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Walking with wapiti: measuring late Holocene climatic variability through Cervus elaphus abundance and stable isotope analysis in the Gulf of Georgia Region

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Walking With Wapiti: Measuring Late Holocene Climatic Variability Through *Cervus elaphus* Abundance and Stable Isotope Analysis in the Gulf of Georgia Region.

By

Angus Michael David Tierney

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Arts

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Walking With Wapiti: Measuring Late Holocene Climatic Variability Through *Cervus elaphus* Abundance and Stable Isotope Analysis in the Gulf of Georgia Region.

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Arts

by
Angus Michael David Tierney
June 2012
Abstract

Native hunters of the Northwest Coast valued the local wapiti subspecies (*Cervus elaphus roosevelti*) greater than any other land animals as a source of both food and raw materials for tools. Wapiti population size depends on the quantity and quality of their preferred foods: easily digestible, high protein plants that occur most abundantly in meadows and thickets, particularly after spring and summer rains. Changing climate regimes affected the productivity of these foods but there is disagreement about whether climate periods with long dry summers helped or hindered wapiti populations on the Northwest Coast. Lepofsky et al. (2005) suggests wapiti abundance increased in periods with persistent summer drought due to increased fire frequency destroying forests and expanding meadows, and increasing the productivity of their preferred foods. While Broughton et al. (2008) suggests wapiti abundance decreased in periods with low spring-summer precipitation due to reductions in the duration and forage quality of the growing season.

The goal of this thesis is to eliminate one of these hypotheses with a systematic analysis of wapiti remains from six sites in western Whatcom County representing 300 to 5300 cal yr BP. Stable isotope analysis of nitrogen and carbon in wapiti bone collagen from contexts closely associated with radiocarbon dates. Mammal remains from levels closely associated to these radiocarbon dates were separated and counted to determine mammal NISP, and wapiti remains were identified to determine wapiti NISP. The relative abundance of wapiti was determined by dividing wapiti NISP by mammal NISP and converting to a percentage for each radiocarbon date, and for each climate period. Relative wapiti abundance was found to be dependent on climate period, with significantly lower wapiti abundance relative to other mammals during hot, dry climate periods. The δ¹³C values are low compared to other regions worldwide and remain stable through time suggesting that closed canopied
temperate rainforests were the dominant terrestrial environment over the last 5300 calendar years. During the Medieval Warm period $\delta^{15}$N values are significantly higher suggesting that the hottest driest conditions of the late Holocene occurred at that time. During the warm dry climate periods such as the Medieval Warm Period, increased seasonality would lead to reduced hunting return and plant forage rates for people.
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I am grateful to the staff at the Center for Archaeology, Materials and Applied Spectroscopy at Idaho State University for conducting the stable isotope analysis. Kelli Barnes was invaluable in answering my questions on stable isotope analysis and in assisting me with the preliminary steps, while Dr. Bruce Finney helped me in interpreting the data.

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Chapter 1. Introduction

Wapiti (*Cervus elaphus*) were the most important terrestrial faunal resource to prehistoric societies in the Gulf of Georgia region of the Northwest Coast, and consequently make up a significant part of most archaeological mammalian faunal assemblages (Harpole and Lyman 1999). Their importance primarily has to do with their size; the native Roosevelt wapiti (*Cervus elaphus roosevelti*) is the largest subspecies of wapiti worldwide, with healthy bulls weighing 700 to 1,000 lbs and cows weighing 400 to 700 lbs (Schwartz and Mitchell 1945). Their large size provides a large return rate for hunters who gain hundreds of pounds of meat by killing a single individual. Along with subsistence, wapiti were also valuable as a source of tool raw material (Thomas and Toweill 1982) and before their extirpation in the 19th century, they were available in the lowlands used by people as primary residence (Harpole and Lyman 1999). Changes in the abundance and availability of wapiti would have critically affected prehistoric indigenous societies.

The coastal Pacific Northwest has been witness to a series of climate shifts during the Holocene which began 11,500 cal yr BP (Calendar years Before Present). Shifts in climate regimes would have affected the abundance of wapiti by altering the quality and quantity of forage, affecting the distribution of habitats, changing the duration of the plant growth season, and changing the predictability and extremes of climate. Yet there is disagreement about whether climate regimes typified by short, wet winters and long summer droughts would result in increase wapiti abundance (Lepofsky et al. 2005), or decreased wapiti abundance (Broughton et al. 2008).
Wapiti are an ecotonal species that eat a mixture of woody plant leaves and shoots (browse) and annual herbaceous forbs and grasses. They maintain the highest population densities in habitats that provide a mixture of these plant types such as meadow-forest ecotones and brushy thickets (Bobek et al. 1984, Lantham et al. 1997, Prokesova et al 2006). In climate regimes typified by long summer drought increased fire frequency would increase the size of these preferred habitats (Marlon et al. 2006, Enache and Cumming 2009). Lepofsky et al. (2005:278) argues that wapiti and deer (*Odocoileus* spp.) are more likely to survive the winter and spring with the increased forage associated with more open ecosystems and meadow-forest edge.

However Broughton et al. (2008:1917) argues that period characterized by summer droughts depress artiodactyl populations (including wapiti) due to reductions in the duration and forage quality of the growing season and the miss-timing of reproduction when seasons favorable for birth are shorter and less regular. Spring and summer rains are important for plants to form new growth which is easily digestible and nutritionally important to nursing cows recovering from winter deprivation (Merrill et al. 1995). Periods of summer drought would also see increased variability of resource distribution which is detrimental to the social bonding of wapiti and results in smaller group sizes and smaller wapiti populations (Jenkins and Starkey 1982, Kamler et al. 2008).

Broughton et al. (2008:1918) also argues that larger mammals such as wapiti are more likely to miss favorable conditions for calving due to their longer and more variable gestation periods. Because of their greater size, Roosevelt wapiti have the longest gestation periods of wapiti subspecies (Schwartz and Mitchell 1945). Recruitment rates for Roosevelt wapiti are also much lower than other subspecies due to fewer cows getting pregnant annually and a lower calf survival rate (Starkey et al. 1982). These characteristics of Roosevelt wapiti make them
particularly sensitive to shorter plant growing season and could result in decreased wapiti abundance during climate periods with long summer droughts.

Paleoclimatologists have divided the Holocene of the coastal Pacific Northwest into periods of hotter, drier condition and cooler, wetter conditions (Ryder and Thompson 1986, Hallet et al. 2003, Grove 2004, Reyes et al. 2006, Arsenault et al. 2007, Koch and Clague 2011). Many different methods are used to reconstruct the climate and environment of different periods (see Chapter 3), but one method that has not been used in climate and paleoenvironmental reconstruction of the coastal Pacific Northwest is stable isotope analysis of terrestrial mammals. The stable carbon and nitrogen isotope signatures of animal bone collagen reflect the average climate and environmental conditions over the life of the individual (Heaton 1999). In hot, dry periods climate and environmental factors result in a net enrichment in the δ^{13}C and δ^{15}N values of plants, while in cool, wet periods these factors result in net depletion of plant δ^{13}C and δ^{15}N values (Van Klinken et al 1994, Amudson et al 2003). Because of this effect, a stable isotope analysis of carbon and nitrogen in wapiti bone collage could independently test the validity of these climate periods as well as measure the relative strength.

