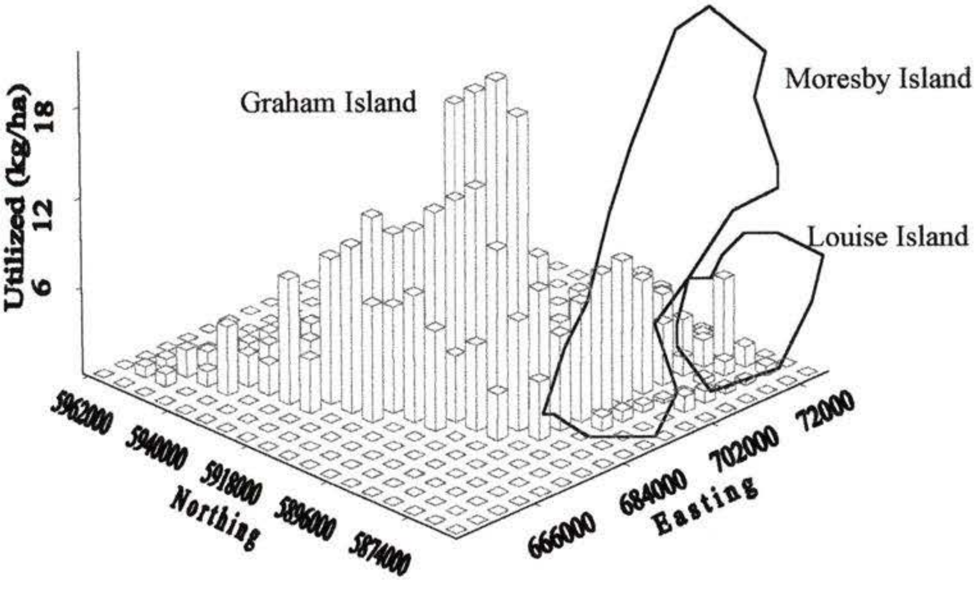
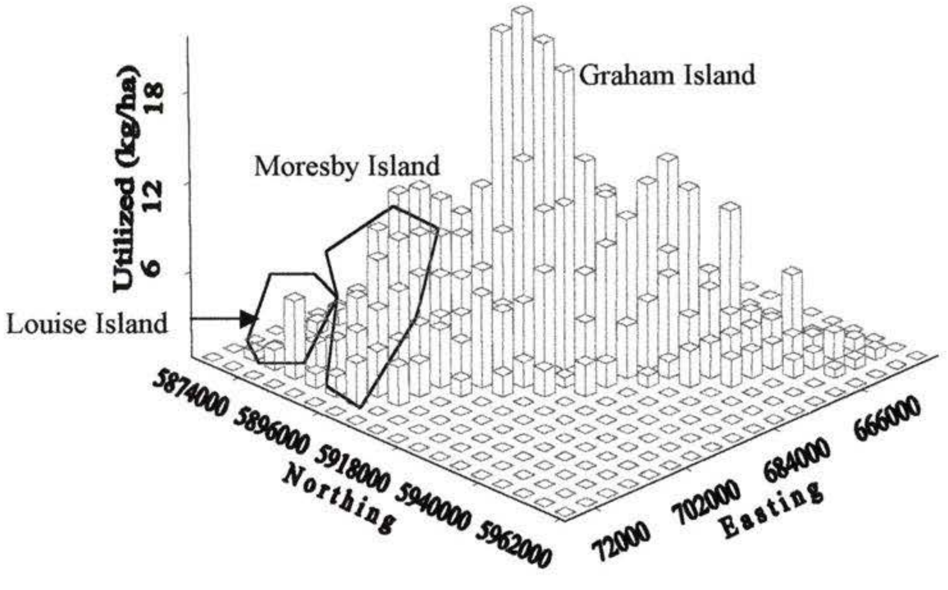


Figure 22: Spatial variation of utilized biomass in old-growth forests on Haida Gwaii, positioned using UTM coordinates in 3-D bar plots.

A: Data shown with x-axis on 225 deg.



B: Data shown with x-axis on 45 deg.



5. Discussion.

5.1. Estimating plant biomass by regression equations.

I used easily measured independent variables such as basal stem, twig, and of point-of-browse diameters to avoid the inherent observer biases in estimating cover. I not only used measurements of the basal stem and twigs diameter on shrubs to estimate biomasses, but I also applied this approach successfully to *Blechnum spicant*. Generally the frond width and length has been used, but to the best of my knowledge, this is the first time that stem diameter has been used to estimate *Blechnum spicant* biomass.

After investigating different estimation models, I chose the power function. Because shrubs grow in a three-dimensional environment and current annual growth occurs at the tip of all branches as well as from new branches, accepting an exponential growth model seemed reasonable. Knowing the difference between estimates of the power function and natural logarithmic transformation models, with and without re-transformation factors, allowed me to compare my results to those of other authors. Models have inherent inaccuracies due to natural variation, as can be seen in the relatively low fit of the model to estimate pre-browsed biomass. This inaccuracy was influenced by varied growth from site to site. Because original data were heteroscedastic, legitimate linear regression models warranted transformations of the data. The power function avoided this step. Whether one can assume a causal relationship between basal stem diameter and biomass that is a necessary assumption for developing regressions is another question (Zar 1984).

During the survey to determine the best function to estimate biomass, I found that the correction factors published by Baskeville (1972) and Sprugel (1983) did not enhance the accuracy of estimates. One reason might be that I did not use log paper but transformed measured data and developed the regression on the computer, a more precise approach.

Site-related factors that normally influence models were not found in this study. Several authors have reported that different habitat types produce different models (Nyberg 1985; Alaback 1986; Alaback 1987; Yarie and Mead 1989; Marshall et al. 1990; Feller 1992; MacCracken and Ballenberghe 1993), but I found that the two different types of habitat I tested could be represented by the same model. One reason for this result could be that the two habitat types were not very different in how they affected plant growth forms. Another reason could be that the plants I used to develop the models all grew on old stumps and tipped over root systems, microhabitats inaccessible to Black-tailed Deer. Because these plants all originated from similar microhabitats, the overall habitat type may have had minimal influence on growth, vigour and form.