In this thesis I will explore how climate regimes during the mid to late Holocene affected wapiti populations on the coastal Pacific Northwest. All dates are presented as calendar years before 1950 AD (cal yr BP) original radiocarbon dates were calibrated into calendar years using OxCal v4.1.7 (Bronk Ramsey 2010). Chapters 2 through 5 provide detailed descriptions of wapiti, prehistoric subsistence, climate, and stable isotope analysis. Chapter 6 details the sampling and methods used to calculate the relative wapiti abundance and to conduct stable isotope analysis. The results of this study are given in Chapter 7, while in Chapter 8 I discuss the implications of
this study in understanding Northwest Coast prehistory, and will explore further avenues for study. Chapter 9 provides a final summary of the main findings and implications of this study.
Chapter 2. Wapiti

In western Washington the largest-bodied terrestrial mammal is the Roosevelt elk or wapiti (*Cervus elaphus roosevelti*). Wapiti are cosmopolitan in North America, adapting to a wide range of environments by modifying their diet, home range size, and group structure (Fryxell et al. 2008, Long et al. 2008, Visscher and Merrill 2009). Dense, closed canopy forests offer protection from predators and weather extremes but forage is low quality and dispersed. In such habitats wapiti respond by ranging over large areas in small groups and eating more shrubs and trees (Kamler et al. 2008, Schaefer and Morrelet 2008, Wilson and Ruff 1999). In more open environments where high quality forage is plentiful, wapiti range over smaller areas in larger groups and eat more grass and herbaceous annuals, (Stubblefield et al. 2006). The optimal environment for wapiti is a patchy environment of both meadows and forest where a mixture of protection and high quality forage sustain the highest population densities (Bobek et al. 1984). This is consistent with Leopold’s law of interspersion where game is found concentrated in edge environments (Leopold 1931:133).

*Cervus elaphus* subspecies

Wapiti are divided into many different sub species that live around the world and vary in some minor respects (Figures 2.1, 2.2). North American elk or wapiti are the same species as Eurasian red deer and were separated 10,000 years ago with the flooding of Beringia (Bryant and Maser 1982). While red deer have a reddish brown coat and weigh between 220 and 550 pounds American wapiti have brown and grey coloring, and most are larger (Clutton-Brock 1986). There
are four extant subspecies in North America: Roosevelt wapiti (*Cervus elaphus roosevelti*) Rocky Mountain wapiti (*C. e. nelsoni*) Tule wapiti (*C. e. nannodes*) and Manitoban wapiti (*C. e. manitobensis*). Rocky Mountain wapiti (*C. e. nelsoni*) weigh between 440 and 770 pounds and are originally from the Rockies but have been introduced around the world after local subspecies were expurgated by humans (Bryant and Maser 1982). Manitoban wapiti survive in pockets in central Canada while the Tule wapiti live in south central California and are similar in size to red deer.

Roosevelt wapiti are indigenous to the Pacific Northwest and are the biggest extant subspecies worldwide with bulls weighing between 700 and 1,000 pounds, and cows weighing between 400 and 700 pounds. (Schwartz and Mitchell 1945). The large size of Roosevelt wapiti and thus smaller surface area to volume ratio makes them more susceptible to heat stress than other wapiti subspecies (Witmer and deCalesta 1983). Roosevelt wapiti have very low reproductive rates when compared to Rocky Mountain wapiti, with 50% of cows pregnant annually compared to 90% of Rocky Mountain wapiti. Recruitment rates of 30% for Roosevelt wapiti calves are also lower than Rocky Mountain wapiti’s 70-90% recruitment rates (Starkey et al. 1982). Their large size and low recruitment rate are adaptations to the the old growth temperate rainforest habitat they evolved in, which is characterized by a mild, stable climate and low forage quality.
Figure 2.1. Modern North American range of *Cervus elaphus* and subspecies distribution (Bryant and Maser 1982:25).

Figure 2.2. Modern European range of red deer (*Cervus elaphus*) and locations of red deer studies (adapted from ICUN 2011). 1, Bialowieza National Forest, a deciduous forest studied in Kalmer (2008); 2, Mountains of Poland, coniferous forest studied in Bobek et al. (1984); 3, Czech Republic deciduous forest studied in Prokesova et al. (2006); 4, Rhum moors studied in Stains et al. (1982); 5, Highland moors studied in Lantham et al. (1997) and Wlodzimierz et al. (2006).
Common Habitats

Wapiti are found in many different environments around the world and in each region, wapiti adapts to the environment by modifying its behavior (Bryant and Maser 1982). Each region has different plants, a different *Cervus elaphus* subspecies and different environmental conditions. In North America, forests cover most of the marginal land that wapiti survive in, yet before they were hunted out they ranged over the continent south of Canadian boreal forests except the humid southeast and deserts (Skovlin et al. 1983). Wapiti habitat includes coniferous and deciduous forests, meadows, moors, seres and wetlands. These habitat types occur in many different regions across North America and Eurasia but each region has a unique mix of plant species that create unique conditions. Understanding how wapiti adapts its behavior to different extant environments allows a better understanding of how the may have responded to past climate changes.

Coniferous Forests

Douglas fir forests cover most of the Cascade and Coast Range mountains which stretch from Northern California into Western British Columbia. The maritime climate of this region is known for high precipitation and mild summers and winters. Forests are important wapiti habitat because they moderate harsh temperatures, prevent snow from piling too deep, and hide wapiti from predators. Yet these forests are poor foraging habitat for wapiti as mature forests lock up most energy into cellulose and little energy goes to edible foliage (Burchard 2003:32). In wet coniferous forests only ferns and a few shrubs and forbs like oxalis peek out under the dark canopies, while in drier areas grasses grow in small tufts (Starkey et al. 1982:353). Areas of old growth where the oldest trees are over 350 years a more substantial understory of seedlings
develops that the density of younger forests prevents (Krukeberg 1991:130). Because wapiti seek out forbs and grass, most of their food comes from where the canopy gives way to riparian zones, meadows, or fire seres.

**Seres**

In heavily forested regions the most important habitat for wapiti are seres created by fires, tree falls, and logging to a lesser extent (Skovlin et al. 1983). Fire scorched forests lose shady canopies while new plants find enriched soils open to sunlight and explode in growth. Seres have an abundance of forbs and shrubs, more grass than forests but less than meadows (Bartos and Mueggler 1980). In the Cascade region these new plants include many of wapiti’s preferred forage such as *Vaccinium spp.* berries, nettles (*Urtica dioica*), oaks (*Quercus spp.*) and fireweed (*Epilobium angustifolium*). Bartos and Mueggler (1980) found that fireweed increased by 60% after fire hit a forest, and new grass growth following fire has over three times more protein (Skovlin et al. 1983). Because of high protein levels and preferred highly digestible forage, seres are an important part of forested wapiti habitat.

**Deciduous Forests**

Deciduous forests are more productive than coniferous forests and are common habitat for wapiti in the Rocky Mountains in the northeastern United States, and red deer in Poland’s Bialowieza National Forest (Bryant and Maser 1982, Anderson et al. 2005, Kalmer 2008). In these regions a continental climate creates temperature extremes between short, hot summers and long, cold winters. In the Rocky Mountains aspen forests mixed with pine cover most of the land, while in Pennsylvania and Bialowieza mixed forests of oak and other hardwoods make up most of the *Cervus elaphus* habitat. Deciduous hardwood forests let more light
through and have less acidic soils than coniferous forests, which allows more shrubs, forbs and grasses to grow. In the winter wapiti rely on the high volumes of woody shoots available in deciduous forests (Delvin and George 1980:98).

**Moors**

The Highlands and islands of Scotland have a similar wet and mild maritime climate to the Northwest coast but instead of vast forests, moors cover the land (Wlodzimierz et al. 2006). Moors consist mainly of heath browse with scattered grasses poking through. In Glenfirshire in the central highlands moors cover 78% of the area while trees only occur on 3% of the land and only in the valleys and grass covered merely 1% of the area (Stains et al. 1982). On the island of Rhum off the coast of Scotland, red deer thrive despite the forests being completely cut down since the early 19th century showing that although forests are beneficial they are not necessary for survival (Wlodzimierz et al. 2006).

**Meadows**

Meadows are important wapiti habitat because of their abundance of good quality forage easily available to wapiti. Dry meadows are dominated by grasses and forbs while in wet meadows small trees and shrubs grow along with reeds, grasses, and forbs. The most productive forage habitat is subalpine meadows which produce an abundance of low trees, berry shrubs, grasses, and forbs. Heavy winter snowpack suppresses slow growing trees and give the advantage to rapidly growing plants, which also provide better quality forage to wapiti (Burchard 2003:42). While most meadows like seres are temporally ephemeral, subalpine meadows are relatively stable and only vary with long term glacial movement (Burchard 2003:46).
Diet of Wapiti

Zoologists divide ruminants into grazers and browsers depending on their foraging preference for grass, forbs, or browse (Nelson and Legee 1982). Browse includes woody plants like shrubs and trees including their shoots, stems, leaves and needles. Grass refers to any graminoid including sedges, rushes and grasses, while forbs are non-woody broadleaved annuals. Grazers are ruminants who eat mostly grass and forbs while browsers diet consists mostly of browse (Merrill et al. 1995, Weckerly 2005). Wapiti are grazers near the middle of the continuum that vary their diet depending on the season (Jenkins and Starkey 1991), region (Nelson and Legee 1982: 323), and sex (Stains et al. 1982; Figure 2.3). Extreme examples highlight wapiti’s dietary plasticity: in the winter Roosevelt wapiti consumed almost 100% browse in overcrowded conditions at Olympic National Park (Schwartz and Mitchell 1945), while red deer hinds subsisted almost entirely on grass on the island of Rhum (Clutton-Brock 1986). In general around 30% of the diet consists of grasses year round (McNamara 1982, Jenkins and Starkey 1991), and more total browse must be eaten when grass is locally insufficient to offset nutritional deficiencies (Weckerly 2005). Wapiti can subsist almost solely on graze or browse but a varied diet of both graze and browse is optimal (Clutton-Brock 1986).
Throughout the year wapiti strive for the highest quality diet but this is limited by the seasonal availability of forage (Marcum 1980, Merrill et al. 1995, Nelson and Legee 1982, Jenkins and Starkey 1991). In winter forage is limited by snowfall to shrub and tree browse with old grasses in the lowlands. When the snow melts in spring, wapiti concentrate on newly growing grasses and forbs (Jenkins and Starkey 1991). Forbs are highly desirable due to higher protein levels and and thinner cell walls making them more nutritious and easier to digest than other plant types, and permitting wapiti to eat a large quantity at once (Merrill et al. 1995). In the summer forbs and shrubs continue growing as grasses begin to mature. Browse becomes important again in the fall as forbs and grass mature and go to seed.

This seasonal dietary variation is evident in Nelson and Legee’s (1982) update of Kufeld (1973) review of Rocky Mountain wapiti diet in western North America. They ranked plants consumed by wapiti as highly valuable, valuable, or least valuable based on percent of total diet and how disproportionately it is eaten compared to its abundance. Figure 2.4 shows how the number of high value species of each type (browse, forbs, and grass) changes through each season. Browse, forbs, and grass all increase in quality and availability in the summer and
decrease in the winter. Only in forbs does the increase in the number of high valued plants eaten directly reflect their abundance and quality while during the winter the number of browse and grass species eaten increases to offset the disappearance of forbs.

![Graph showing the seasonal diet of Rocky Mountain wapiti](image)

**Figure 2.4.** Rocky Mountain wapiti seasonal diet (adapted from Nelson and Legee 1982: 344).

Marcum (1980) has quantified the proportion of diet per food type for Rocky Mountain wapiti for the summer and fall and it is very similar to Nelson and Legee (1982) in the order of plant type importance. In Marcum’s (1980) study wapiti’s summer diet is 51% forbs, 36% browse, and 13% grass (Figure 2.6), which fits Nelson and Legee’s (1982) order with forbs ranked first browse second and grass third. In the fall forbs drop to 21% of the diet, browse stays the same at 36%, and grass jumps to 50% of the diet. This is mirrored in Nelson and Legee’s (1982) study where the amount of forbs eaten decreases as grass increases. However the number of browse species eaten drops from 16 to 5 while remaining stable at 36% of the diet between summer and fall. Heavy concentration on a few browse species in the fall has also been observed in western Washington (Merrill et. al. 1995). These studies follow the expected pattern of wapiti
adapting their diet to what is seasonally available while seeking out the most easily digestible plants with the highest protein levels.

Differences in climate and region affect wapiti diet but more important is differences in habitat type. Wapiti prefer to forage in open habitats that are richer in forbs and grass than in closed forested habitats heavier in browse. These preferences are reflected when contrasting diets of Rocky Mountain wapiti versus Roosevelt wapiti. Jenkins and Starkey (1991) reviewed studies of Roosevelt wapiti diet in the maritime arboreous ranges extending from Vancouver Island to northern California. Figure 2.5 graphs averages of the percentage of total diet for types of plant per season for Roosevelt wapiti. Dense coniferous forests cover most of this region and thus browse plants are a large part of the diet year round and ferns a small but important part of the diet. The only major seasonal variation comes with forbs and conifers which switch in their relative importance between summer and winter, with conifers eaten as a last resort in winter while forbs are only plentiful in the summer. This subdued seasonal variation likely reflects the subdued seasonal variation of the maritime climate.