5.2. Comparing biomass estimates with other areas.

On Haida Gwaii, the estimates of aboveground biomass (0-2137 kg/ha) fluctuated even more than reported from surrounding areas. In southeast Alaska, Alaback (1982) found understory (aboveground) biomass varied between 500 kg/ha and 600 kg/ha in forests older than 250 years. On northern Vancouver Island, Harestad (1979) found that the amount of available food during the winter varied from approximately 30 -700 kg/ha. Also, my estimates of aboveground biomass (maximum aboveground biomass =2100 kg/ha, mean = 300 kg/ha, SD = 400 kg/ha) and available biomass (maximum available biomass = 100 kg/ha, mean = 10 kg/ha, SD = 20 kg/ha), were considerably less on Haida Gwaii, than these two areas. I did not consider the influence of snow cover in my estimates of available biomass, so the amount decreases even further during periods with heavy snowfall. Another difference is that I did not include *Gaultheria shallon* in the biomass estimates, which makes direct comparisons problematic.

To my knowledge, no quantified understory biomass estimates exist for old-growth forests on Haida Gwaii. In Sewell Inlet, Moresby Island, estimates of some shrub and herbaceous plants species exist for areas re-planted in 1982, 1988, and 1989 (Bennet 1996). Western Forest Products, Ltd. established three deer exclosures (0.6 ha, 10 ha, 20 ha) to study the effect of deer browsing on forest regeneration. Because this study focused on a different seral stage, direct comparisons with my findings are not possible. One aspect that was consistent with my study was the considerable variation in shrub and herbaceous plant biomass (kg/ha) on the three sites (616, 84, and 140 kg/ha) when Bennet revisited the sites in 1996.

The fern community on Haida Gwaii was most likely decimated by browsing, and I found *Polystichum munitum* in only eleven plots. This species was earlier listed as the most common fern on the islands (Calder and Taylor 1968). In the three deer exclosures built by Western Forest Products Ltd., *Polystichum munitum* constituted 2 % of the biomass and *Blechnum spicant* 1 % of the biomass (Bennet 1996). In my study, *Blechnum spicant* was present on most sites, but the rosettes were rarely larger than approximately 10-15 cm in diameter, similar to what Pojar et al. (1980) found. Even though forests of Nova Scotia are quite different, fern biomass there (Telfer 1972) corresponded to the maximum estimate (76 kg/ha) of *Blechnum spicant* on Haida Gwaii. In southeast Alaska, *Blechnum spicant* constituted 0.6 % of the understory biomass (Alaback 1982), but made up 1.2 % on Haida Gwaii. This percent difference between Alaska and Haida Gwaii could be an artefact of fewer species present in the understory on Haida Gwaii, causing the percentage to be larger even though the estimated amount might be smaller.

Vaccinium parvifolium, the most common species in the understory of old-growth forests on Haida Gwaii, is also one of the important winter forage species for deer (Cowan 1945; Pojar et al. 1980; Kirchhoff and Larsen 1998; Parker et al. 1999). In southeast Alaska, this species was estimated to produce up to 2681 kg/ha depending on substrate (Alaback and Sidle 1986), but estimated average aboveground biomass in old-growth was 24 kg/ha (Alaback 1984). The maximum aboveground biomass estimate on one sampling site on Haida Gwaii was 2134 kg/ha, but the overall was average 258 kg/ha (SD = 388, n = 110) and the overall median estimate was 59 kg/ha. The amounts of *Vaccinium parvifolium* on Haida Gwaii seem comparable to nearby southeast Alaska.

Only a small part of *Vaccinium parvifolium* was available as deer forage. The median amount of the estimated available biomass of *Vaccinium parvifolium* on Haida Gwaii was 1.2 kg/ha. On Vancouver Island, *Vaccinium parvifolium* was the most sought-after shrub species, and evidence of browsing was present on most plants (Cowan 1945). *Vaccinium* spp. were present in 60 % of plots in old-growth stands in southeast Alaska (Wallmo and Schoen 1980), making it not quite as common as on Haida Gwaii (98%).

Also in Alaska, Wallmo and Schoen (1980) reported that *Cornus canadensis* grew in 50 % and *Menziesia ferruginea* in 7.5 % of the plots, which indicates that *Menziesia ferruginea* was more abundant on Haida Gwaii than in southeast Alaska. Compared to Haida Gwaii, *Cornus canadensis* grew in 38 % of the plots and *Menziesia ferruginea* in 20 %. Cowan (1945) reported that *Gaultheria shallon* was browsed in 32 % of his plots, but present in 90%. I found that *Gaultheria shallon* was browsed in 95 % of the sampling sites (n = 22) and present in 31 % (n= 71). Because *Gaultheria shallon* is not the first choice (Pojar et al. 1980) of forage for deer, this difference could indicate that browse pressure is higher on Haida Gwaii.

Reforestation with *Thuja plicata* poses a problem on Haida Gwaii because Black-tailed Deer browse it heavily (Henigman and Martinz 2000). On Vancouver Island, Cowan (1945) found that 87% of *Thuja plicata* in his plots showed sign of browsing. Even though *Thuja plicata* is often a prominent member of the canopy, I found only *Thuja plicata* saplings in one sampling site and seedlings in 37 sites. Compared to findings in other areas where large percentage of the understory biomass is made up of crown species (Telfer 1972), the situation on Haida Gwaii differs. When deer browsing inhibits recruitment of *Thuja plicata* to the canopy, the climax forest species composition will change. Such browsing - induced changes have been observed in other areas of North America (Stromayer and Warren 1997).

My study showed that biomass varies incredibly regardless of geographic location, biogeoclimatic site series, and topography (Table 4, Table 6). This variation was most likely a result of factors such as the substrate (Alaback 1987), forest mosaic (Kirchhoff 1994) and browse pressure (Pojar et al. 1980). For example, the substrate influences the biomass estimates in the understory in southeast Alaska, where decomposed logs produced twice as much *Vaccinium parvifolium* biomass as root mounds, and fifty times more than on sites with duff (Alaback and Sidle 1986). Similar differences occurred for *Menziesia ferruginea* except that duff was the poorest growing medium. Because I did not distinguish between substrates, it was not possible to investigate these relationships in my study. Finally, the understory biomass in southeast Alaska correlated negatively with the density of canopy closure (Alaback 1982), another parameter that could influence the biomass estimates regardless of the browsing pressure.

Theoretically, a variety of understory species is important to deer because it spreads the prime nutritional stages of growth over a longer period (Wallmo and Schoen 1980), and noxious chemicals present in plants are diluted when consumed with a diet of mixed forage (MacArthur et al. 1993). This species diversity does not exist in old-growth forests on Haida Gwaii where I found three species of *Vaccinium*, *Menziesia ferruginea* and very few *Rubus spectabilis* and *Thuja plicata* (saplings). Moreover, overall species diversity was most likely impoverished even before the arrival of Black-tailed Deer because of its off-shore location (Banner et al. 1984). This impoverished flora may imply that the nutritional plane of deer on Haida Gwaii is lower than other areas. The role of a mixed diet for dealing with anti-quality compounds might not be as important on Haida Gwaii because, for example, monoterpene levels in *Thuja plicata* were found to be lower on Haida Gwaii that on the adjacent mainland (Vourc'h and Martin 1999).

Relationships between controlling factors and associated response variables are complex in many ecosystems (Garvey et al. 1998). The understory in forests is known to vary considerably (Ovington 1962), and biomass varies with canopy closure among other factors (Peek et al. 1971; Dodd et al. 1972; Messier et al. 1989; Chang et al. 1995; Saunders and Puettmann 1999). In this study, no correlations between canopy closure and understory biomass were found to explain the variation (Table 6).

Pojar and Banner (1982) observed an uneven impact of browsing on Haida Gwaii and attributed it to settlement, colonization unevenness, and general biogeographical principles. Except for Moresby Island, I was unable to find any general difference between deer densities based on distance or remoteness at least in old-growth forests (Figure 15), and I believe that enough time has passed to erase initial colonization unevenness.

In Alaska, topography influences plant growth, and for example, south-facing slopes had longer growing seasons (Klein 1965). One would think that a prolonged growing season would cause an increase in biomass. I did not find any differences between the north- and south-facing slopes amounts of aboveground ($U = 1056$, $p = 0.237$, $n = 99$), utilized ($U = 801.5$, $p = 0.606$, $n = 83$) and available ($U = 812$, $p = 0.674$, $n = 83$) biomass. Perhaps, the slope differences in my study sites were not as pronounced as those studies by Klein (1965).

When understory is scarce, only a few deer can maintain a denuded understory, so that any site variation that might have existed would be erased. It has long been known that deer will use forests without forage in the winter (Hamerstrom and Blake 1939), and it is generally accepted that thermal cover is one of the factors that drive deer into the forest when it is cold (Bunnell 1990). During the winter, deer reduce food intake (Jones 1975), reduce their metabolic rate (Bunnell 1990) and they can lose up to 30% of their weight without affecting survival (Potvin and Hout 1983). Site fidelity was the dominating response to major habitat changes on Vancouver Island (McNay 1995), so incremental changes such as over browsing must be unnoticed by deer. Thus Black-tailed Deer might habitually use the same old-growth forest stands regardless of the amount of food, contrary to what would be predicted by optimal foraging theory. Probably, deer rely on sources outside the old-growth stands and only use these for thermal protection.

The initial, unexploited niche that deer used on their arrival to Haida Gwaii has changed because of the high browse pressure. Because there is only one major herbivore, the Black-tailed Deer, only they could be responsible for changes to their realized niche. A change had to take place because the deer had only two options; either die of starvation or changes their diet. It has been shown that diet composition of Roe Deer change with increased population density (Maizeret et al. 1989) from a more nutritional diet to a less nutritional diet.

Fallow deer (*Dama dama*) foraging strategy was described as a biased random walk without complex search mechanisms, and this inhibited their ability to detect and exploit food patches (Focardi et al. 1996). The authors argued this strategy was justified by the fact that the food source was very common and of relative poor nutritional value. It could then be argued, because of the heavy exploitation of the most valued foods on Haida Gwaii, that deer are forced to utilize less nutritional but widely occurring species, and consequently could be expected to follow a similar forage strategy here.

5.3. Estimating relative deer densities, topography and remoteness.

Topography can influence pellet deterioration rates, and can hence affect pellet group estimates. Because moisture regimes influence the deterioration rate (Harestad and Bunnell 1987), pellets on north-facing slopes might deteriorate faster than pellet on south-facing slopes. However, I did not find such differences, suggesting that either the difference in deterioration rates is small or non-existent.

Areas with no road access on Moresby Island showed some differences in aboveground biomass and relative deer density. Generally, I did not find any differences between sampling sites close to villages and those further away, or between remote areas and easily accessed areas. Furthermore, the spatial distribution shows that relative deer density was highest in easily accessible areas. Daufresne and Martin (1997) detected a difference between survival of *Thuja plicata* saplings in remote areas on Haida Gwaii, and they suggested that it was the result of different browsing pressure. If the severe winters before my study had drastically reduced Black-tailed Deer populations, as anecdotal evidence suggests, that could explain why I did not find any general difference when comparing remote areas with easily accessed areas. A drastic decline in Black-tailed Deer killed by hunters was not seen in the 1999/2000 hunting season (Sean Sharpe, pers. comm., 2001), which might or might not support the notion that deer density had declined in the years before this study. Because Daufresne and Martin (1997) did not measure relative deer density, the deer densities could have been similar, and the difference in *Thuja plicata* survival rate caused by other factors.