![Figure 2.5. Roosevelt wapiti seasonal diet (Jenkins and Starkey 1991:264).](image-url)
Conifers and ferns are never as important for Rocky Mountain wapiti but conifers constitute 25% of the winter diet for Roosevelt wapiti. Rocky Mountain wapiti eat aspen, willow, oak and chokecherry shoots in the winter where these plants grow abundantly (Bartos and Mueggler 1980). These species are mostly absent in Roosevelt wapiti range (Nelson and Legee 1982). In the spring there are few high value species of browse and forbs. By contrast, shrub browse comprise 30% of the spring foods eaten by Roosevelt wapiti (Jenkins and Starkey 1991). These disparities likely reflect local environmental differences in the foods that are available.

The difference that local environments make on wapiti diet for Rocky Mountain wapiti and Roosevelt wapiti diet is portrayed in Figure 2.6 derived from Marcum (1980) and Jenkins and Starkey (1991). The regions are both forested mountains but Jenkins and Starkey reviewed studies from mild and wet coastal mountains while Marcum studied drier continental Montana mountains with hot summers and cold winters. Overall Roosevelt wapiti are eating more browse while Rocky Mountain wapiti are eating more grass, reflecting differences in climate and plant availability.
Figure 2.6. Comparison of *C. e. roosevelti* and *C. e. nelsoni* diet. Dietary proportions for *C. e. nelsoni* from Marcum (1980) and dietary proportions for *C. e. roosevelti* from Jenkins and Starkey (1991).

Two studies of elk diet in different habitats within Washington State reveal the significant impact of different canopy conditions and vegetation communities (Figure 2.7). Merrill et al. (1995) studied wapiti diet on Mount St. Helens just west of the Cascade Range in southwestern Washington State where 85% of their home range was in the early stages of forest succession following the volcanic eruption. In the Hoh Rainforest on the Olympic Peninsula of Washington State over 65% of wapiti range is closed canopy old growth forest and the other 35% consist of early to mid seral forests (Leslie et al. 1984:763). Here, ferns are a significant percentage of the diet, as much a grass or browse in the summer while on Mount St. Helens they are little more than a statistical anomaly. Overall the Hoh rainforest wapiti are consuming much more browse and ferns, while the Mt. St. Helens wapiti are consuming more grass and browse. Wapiti likely responded similarly to climate changes in western Washington that altered the availability of forage classes.
Figure 2.7. Roosevelt wapiti diet in a closed canopy temperate rain forest and an early succession open landscape, both in Washington State. Closed canopy dietary proportions from Merrill et al. (1995) and open landscape dietary proportions from Leslie et al. 1984.

Home Range and Habitat

One way that wapiti adapt behaviorally to their environment is by changing the size of their home range, defined as the area in which an individual forages (Anderson et al. 2005, Kamler et al. 2008). The size of their home range is determined by available biomass, sex, and mixture of habitat types. When habitat patches are richer and closer together, wapiti can get all their needed food within a smaller area, while an area with poor and distant habitat patches will require wapiti to forage over a larger area (Kamler et al. 2008, Schaefer et al. 2008). This results in the largest home ranges in unbroken old growth forests, while the smallest home ranges are found in areas with a heterogeneous mixture of forests and open habitats.

This association of home range size with habitat patchiness has been well documented in European red deer (Kamler et al. 2008). Mean home range size for stags is 36 km$^2$ in Bialowiezia National Park, which has the largest tract of old growth forest in Europe, with few breaks in the
dense canopy. Other areas in Europe report home range sizes between 11.8 km$^2$ and 1.1 km$^2$ with the smallest average home range on the isle of Rhum on Scotland at 1.1 km$^2$. These other regions are much more mixed in habitat types than Bialowiezia except Rhum which is almost entirely unforested.

North America’s Roosevelt wapiti also have larger home ranges in heavily forested areas. Home ranges are larger in the old growth forest of Washington’s Hoh Rainforest than in open coastal meadows in California or managed forests in Oregon (Jenkins and Starkey 1991). In such heavily forested areas wapiti preferentially forage in the few meadows and clearcuts that break through the old growth forest (Weckerly 2005). This can also be seen in alpine Idaho where although meadows covered only 1-2% of the study area, they provided 20% of the volume of their total diet (Hayden-Wing 1980a:40). In both areas within meadows foraging is concentrated on forbs and grasses on the periphery of the forests, to more quickly escape predators.

In the North American interior, Anderson et al. (2005) found that forage biomass is negatively correlated with Rocky Mountain wapiti home range size while percent of land covered in forest is positively correlated (Table 2.1). Of the three studied sites, Wisconsin has the smallest mean home range, the lowest percent forest cover and the most heterogeneous landscape with deciduous and coniferous forests and lots of wetlands. This diversity of patch types enables wapiti to find all the different types of plants they need in a relatively small area.
Table 2.1. Seasonal Home Range Sizes and Forest Cover (Anderson et al. 2005).

<table>
<thead>
<tr>
<th>Region</th>
<th>Winter Home Range km²</th>
<th>Summer Home Range km²</th>
<th>Percent Forest Cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yellowstone</td>
<td>180</td>
<td>135</td>
<td>90%</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>28</td>
<td>21</td>
<td>65%</td>
</tr>
<tr>
<td>Alberta</td>
<td>101</td>
<td>53</td>
<td>80%</td>
</tr>
</tbody>
</table>

The effects of biomass are also clear with the decrease in home range size from winter to summer (Table 2.1). This is due to the increase biomass availability and increased plant diversity allowing wapiti to meet dietary requirements in a smaller area. For migratory wapiti this is most evident with the seasonal shifts in home range size from summer ranges to winter ranges. In Yellowstone and Wisconsin the summer home range is 3/4 the size of the winter home range, while in Alberta, it is half the size.

Size differences between sexes and subspecies also influence habitat use and home range size, with stags eating a lower quality diet with more browse (Staines et al. 1982, Clutton-Brock 1986, McCorquodale 2003). Red deer stags are about 70% larger than hinds, (Clutton-Brock 1986), while Roosevelt wapiti bulls are about 40 to 70% larger than cows (Skovlin and Mitchell 1945). Larger bodies require a higher caloric input which results in males eating more browse than females (McCorquodale 2003, Stains et al. 1982). This size hypothesis also partly explains why Roosevelt wapiti are considered to be more heavily browsers than other wapiti sub species (Jenkins and Starkey 1991).
Table 2.2. Stag and Hind Home Range Sizes in Km$^2$ (Kamler et al. 2008:79).