5.4. Pellet group and biomass correlations.

I had expected to find relationships between aboveground, utilized and available biomass and relative deer density, similar to those demonstrated in Alaska. For example, in Alaska, deer density increased significantly with increased biomass of *Vaccinium parvifolium* (Kirchhoff 1994). I did not find a correlation between aboveground biomass 78
? utilized
and PG/ha (Table 5), but available biomass was weakly but statistically significantly correlated (Table 5). Part of the problem may be the temporal difference between the biomass estimates and the relative deer density estimates. For example, pellet groups persisted up to two years in the forests of Vancouver Island (Harestad and Bunnell 1987), and 6-8 months in the forests of southeast Alaska (Rose 1982; Schoen et al. 1985). The biomass estimates, on the other hand, reflect browsing history from at least the last seven years (Engelstoft, unpublished data). Accordingly, I developed a model as a framework for discussing potential causes of variation found in this study (Figure 23).

Figure 23: Conceptual model used to explain differences between high and low estimates of available biomass and pellet group densities.

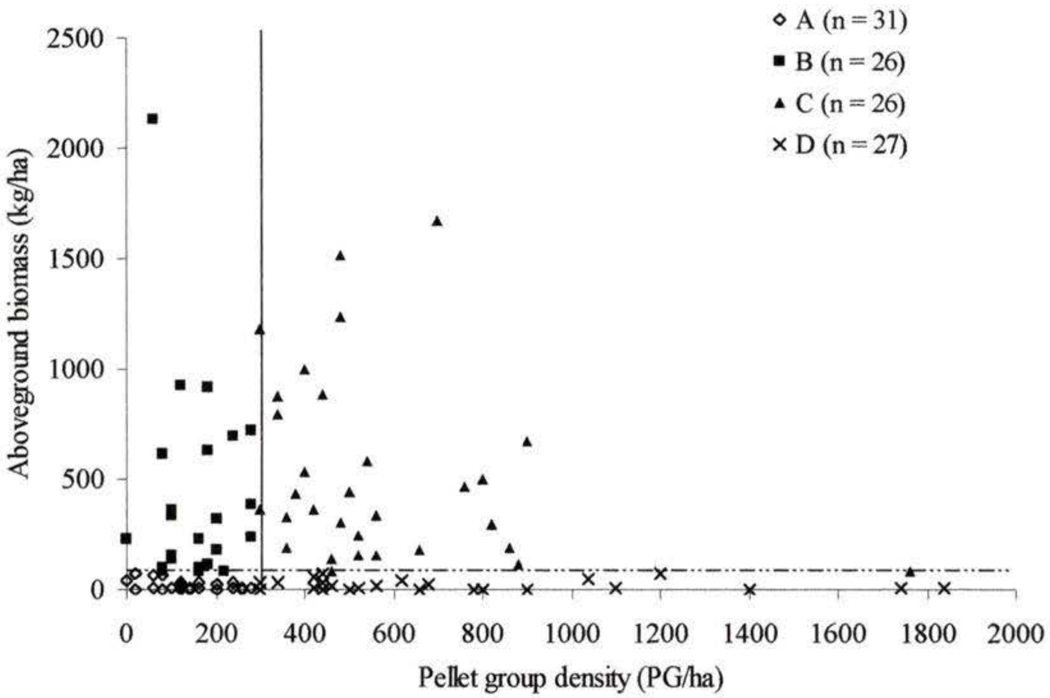
B: low PG/ha & high biomass	D: high PG/ha & high biomass
- Deer arrived recently - Browse out of reach - Forest mosaic	- Deer arrived recently - Browse out of reach - A heavily used corridor - Forest mosaic
A: low PG/ha & low biomass	C: High PG/ha & low biomass
- Long browse history but deer population crashed. - Poor growth condition - Few deer suppress vegetation	- Long browse history - Poor growth condition - A heavily used corridor

A site with high estimated aboveground biomass and high relative deer density might have experienced a recent invasion of deer, with the aboveground vegetation out of reach to the deer (Figure 23, D). Also, a few deer using an area intensively could result in a high pellet group count. A high pellet group count can also be the result of many deer using the area less intensively, for example in a heavily-used corridor. Finally, the surrounding forest mosaic influences the use of an area. In large homogeneous old-growth stands, like the sampling sites on the west coat of Moresby Island, the area must provide thermal cover, food and water (Bunnell 1990). In forest stands with diverse seral stages, the old-growth forest might only provide thermal cover and other seral stages supply food during most winters. This could cause an area with little understory to receive high use. The reason that a site falls in the A quadrant (Figure 23) could be either that it is a poor growing site and hence receives little use because there is no food, or a few deer are able to suppress any growth by browsing all current annual growth in a short time. It is important to recognize that substrate is controlling the growth potential of a site (Alaback and Sidle 1986), so sites with good growth will respond more quickly to a browse release than poor growing sites.

It did appear that aboveground biomass amounts were suppressed to a very low level when pellet group densities were greater than 950 PG/ha (Figure 12, Figure 17). Interestingly, four of the seven sampling sites (100, 101, 104, 105)(Figure 8) with more than 950 PG/ha were from the southeast corner of Moresby Island, an area with relative low canopy closure (<44 %). However, the stand is adjacent to an area with substantial logging, and possibly deer in the area seek refuge in this old-growth forest especially if site fidelity is different on Haida Gwaii than on Vancouver Island (McNay 1995). The remaining three sampling sites (52, 54, 92) in the same PG/ha range are also located in areas with substantial logging. However, many of the other sites are situated similarly, so there are also other factors that cause these high densities.

I divided the data using the median measurement into four almost equal groups of sampled sites ($n_A = 31$, $n_B = 26$, $n_C = 26$, $n_D = 27$; Figure 24). This partitioning of the data did not reveal any strong correlations between PG/ha and biomass that could be used to develop predictive models. Only utilized biomass of *Blechnum spicant* in group "B" correlated significantly with PG/ha ($r^2 = 0.495$, $p = 0.016$, $n = 23$).

Figure 24: Estimated aboveground biomass versus estimated pellet group densities grouped into four groups using median measurments of both pellet groups (solid line) and aboveground biomass (stipled line) as dividing points.