<table>
<thead>
<tr>
<th>Region</th>
<th>Stag</th>
<th>Hind</th>
<th>H/S</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bialowieza, Poland</td>
<td>36</td>
<td>8.4</td>
<td>23%</td>
</tr>
<tr>
<td>Monfrague, Spain</td>
<td>6.6</td>
<td>2.6</td>
<td>39%</td>
</tr>
<tr>
<td>Jeseniky Mts, Czech R.</td>
<td>2.6</td>
<td>1.05</td>
<td>40%</td>
</tr>
<tr>
<td>Bavarian Alps, Germany</td>
<td>2.5</td>
<td>1.2</td>
<td>48%</td>
</tr>
<tr>
<td>South Argyll, Scotland</td>
<td>11.2</td>
<td>7.1</td>
<td>63%</td>
</tr>
<tr>
<td>Isle of Rhum, Scotland</td>
<td>1.1</td>
<td>1.8</td>
<td>164%</td>
</tr>
</tbody>
</table>

Because stags forage more in forests where food is more dispersed and low quality, they almost always have a larger home range than hinds (Table 2.2). Kamler et al. (2008) found that in the old growth deciduous forest of Bialowieza, hind and stag home range size differences are bigger than anywhere else in Europe. There, hind home ranges average 8.4 km$^2$ while stags average 36 km$^2$, about four times larger than anywhere else in Europe, except the Isle of Rhum. Larger hind home range size on the Isle of Rhum may be due to the high red deer density of 14 per km$^2$, and a unique population adapted to no forest cover. There are many complicating reasons for range size such as interspecies and intraspecies competition, breeding opportunities, and rearing young (Staines et al. 1982, Kamler et al. 2008), but differences in forage environment have the greatest influence.

Population Density

Wapiti population density is highest where the landscape provides a good mix of habitats and lowest where habitats are homogenous as in heavily forested regions. However forests also provide shelter from extreme weather and concealment from predators. In the mountains of Poland, Bobek et al. (1984) found that red deer density is maximized in regions that are covered 40% by forests and 60% by openings. The optimal balance of food and cover is also met in brushy thickets. The highest red deer densities were found in habitats with 60 to 80% dense shrub
cover in a deciduous lowland forest in the Czech Republic (Prokesova et al. 2006). Similar patterns are found in Scotland where the highest red deer densities are in open thickets with trees young enough to easily forage and before canopies develop (Lantham et al. 1997). In Oregon, wapiti preferentially forage in brushy clear-cuts over new clear-cuts or pole sapling stands (Witmer and deCalsetra 1983). Such habitat provides the perfect mix of food availability and protection.

Plant species composition is another important factor influencing red deer density. In the Polish mountains, red deer showed a strong affinity for deciduous forests which produce a higher quantity of forage than coniferous forests, particularly in the winter (Bobek et al. 1984). Thus, red deer population density is negatively correlated with coniferous forest cover (e.g. spruce and pine trees). In an entirely deciduous forest such as the lowland Czech forest, red deer density was found to have a positive correlation with increasing stand diversity as the number of deciduous species increased (Prokesova et al. 2006). Wapiti meet micronutrient requirements sooner by eating a greater diversity of plants due to the variable amounts vitamins and minerals present in different species. (Hunter et al. 1980:105). This shows that population density increases with more deciduous trees, and with increased deciduous species richness.

Most studies on wapiti and red deer emphasize the importance of open habitat for forage, but some stress the importance of old growth forests (Starkey et al. 1982, Witmer and deCalesta 1983, Kamler et al. 2008). Roosevelt wapiti in western Oregon manage the heat stress from their large size by sheltering in old growth forests during mid day and throughout late spring to early fall (Witmer and deCalesta 1983). Roosevelt wapiti in the old growth Hoh rainforest had larger group sizes than would be expected in the, homogenous closed canopied forest (Jenkins and
Starkey 1982). Similarly, in Bialowieza National Forest, red deer population densities and home ranges were larger in old growth coniferous forests than in deciduous and regenerating forests (Kamler et al. 2008). The stability of resources in old growth forests favors long-term social bonding and cohesiveness of large wapiti groups which is reflected in higher population densities, and larger group sizes than in more variable environments.

Red deer population density is also influenced by climatic factors (Lantham et al. 1997). In the plantation forest of Scotland, red deer density was found to be positively correlated with mean daily temperature, and negatively correlated with snow depth in winter and wind speed in summer. Winter snow depth was also found to have a strong negative correlation with population growth in the Rocky Mountains both in Montana (Creel and Creel 2009) and in Alberta (Hebblewhite 2005). Snow covers forage, making it unavailable and restricts movement which leaves wapiti more vulnerable to predators. Snow depth is a strong determinant of population growth in regions with winter snow accumulation, indicating wapiti’s preference for temperate and mild climates.

**Expectations for Wapiti Availability with Climatically Induced Resource Variation**

Warm and dry climate conditions have both positive and negative consequences for wapiti population and their availability to human hunters (Table 2.3), so it is not immediately clear whether wapiti abundance would increase as Lepofsky et al. (2005) argues, or whether they would decrease as Broughton et al. (2008) argues. Increased fire frequency in a warmer, drier climate can increase the productivity of the environment by expanding the size and number of seres and meadows (Lepofsky et al. 2005). These habitats have more grass, forbs and deciduous browse which are more easily digested and have a higher ratio of edible to inedible biomass
(Merrill et al. 1995). Fires also increase the protein content of grass (Walter and Leslie 2009), so meadows would be more nutritious in periods of increased fire frequency. Warmer conditions would melt snow earlier in the spring, allowing wapiti to migrate earlier to forage in rich subalpine meadows (Adams 1982). Migration timing depends on snow depth and except for large stags, rocky mountain wapiti can’t move through snow depths over 122 centimeters. Besides restricting movement, snow also covers the forbs and grass forcing them to rely on browse. Early migration can offset the late winter food shortage that weakens wapiti.

Wapiti are most vulnerable to predation during the spring migration due to being weakened from winter fasting and having to protect and nourish new calves (Weaver 1980:29). Calving occurs in the spring while wapiti are migrating slowly to their summer range. Wolves focus on hunting spring migrating wapiti and half their kills consist of newborn calves (Wright et al. 2006). Pregnant cows rely on calving to occur simultaneously with the peak in spring foraging quality, in order to adequately nourish calves. If these peak conditions pass before calving occurs calf mortality could rise.
Table 2.3. Expectations of a Warm, Dry Climate on Coastal Pacific Northwest Wapiti.