That understory biomass varies in old-growth forest is well known (Alaback and Sidle 1986), but the cause of this variation is not understood on Haida Gwaii. The large variability of understory biomass at low relative deer densities (Figure 12) might reflect local population oscillations of Black-tailed Deer combined with local soil nutrient and light regimes. These compounding factors might also explain why I did not find correlation between percent canopy closure and aboveground biomass estimates (Table 5).

5.5. Population dynamics.

Deer densities on Haida Gwaii appear to be lower than those in adjacent areas. The maximum estimate of 61 deer/km^2 is well below the maximum of 100 deer/km^2 reported in southeast Alaska (Kirchhoff 1994), and that expected in good quality, old-growth forest winter ranges on Vancouver (Bunnell 1990). The average deer density I estimated (13 deer/km^2) was considerably lower than on the smaller islands (Baltzinger and Martin 1998), and lower than the average (35.6 deer/km^2) found in southeast Alaska (Kirchhoff 1994), but much higher than one that Cowan (1945) reported from old-growth forests on the east coast of Vancouver Island. A rough estimate from the Tsitika Valley on Vancouver Island was 18 deer/km^2 (Smith and Davies 1975), which is more comparable with the average estimates from Haida Gwaii. The high variation between sampling sites on Haida Gwaii was similar to the situation in southeast Alaska (Kirchhoff 1994).

Peek (1980) grouped studies that tried to explain regulation of ungulate populations into two general models. One model suggests that predators control ungulate populations, and the other suggests that it is an interaction between ungulates and their habitat via such mortality factors as starvation. The population of deer on Haida Gwaii probably follows the latter model, which seems to make sense because there are no predators here.

Similar to the Himilyan Thar (*Hemitragus jemlahicus*) introduced into New Zealand (Caughley 1970), deer on Haida Gwaii probably went through four phases. The first phase was the irruption of the population, followed by a levelling off, followed by a population crash. The fourth phase was the equilibrium between vegetation biomass and herbivore density, with browsing as the driving force. Vegetation biomass must be the density-dependent factor that constitutes the ultimate self-regulating mechanisms for population dynamics (Maizeret et al. 1989).

Unfortunately, the deer population on Haida Gwaii has not been monitored continually. However, in the mid-1970's the pellet group density averaged 926 PG/ha for elevations below 450 m (Hatter and Steiger 1974). These estimates are well below the average of 402 PG/ha (SD = 362) found in my study, and this could suggest a decline in deer populations between then and now. A declined in numbers of deer killed by hunters, regardless of an increase in effort, also points towards a population decline in the past decades. Hunting statistics might not be a good indicator because they depend strongly on the socio-economic situation, which has forced many people to leave the islands (Sean Sharpe, pers. comm. 2001). Local hunters had noticed a considerable die-off in the two winters before this study. If my surveys followed immediately after a population crash, any correlation between vegetation biomass and relative deer density that might have been present would most likely have been erased. There simply has not been enough time for the vegetation to respond to the browse release (Figure 23).

After the initial introduction of Black-tailed Deer, colonization of the islands might have followed the "rolling wave of density" model put forth by Caughley (1970) and Riney (1964). What controlled the Black-tailed Deer population after it was established? Klein and Olson (1960) suggested that the severity of the winter controlled the deer population in southeast Alaska, and long-term monitoring programs in Poland and Belarus showed also that severe winters decimated Roe Deer populations (Jedrzejewska et al. 1997). On the other hand, Maizeret et al. (1980) concluded that ultimately density-dependent factors are the mechanisms that regulate populations. Considering the low amount of available biomass in potential winter ranges, it seems that winter forage might be the controlling factor on Haida Gwaii.

5.6. Management recommendations and future research.

Efficient management of deer populations requires an understanding of the population (Caughley 1976), so the first step to manage the deer on Haida Gwaii is to gather relevant population information. Because no reliable information on population trends exists for the islands, it is paramount to initiate a monitoring program. This is relatively easily accomplished by establishing pellet group inventory sites throughout the islands following the Resource Inventory Committee standards (Resource Inventory Committee 1998). Subsequently, it is necessary to establish at which the level the deer population is acceptable, and determine how to reach this goal. Another option is to develop a model that incorporates the forest stand mosaic, stand age, relative deer density and available biomass to predict the temporal and spatial deer population fluctuations. This would provide managers with another tool to manage the deer population and predict temporal changes.

This project was planned to look at a selected group of species that was known to be an important component of the deer diet in other areas. Because it was initially thought to be too time consuming to estimate *Gaultheria shallon* biomass, I opted for surveying this species in a different way. In retrospect it would have been better to develop a procedure to estimate *Gaultheria shallon* biomass, so it could have been included in the total understory biomass. Future research should investigate the geographic biomass distribution of the understory shrubs, including *Gaultheria shallon*, on Haida Gwaii.

The variability of understory biomass and relative deer density could be investigated further in an attempt to understand why some areas have relatively large amounts of biomass or pellet groups whereas others close by do not. It is interesting that I did not find a correlation between canopy closure and aboveground biomass, and this warrants further attention. A study on gap dynamics could shed light on the canopy recruitment and further our understanding of browsing's impact on the climax forest.

Finally, to manage the deer population on Haida Gwaii it will be necessary to investigate population processes. To know a population size gives no information about rate of change of the population, which is a function of age distribution, sex ratio, fecundity and survivorship (Caughley 1970). So, in addition to monitoring the deer population, studies will be needed at the "process" level.

6. Conclusions.

Because "forest fragments and islands may be at greatest risk for loss of tree species from deer browsing" (Stromayer and Warren 1997), Haida Gwaii, as an island with a highly fragmented forest, can expect changes in the climax forest if current browsing pressure persists. The lack of saplings of canopy species such as *Thuja plicata* in the understory supports this prediction. The understory already appears to have undergone substantial changes on Haida Gwaii compared to an earlier report by Hopkinson (1931), and the results reported by Pojar et al. (1980) when comparing understory on Haida Gwaii with the mainland of British Columbia. The well documented correlation between canopy closure and aboveground biomass estimates, which is found in many other (Dodd et al. 1972; Messier et al. 1989; Saunders and Puettmann 1999), is also lacking. Even though amount of understory biomass varies tremendously at low relative deer densities, it appears to taper off at higher densities (Figure 12). It appears that browsing is capable of suppressing the forest understory. Because low biomass also occurs at low deer densities, other factors also may influence the amount of understory. The low amounts of available biomass in the old-growth stands likely cause Black-tailed Deer to starve during severe winters when they seek thermal cover in these stands. Winter ranges do not provide much food for the Black-tailed Deer to survive on, and this low amount of food most likely influences their survival during severe winters.

? long term maybe

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Appendix

Appendix 1: Biomass estimation (kg/ha) and pellet group (PG) counts on sampling sites on Haida Gwaii, March and April, 2000. Empty cell indicate no data. (AG=Aboveground biomass, AV = available biomass, UT = utilized biomass, Cc = *Cornus canadensis,* Bs = *Blechnum spicant,* Vp = *Vaccinium parvifolium,* Vx = *Vaccinium ovalifolium/alaskaense,* Mf = *Menziesia ferruginea,* Tp = *Thuja plicata,* Gs = *Gaultheria shallon.* Gs followed by "s" and "t" denote shrub plot or transect sampling, e.g. GS-t, and for other species "s" preceding species name indicate seedling e.g. sTp).

site #	Zone	Easting	Northing	PG/ ha	Cc AG^1	Bs AG^1	Vac AG^2	Mf AG	Tp AG^1	sTp AG^1	Rs AG^1	Total Ag	Cc AV	Bs AV	Vac AV	Mf AV	Rs Av	Total AV	Cc UT	Vac UT	Mf UT	Bs UT	Total UT	Gs s-AG	Gs-S UT	Gs t-PG
7	8	687220	5918220	240	0	0	700	0	0	0	0	766	1	0			0		0			0				0
8	8	687960	5920400	100	0	0	147	0	0	0	0	156	0	0	2	0	0	2	0	7	0	0	7			0
9	8	687350	5918400	300	0	0	1183	0	0	0	0	1298	0	0			0		0			0				0
10	8	688300	5920160	400	0	0	530	0	0	1	0	592	0	1	13	0	0	15	0	8	0	0	9			0
11	8	689960	5909350	60	0	0	2134	0	0	0	0	2391	1	1			0		0			0				0
12	8	689960	5909650	480	0	0	1512	0	0	0	0	1708	0	1	16	0	0	17	0	3	0	3	5			0
15	9	308281	5901949	0	0	0	40	0	0	0	0	45	0	2			0		0			4				95
16	9	308281	5901299	460	0	0	140	0	0	0	0	152	0	25			0		0			21				51
17	8	687630	5888730	820	2	0	284	11	0	0	0	326	0	0	4	0	0	4	1	4	1	0	5			0
18	8	683320	5922420	760	0	0	470	0	0	0	0	518	0	0	10	0	0	10	0	13	0	0	13			0
19	8	683450	5922380	900	0	0	669	0	0	0	0	745	0	0	0	0	0	0	0	12	0	0	12			0
20	8	683540	5922560	540	0	0	583	0	0	0	0	648	0	0			0		0			0				0
21	8	683380	5922530	160	0	0	230	0	0	0	0	249	0	1			0		0			1				0
22	8	663616	5934816	280	0	0	7	0	0	0	0	7	0	0			0		0			1				0
23	8	663746	5934576	280	0	0	236	0	0	0	0	272	0	1			0		0			2				0
24	8	663896	5935768	700	0	9	1669	0	0	0	0	1991	0	6			0		0			3				0
25	8	663720	5935658	380	1	0	432	0	0	0	0	485	1	0			0		0			0				1
27	8	676590	5920157	340	0	0	880	0	0	0	0	994	0	0	32	0	0	32	0	11	0	0	11			0
28	8	676180	5919940	480	0	0	307	0	0	0	0	334	0	0	9	0	0	9	0	10	0	0	10			0
29	8	676518	5920964	360	0	1	187	0	0	0	0	210	0	1			0		0			0				0
30	8	676612	5920780	480	0	0	1239	0	0	0	0	1446	0	0			0		0			0				0
31	8	664160	5935084	360	6	1	312	0	0	0	0	359	1	0	5	0	0	7	14	0	0	0	15			0
32	8	664036	5935324	520	0	0	245	0	0	0	0	279	0	0	1	0	0	1	0	1	0	0	1			0
33	8	692440	5921080	180	0	0	114	0	0	0	0	131	0	0	2	0	0	2	0	3	0	0	3			0
34	8	692340	5921260	60	0	0	62	0	0	0	0	68	0	0	4	0	0	4	0	0	0	0	0			0
35	8	692380	5920940	560	1	3	332	0	0	0	0	372	0	2			0		1			2				1
36	9	305200	5941470	120	0	0	0	0	0	0	0	0	0	0			0		0	0	0	0	0			0
37	8	692640	5921040	440	0	1	26	0	0	4	0	32	0	0	9	0	0	13	0	0	0	1	1			0
40	8	665268	5936220	60	0	11	12	0	0	0	0	24	0	3			0		0			8				0
41	8	665100	5936072	800	3	6	502	0	0	0	0	572	0	5			0		0			1				0
42	8	664960	5935300	0	0	1	230	0	0	0	0	255	0	0	2	0	0	3	0	1	0	0	1			0
43	8	664700	5935600	240	0	4	31	0	0	0	0	37	0	1	2	0	0	2	0	2	0	3	5			0
44	8	665360	5935920	80	0	2	617	0	0	0	0	698	0	1	11	0	0	12	0	2	0	1	2			0
45	8	665340	5935540	120	0	11	34	0	0	0	0	47	0	7	3	0	0	10	0	1	0	4	5			0
46	8	666400	5928620	300	0	2	30	0	0	0	0	35	0	1	1	0	0	2	0	2	0	1	3			0
47	8	667658	5928300	660	0	3	0	0	0	0	0	3	0	1	0	0	0	1	0	0	0	2	2			0
48	8	666680	5928380	140	0	1	1	0	0	0	0	2	0	0			0		0			1				0
49	8	666920	5928466	160	0	1	5	0	0	0	0	7	0	0			0		0			1				0
50	8	680200	5918160	400	2	3	987	9	0	0	0	1109	1	1	23	2	0	27	2	2	0	2	6			18
51	8	685560	5935180	20	3	1	35	34	0	1	0	76	1	1	3	2	0	6	0	0	0	0	1	777	1	832
52	8	686330	5936320	1200	0	1	70	0	0	5	0	85	0	1	0	0	0	6	0	2	0	0	3	124	3	119
53	8	689960	5910380	440	3	0	885	1	0	0	0	977	2	0	21	0	0	23	1	2	0	0	3	0	0	1