<table>
<thead>
<tr>
<th>Warm, Dry Climate</th>
<th>Positive Consequences for Wapiti Availability</th>
<th>Negative Consequences for Wapiti Availability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Higher Temperatures</td>
<td>No direct benefit.</td>
<td>Warm climate increases heat stress on wapiti(^1).</td>
</tr>
<tr>
<td>Resource Distribution</td>
<td>Resources are more concentrated, decreasing wapiti home range and increasing population density(^5,6).</td>
<td>Increased resource distribution variability decreases wapiti group size and population density(^2,3).</td>
</tr>
<tr>
<td>Increased Fire Frequency</td>
<td>Fires increase the number and size of seres and meadows, increasing the amount and quality of forage(^9).</td>
<td>New seres leave wapiti exposed to predators and take a few years for the optimal brushy habitats to form(^1,5).</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fires burn up wapiti and are slow to recover their population(^2).</td>
</tr>
<tr>
<td>Forage Plant Type</td>
<td>Seres and meadows have more grass forbs, and deciduous browse, the preferred forage of wapiti(^4,5).</td>
<td>No detriment.</td>
</tr>
<tr>
<td>Forage Quality</td>
<td>Fire increases the protein content of grass, important for healthy wapiti(^3).</td>
<td>Less rain causes plants to thicken cell walls, and lower in vitro dry matter digestibility(^7).</td>
</tr>
<tr>
<td>Spring Plant Growth Timing</td>
<td>Warmer climate would shorten the winter fasting season allowing more wapiti to survive the winter(^13).</td>
<td>Less precipitation in the spring and summer would shorten the plant growth season, reducing the quality and quantity of wapiti forage(^10).</td>
</tr>
<tr>
<td>Migration Timing</td>
<td>Warm climate melts snow allowing earlier migration to subalpine meadows(^11).</td>
<td>Earlier snow melt would cause calving to occur after ideal conditions have passed and forage has dried and matured(^12).</td>
</tr>
</tbody>
</table>

\(^1\)Witmer and deCalesta 1983; \(^2\)Jenkins and Starkey 1982; \(^3\)Kamler et al. 2008; \(^4\)Bobek et al. 1984; \(^5\)Prokesova et al. 2006; \(^6\)Anderson et al. 2005; \(^7\)Merrill et al. 1995; \(^8\)Walter and Leslie 2009; \(^9\)Lepofsky et al. 2005; \(^10\)Broughton et al. 2008; \(^11\)Adams 1982; \(^12\)Weaver 1980; \(^13\)Jenkins and Starkey 1991.

High fire frequency in warm, dry periods has negative consequences for prehistoric Roosevelt wapiti population. High fire frequency would increase the variability of resource distribution, which is detrimental to long term social bonding and result in smaller, more dispersed wapiti herds (Witmer and deCalesta 1983). Fires would also be large-scale landscape devastating events due to the high volume of wood biomass in old growth forests, killing many Roosevelt wapiti which are slow to recover their population relative to other wapiti subspecies.
(Jenkins and Starkey 1982). Landscapes following a forest fire are also not immediately beneficial to wapiti; it takes a few years for seres to mature into the optimal wapiti habitat of brushy thickets. These negative consequences of a warm dry climate could outweigh the benefit of larger and more abundant meadows.

The resource stability and climate moderating effect of old growth forests promotes high population densities of wapiti. This climate moderating effect is important to Roosevelt wapiti in the summer and although red deer in Scotland exhibit higher population densities in warm weather (Lantham et al. 1997), Roosevelt wapiti are 2 to 5 times larger causing them to release excess heat less efficiently (Witmer and deCalesta 1983). A warmer climate would further stress Roosevelt wapiti during summer months and increase the importance of old growth forest. This shouldn’t critically affect wapiti population because even if increased forest fires in warm dry periods decreased old growth forest coverage, there was no shortage of old growth prehistorically.

Overall warm, dry conditions create an environment with more preferred plant types, and shorter the duration of winter fasting. The main disadvantage is the direct impact of higher temperatures and decreased precipitation on plants and wapiti, and the increased variability on resource distribution. In more open landscapes with an abundance of forbs, grasses and deciduous browse wapiti have a higher quality diet with less browse. When climate changes favor more open landscapes wapiti diet should improve resulting in higher population density. However, warmer drier conditions cause many problems for wapiti populations including a shortened spring plant growth season, increased resource variability, and more devastating wildfires which lower wapiti survival and decrease wapiti population density. This would decrease the availability of
wapiti to human hunters who would have to increasingly turn to more marginal resources to make up the difference.
Chapter 3. The Prehistoric Hunters of Wapiti

Wapiti are the largest common land mammals along much of the Northwest Coast of North America and make up a large part of most mammalian faunal assemblages (Ames and Maschner 1999:119). They are an important food resource to prehistoric hunters mainly because of their size, which allows a large meat yield per individual killed. By hunting the largest bodied prey available hunters seek to maximize their energy return, which is the prediction set out in the Prey Choice Model from Optimal Foraging Theory (MacArthur and Pianka 1966). Smaller prey will be increasingly included when the encounter rate of large prey drops, which is based on the population density of the prey in areas that humans are hunting for them. Because wapiti are the largest terrestrial mammal they would be hunted over smaller mammals, and the hunting of smaller mammals would be contingent on the rarity of wapiti.

Despite the high energetic return of hunting wapiti, their subsistence importance relative to the rich marine and anadromous resources of the region is unknown. Wapiti were most important during the winter when they are one of the few fresh food sources left to offset depletions in stored reserves. In winter wapiti are also more available as migratory wapiti move out of the mountains into lowlands seeking snow-free grass (Adams 1982). The development and increased use of storage and mass capture technology over time intensified the subsistence focus on marine resources, yet the hunting of wapiti and other terrestrial game always remained an important part of the subsistence strategy of prehistoric societies on the Northwest Coast.
Gulf of Georgia Archaeology

In the Gulf of Georgia region prehistorians recognize five cultural periods during the Holocene distinguished by differences in technology, subsistence strategy, and social practices (Table 3.1). Within the Gulf of Georgia there are a few geographic subregions including southeastern Vancouver Island, the Gulf and San Juan Islands, and the Fraser River Delta region on the mainland (Figure 3.1). In all these areas, changes in technology, subsistence strategy, and the abundance of humans affected the populations of prey animals humans relied on.

Figure 3.1. The Gulf of Georgia Region on the Northwest Coast.

During the Old Cordilleran period most societies were highly mobile foragers with great flexibility in resource gathering and a broad spectrum diet that emphasized terrestrial resources (Table 3.1; Ames and Maschner 1999). At Glenrose Cannery wapiti were the most important land mammal with the highest weight, while all other faunal remains constitute less that 10% of the
weight of wapiti remains (Matson 1976:95). During the St. Mungo period wapiti became a secondary resource as people lived in semi-sedentary villages and rely more on marine resources (Ames and Maschner 1999, Coupland 1998). This resulted in decreased reliance on wapiti for food, yet they remained an important part of the subsistence economy (Hanson 1991:213). Increased sedentism would cause resource depression near settlements as wapiti learned to avoid them, forcing hunters to travel further to hunt wapiti.