Appendix 1 continued.

site #	Zone	Easting	Northing	PG/ ha	Cc AG^1	Bs AG^1	Vac AG^2	Mf AG	Tp AG^1	sTp AG^1	Rs AG^1	Total Ag	Cc AV	Bs AV	Vac AV	Mf AV	Rs Av	Total AV	Cc UT	Vac UT	Mf UT	Bs UT	Total UT	Gs s-AG	Gs-S UT	Gs t-PG
54	8	685420	5935380	100	0	0	142	0	0	0	0	158	0	0	4	0	0	4	0	1	0	0	1	382	3	265
55	8	686230	5936500	200	0	2	180	0	0	0	0	205	0	0	0	0	0	0	0	1	0	2	3	481	4	527
56	8	658220	5959600	120	0	7	7	0	0	0	0	15	0	2	0	0	0	2	0	1	0	5	6	62	2	32
57	8	659640	5960420	1100	0	2	5	0	0	0	0	8	0	2	0	0	0	2	0	0	0	1	1	12	7	0
58	8	659960	5960680	200	0	1	320	0	0	0	0	366	0	0	1	0	0	1	0	1	0	0	1	0	0	0
59	8	660380	5960480	520	0	0	158	0	0	0	0	177	0	0	0	0	0	0	0	0	0	0	0	0	0	0
60	8	659120	5959580	120	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0
61	8	658700	5959950	260	0	1	10	1	0	0	0	14	0	0	0	0	0	1	0	2	0	1	3	302	29	425
62	8	652500	5957490	440	0	2	0	0	0	0	0	2	0	1	0	0	0	1	0	0	0	1	1	0	0	0
63	8	652680	5957630	900	3	2	0	0	0	0	0	5	1	1	0	0	0	2	0	0	0	1	1	0	0	0
64	8	652900	5957630	800	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
65	8	654730	5958630	780	0	3	1	0	0	2	0	5	0	2	0	0	0	4	0	0	0	1	1	0	0	0
66	8	655080	5958340	440	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
67	8	655500	5958500	100	0	5	7	0	0	0	0	13	0	3	0	0	0	3	0	1	0	2	3	0	0	0
68	9	316620	5862040	560	0	0	12	0	0	0	0	14	0	0	1	0	0	1	0	1	0	0	1	0	0	0
69	9	316600	5862480	520	0	2	5	0	0	0	0	8	0	2	0	0	0	2	0	0	0	0	1	0	0	0
70	9	319120	5863120	440	0	3	1	0	0	0	0	4	0	1	0	0	0	0	0	1	0	2	3	0	0	0
71	9	319800	5863440	260	0	2	1	0	0	0	0	3	0	0	0	0	0	0	0	0	0	1	2	0	0	0
72	9	317340	5870060	680	10	2	5	0	0	0	0	17	3	2	0	0	0	5	16	1	0	0	17	544	2	715
73	9	317300	5869740	500	3	0	0	0	0	0	0	4	2	0	0	0	0	2	1	0	0	0	1	235	2	306
74	9	316080	5869910	140	0	2	1	0	0	0	0	3	0	1	0	0	0	1	0	0	0	1	1	0	0	0
75	9	316080	5869810	300	0	1	1	0	0	2	0	3	0	1	0	0	0	2	0	0	0	0	0	0	0	0
76	9	304360	5874940	120	0	3	8	0	0	0	0	12	0	3	1	0	0	5	0	0	0	0	0	437	4	752
77	9	304660	5875060	80	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	8	676000	5916840	280	3	7	716	0	0	0	0	787	0	4	8	0	0	12	1	1	0	3	6	0	0	6
79	8	676240	5916000	180	1	2	628	0	0	0	0	695	0	1	11	0	0	12	0	1	0	1	2	0	0	0
80	8	674180	5917860	80	0	0	86	0	0	0	0	95	0	0	2	0	0	2	0	1	0	0	1	0	0	0
81	8	674520	5918160	260	0	0	2	0	0	0	0	0	0	0	5	0	0	5	0	7	0	0	7	0	0	0
83	9	307250	5898850	100	0	1	159	0	0	0	0	178	0	1	1	0	0	2	0	0	0	0	1	0	0	0
84	9	306250	5898600	340	0	2	36	1	0	0	0	42	0	1	2	0	0	3	0	1	0	1	3	0	0	0
85	9	305200	5895700	620	0	0	44	0	0	0	0	48	0	0	2	0	0	2	0	4	0	0	4	0	0	0
86	9	305400	5895500	200	0	0	25	0	0	0	0	28	0	0	4	0	0	4	0	2	0	0	2	0	0	0
89	8	697302	5909680	120	18	8	867	0	0	1	0	978	2	7	7	0	0	17	59	3	0	2	63	0	0	0
90	8	674140	5928100	160	0	1	32	0	0	0	0	36	0	1	7	0	0	8	0	1	0	0	1	0	0	0
91	8	674440	5928380	80	6	0	85	1	0	1	0	93	1	0	1	0	0	4	7	2	0	0	9	0	0	0
92	8	673420	5930040	120	0	2	13	0	0	0	0	15	0	1	0	0	0	2	0	1	0	1	3	0	0	0
93	8	673360	5930160	160	4	1	1	0	0	0	0	6	1	1	0	0	0	2	4	0	0	0	5	0	0	2
94	8	691750	5910320	1760	1	0	81	0	0	0	0	87	1	0	0	0	0	0	0	14	0	0	14	0	0	0
95	8	688250	5908840	860	0	0	190	0	0	0	0	199	0	0	9	0	0	9	0	22	0	0	22	0	0	0
96	8	687570	5927200	440	1	6	65	0	0	5	0	85	1	5	0	0	0	12	0	1	0	0	2	333	14	272
97	8	687680	5926910	460	1	3	4	0	0	13	0	21	1	1	0	0	0	15	0	2	0	1	3	62	7	172
98	8	688200	5928050	220	7	10	74	0	0	2	0	100	1	8	3	0	0	14	4	5	0	2	11	417	30	469