Table 3.1. Cultural Phase Subsistence Strategies in the Gulf of Georgia Region.

<table>
<thead>
<tr>
<th>Cultural Phase</th>
<th>Broad Trends in Subsistence Strategy</th>
<th>Evidence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old Cordilleran</td>
<td>Mobile Broad Spectrum Foragers focused on Terrestrial resources.</td>
<td>Live weight of mammal bones at Glenrose Cannery outweighs that of fish bone, and relatively few shellfish are present(^1).</td>
</tr>
<tr>
<td>11500 to 6400 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>St Mungo</td>
<td>Semi-sedentary broad spectrum foragers with marine emphasis.</td>
<td>Stable isotope analysis of burials shows 90-100% reliance on marine protein(^2). Appearance and increased frequency of fish nets, harpoons, and pit houses(^3).</td>
</tr>
<tr>
<td>6400 BP to 3700 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Locarno Beach</td>
<td>Semi-sedentary collectors with marine emphasis.</td>
<td>Appearance and increased frequency of storage boxes, plank houses, fish weirs, composite toggling harpoons(^3).</td>
</tr>
<tr>
<td>3700 to 2400 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Marpole</td>
<td>Greater access to long distance resources and earliest evidence for prairie management</td>
<td>Increased frequency of tools to make large dugout canoes and obsidian(^4). Prairie adapted plants in a western hemlock forest zone(^5).</td>
</tr>
<tr>
<td>2400 to 1500 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gulf of Georgia</td>
<td>Further intensification of marine resources and highest precontact human population.</td>
<td>Appearance of the herring rake(^3). Increased frequency of fortifications(^3).</td>
</tr>
<tr>
<td>1500 BP to 150 BP</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

During the Marpole period there is increased use of large dugout canoes and greater interregional trade (Ames 1994). This allowed easier exploitation of distant wapiti and other resources from many different habitats. The earliest evidence of prairie maintenance through anthropogenic fire also occurs in this period which increased the size, abundance and production of prairies thus increasing the health and size of wapiti populations (Weiser and Lepofsky 2009:185). Many economically important plant and animal species co-occur in prairies and expanding their production increases the availability of wapiti to humans (Boyd 1999:94).

On the Northwest coast, human populations continued to increase over time, requiring further intensification of marine resources, (Croes 1995:4). In other regions, increased hunting pressure from large human populations outpaced the regeneration rate of prey, resulting in decreased encounter rates (e.g, Grayson 2001). Resource depression is common in larger animals such as wapiti that tend to have fewer offspring and longer time between births (Lupo 2007). Yet a review of faunal assemblages from archaeological sites across the Northwest Coast found that resource depression did not occur in artiodactyls such as wapiti, and instead artiodactyls increase over time (Butler and Campbell 2004). The pre-contact indigenous population size is estimated to be around 300,000 people, large enough to potentially cause resource depression (Haggan 2006:8). That hunting pressure did not cause resource depression, may be due to flexible resource use along with beliefs and social institutions that placed harvesting restraints on individuals (Campbell and Butler 2010).

Wapiti remains are common in Northwest Coast archaeological faunal assemblages. Of all mammalian resources, Wapiti and deer are the most abundant in terms of NISP (number of identified specimens) at 21 of 25 sites reviewed by Butler and Campbell (2004) across the Northwest Coast, while seal and dog are the next most abundant. Similar results are found more
locally in sites within the Fraser River Delta region where wapiti, deer, and harbor seal are the three most important mammalian food resources, with wapiti the most common of the three (Hanson 1981, Matson 2010).

Although deer and wapiti remain important through these cultural periods, there are some important differences in mammal ubiquity measured in NISP (Table 2.2). During the Old Cordilleran wapiti are the most abundant mammal by far until the St. Mungo period when deer and beaver become nearly as important as wapiti. Beaver all but disappear during the Locarno Beach period and remain rare or absent subsequently, while deer and wapiti remain important, and at local sites there is an increase in canids. Deer in most areas supersede wapiti in importance in the Marpole period except at Semiahmoo, while in the Gulf of Georgia period canids and cervids both increase in ubiquity but canids increase more. Throughout the culture phases, marine mammals remain consistently less important than cervids in local sites and are usually far less common.

The St. Mungo period occurs during the Altithermal climate period when the climate was much hotter and drier than historic conditions (see Chapter 4). These climate conditions would adversely affect cervids more than smaller mammals due to increased mistiming of births with shortened favorable conditions (Broughton et al. 2008). This may explain the appearance of a large percentage of beaver in St. Mungo mammalian faunal assemblages.
Table 3.2. Mammalian Faunal Assemblages in the Fraser River Delta by Culture Period.

<table>
<thead>
<tr>
<th>Culture Period</th>
<th>Sites</th>
<th>Mammalian Faunal Assemblages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old Cordilleran</td>
<td>Glenrose Cannery (DgRr 6)</td>
<td>Wapiti are most common followed distantly by deer, seal, and beaver&lt;sup&gt;1&lt;/sup&gt;</td>
</tr>
<tr>
<td>11,500 to 6,400 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td>St. Mungo</td>
<td>Glenrose Cannery (DgRr 6) &amp; St. Mungo</td>
<td>Wapiti are the most common followed closely by deer and beaver at both sites&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>6,400 BP to 3,700 BP</td>
<td>(DgRr 2)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ferndale (45WH34)</td>
<td>Wapiti rank a close third behind deer and beaver&lt;sup&gt;3&lt;/sup&gt;</td>
</tr>
<tr>
<td>Locarno Beach</td>
<td>45WH100 &amp; 45WH114</td>
<td>Wapiti are most common followed by deer, then canids&lt;sup&gt;4&lt;/sup&gt;</td>
</tr>
<tr>
<td>3700 to 2400 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cherry Point (45WH1)</td>
<td>Wapiti and deer are equally most common followed distantly by canids and seals&lt;sup&gt;5&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Hanson and VanGaalen</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cherry Point (45WH1)</td>
<td>Canids are most abundant by far followed by deer, wapiti, then seal&lt;sup&gt;6&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td>Dubeau</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Semiahmoo (45WH17)</td>
<td>Canids are most abundant followed by deer, then wapiti&lt;sup&gt;7&lt;/sup&gt;</td>
</tr>
<tr>
<td>Marpole</td>
<td>Cates Park, Crescent Beach (DgRr 1)</td>
<td>Deer are the most common mammal&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>2400 to 1500 BP</td>
<td>&amp; Glenrose Cannery (DgRr 6)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Cherry Point (45WH1)</td>
<td>Canids increase from ½ to 2/3 of the mammalian assemblage, deer remain the same while wapiti and</td>
</tr>
<tr>
<td></td>
<td>Dubeau</td>
<td>seal decline</td>
</tr>
<tr>
<td></td>
<td>Semiahmoo (45WH17)</td>
<td>Wapiti are most common mammal&lt;sup&gt;7&lt;/sup&gt;</td>
</tr>
<tr>
<td>Gulf of Georgia</td>
<td>45WH111</td>
<td>Wapiti, deer, dog, and porpoises are the most common mammals&lt;sup&gt;4&lt;/sup&gt;</td>
</tr>
<tr>
<td>1500 BP to 150 BP</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Semiahmoo (45WH17)</td>
<td>Canids make up 2/3 of mammalian assemblage wapiti are second in abundance, then deer&lt;sup&gt;7&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Birch Bay (45WH9)</td>
<td>Deer, canids, and wapiti are the most common mammals with canids increasing from an earlier</td>
</tr>
<tr>
<td></td>
<td></td>
<td>component&lt;sup&gt;8&lt;/sup&gt;</td>
</tr>
</tbody>
</table>