site #	Zone	Easting	Northing	PG/ ha	Cc AG[1]	Bs AG[1]	Vac AG[2]	Mf AG	Tp AG[1]	sTp AG[1]	Rs AG[1]	Total Ag	Cc AV	Bs AV	Vac AV	Mf AV	Rs Av	Total AV	Cc UT	Vac UT	Mf UT	Bs UT	Total UT	Gs s-AG	Gs-S UT	Gs t-PG
99	8	696640	5909270	300	1	2	342	16	0	0	0	362	1	2	4	0	0	7	0	3	0	0	4	0	0	0
100	9	316720	5882480	1740	0	14	5	0	0	3	0	23	0	4	1	0	0	8	0	1	0	10	11	115	6	137
101	9	316940	5882580	1400	0	1	0	0	0	1	0	3	0	1	0	0	0	2	0	1	0	0	1	58	3	147
102	8	698850	5910550	180	1	1	916	0	0	0	0	918	1	0	17	0	0	18	0	6	0	0	6	0	0	0
103	8	698850	5910800	420	1	0	356	0	0	1	0	358	0	0	5	0	0	6	0	11	0	0	11	0	0	0
104	9	315060	5882300	1040	0	2	48	0	0	0	0	57	0	1	0	0	0	1	0	2	0	1	4	0	0	0
105	9	315220	5882500	1840	0	1	5	0	0	0	0	6	0	0	0	0	0	0	0	2	0	1	2	0	0	0
106	8	684900	5887150	880	0	0	44	73	0	0	0	120	0	0	0	92	0	86	0	22	0	0	22	0	0	0
107	9	321400	5887250	660	0	0	179	0	0	0	0	202	0	0	0	0	0	0	0	3	0	0	3	159	14	62
108	9	301950	5887500	200	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0	3	0	0	3	12	0	1
109	9	306420	5896980	160	1	0	80	2	0	0	0	90	0	0	10	0	0	10	0	3	0	0	3	0	0	0
110	8	682100	5882750	20	0	1	1	0	0	0	0	3	0	1	0	0	0	0	0	2	0	1	2	0	0	0
111	8	681450	5883350	140	0	4	5	0	0	0	0	9	0	1	2	0	0	3	0	1	0	3	3	0	0	0
112	8	681450	5882600	160	3	2	94	0	0	4	0	113	1	2	0	0	0	6	1	2	0	0	3	0	0	3
113	8	681400	5882100	100	0	1	362	0	0	0	0	410	0	1	0	0	0	1	0	2	0	0	2	0	0	4
114	8	680050	5880650	420	0	1	7	0	0	0	0	9	0	0	0	0	0	0	0	5	0	1	5	0	0	0
115	8	680000	5881050	100	0	0	315	19	0	0	0	379	0	0	0	0	0	0	0	2	1	0	3	12	10	0
116	8	679350	5879300	420	0	3	60	0	0	0	0	70	0	2	0	0	0	2	0	2	0	1	3	0	0	2
117	8	679800	5879050	80	1	2	65	0	0	1	0	76	0	1	0	0	0	2	0	0	0	1	1	0	0	0
118	8	678250	5880600	280	0	0	383	0	0	0	0	435	0	0	0	0	0	0	0	1	0	0	1	0	0	0
119	8	683400	5882500	240	0	3	12	0	0	0	0	15	0	2	0	0	0	3	0	1	0	1	2	0	0	0
120	8	684250	5882200	120	0	4	5	17	0	0	0	27	0	3	0	3	0	3	0	6	1	1	8	0	0	0
121	8	666780	5918380	560	4	0	145	6	0	6	0	177	2	0	0	1	0	6	0	12	1	0	14	242	48	64
122	8	680760	5916950	340	1	3	127	663	1	3	0	798	1	1	2	1	0	9	0	6	1	2	8	115	2	51
123	8	699350	5880050	500	8	0	74	371	0	0	0	462	1	0	0	0	0	0	0	8	2	0	10	311	10	546
124	8	684750	5886750	460	0	76	71	0	0	0	30	178	0	76	0	3	30	93	1	4	0	0	5	0	0	0
Average				402	1	2	234	11	0	1	0	276	0	2	3	1	0	7	1	3	0	1	5	73	3	55
Standard deviation				362	2	8	381	72	0	2	3	432	1	8	6	10	3	14	6	4	0	2	8	158	8	159
Max				1840	18	76	2134	663	1	13	30	2391	3	76	32	92	30	93	59	22	2	21	63	777	48	832
***N*[3]**				110	110	110	110	110	110	110	110	110	110	110	91	91	110	91	110	92	92	110	92	71	71	110
***n*[4]**				108	43	86	109	19	1	35	1	109	42	102	80	20	1	79	18	87	14	83	91	21	20	37
Median				300	0	1	68	0	0	0	0	86	0	1	0	0	0	3	0	1	0	0	3	0	0	0

[1] included in total available biomass estimate

[2] not included in the total utilized biomass estimate

[3] number of sites surveyed

[4] number of sites where plant or PG occurred

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Title of Thesis:

Effect of Sitka Black-tailed Deer (Odocoileus hemionus sitkensis) on understory in old-growth forest on Haida Gwaii (Queen Charlotte Islands), British Columbia

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