It is unlikely that environmental conditions have anything to do with the increase in canids starting in the Marpole and continuing through the Gulf of Georgia Period. Most if not all of the canids included represent domesticated dogs (*Canis fammiliaris*) which were valued for hunting.
as well as for wool and rarely used as a food source (Suttles 1990). The increased relative abundance of canids then is not a direct result of resource depression or climate, but could be related to increased hunting of cervids, increased wool production, and/or larger human populations that support more dogs.

Wapiti remain consistently a common part of archaeological faunal assemblages despite thousands of years of use by increasing human populations. Yet through time there is variation in the abundance of wapiti relative to other mammals. In Fraser River Delta mammalian faunal assemblages, deer and canids compete with wapiti for most abundant mammal, while beaver are only important early on and sea mammals are rarely very common. Climate is a possible cause for these variations in relative mammalian abundance; climate changes affect the environment by altering the abundance and distribution of resources important for both prey animals and human societies. When climate conditions are detrimental to wapiti their population density will decrease, the encounter rate for hunters will drop, and smaller prey will be increasingly hunted.
Chapter 4. Holocene Climate History

Dynamic fluctuations in moisture and temperature have driven glacial advances and retreats, changing fire frequency, and biome fluctuations during the Holocene in the Pacific Northwest (Table 4.2). Scientists have documented these changes on the coastal Pacific Northwest through a variety of ways including mapping glacial movements, dendroclimatology, pollen and charcoal cores, soil salinity, and choronomids (Table 4.1). Combining results from these independent methods climate scientists agree on three unique periods that make up the Holocene: the early or Xerothermic, the middle or Altithermal, and the late or Neoglacial. Open parklands dominated much of the land during the early and middle Holocene. With the beginning of the Neoglacial the climate grew colder and wetter, thus precipitating the expansion of closed canopied forests. The Neoglacial was much cooler and wetter overall and is also a period of dynamic fluctuation in temperature and humidity. Recently, these Neoglacial fluctuations have been subdivided into shorter periods: the warm, dry Fraser Valley Fire Period and Medieval Warm Period, and the cool, wet 1st Millennium Advance and Little Ice Age. During cooler, wetter periods closed canopied forests of shade tolerant plants expanded while in warmer, drier periods these forests broke up into patchy open canopied forests.

Paleoclimatologist use a variety of methods to document past environments and climates (Anderson et al. 2007:2). The most commonly used method is analysis of pollen and charcoal cores, usually taken from either a bog or a lake, when paired with radiocarbon dating they reveal temporal variation in vegetation and fire frequencies. Pollen and macrofloral remains preserved in the sediment are identified and allow the inference of variations in the relative abundance of vegetation types (Galloway 2007, Brown 2008). Plant species prefer different climate conditions, and the relative abundance of plants with similar climate preferences indicates the climate conditions (Table 4.1). Often pollen cores are taken near glacial moraines, where they preserve
evidence of vegetation sequences such as changes from forests to subalpine meadow (Evans 1997). Charcoal is also preserved in the sediment and can give a rough measurement of the frequency and strength of local fires (Marlon et al. 2006). Glacial advances occur due to colder summers, wetter winters, or both. Wood trapped in glaciers can determine when glacial advances overrode forests. (Ryder and Thompson 1986). Tiny insects known as chironomids are very sensitive to changes in temperature and measuring the relative abundance of different species preserved in lake or bog sediments indicates the mean July air temperature when they lived (Pellatt et al. 2000, Palmer et al 2002). Paleoclimatic records from western Washington, southwestern British Columbia, and further north along the coast show similar trends throughout the Holocene (Figure 4.1).
Table 4.1. Plant Species Used as Climate Indicators in Pollen Cores.

<table>
<thead>
<tr>
<th>Latin Name</th>
<th>Common Name</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Thuja plicata</em></td>
<td>Western Red Cedar (Giant Arborvitae)</td>
<td>Prefers moist to wet soils, or dry if soil is very rich. Found most often in shaded forests.</td>
</tr>
<tr>
<td>or <em>Cupressaceae</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cyperaceae</em></td>
<td>Sedge</td>
<td>Found in very wet and sunny meadows.</td>
</tr>
<tr>
<td><em>Picea sitchensis</em></td>
<td>Sitka spruce</td>
<td>Moist well-drained sites in full sun, often on floodplains.</td>
</tr>
<tr>
<td><em>Tsuga heterophylla</em></td>
<td>Western Hemlock</td>
<td>Climax species: grows well in full shade, dry to wet forests.</td>
</tr>
<tr>
<td><em>Tsuga mertensia</em></td>
<td>Mountain Hemlock</td>
<td>Grows in High elevation wet, shady and cold forests.</td>
</tr>
<tr>
<td><em>Alnus rubra</em></td>
<td>Red Alder</td>
<td>Pioneer species found in moist forests and stream banks, fixes nitrogen.</td>
</tr>
<tr>
<td><em>Pseudotsuga</em></td>
<td>Douglas Fir</td>
<td>Pioneer species: Highly tolerant of extremely dry to moist soil, but prefers sunny open places, fire tolerant.</td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>Lodgepole or Shore Pine</td>
<td>Highly adaptable but most often in dry sunny places or where fires are frequent.</td>
</tr>
</tbody>
</table>

\(^1\)From Pojar and Mackinnon 1994.

Xerothermic (11,500 to 7,000 Cal. yr. BP)

The Holocene began around 11,500 cal yr BP (calendar years before 1950 AD) as glaciers receded from the last ice age (D.G. Anderson et al. 2007). The early Holocene period between 11,500 to 7,000 cal yr BP is often referred to as the Xerothermic in reference to the warm dry conditions (Table 4.2), yet climate did fluctuate within this period (Moss et al. 2007). Across North America, average annual temperature rose 3 to 4 degrees C from 14 to 10,000 cal yr BP, then rose another 1 degree C between 10 to 8,000 cal yr BP before gradually cooling off for another 2,000 years (Viau et. al. 2006). In the North Cascades in British Columbia, the average July temperature was 12.8 degrees C at 11,500 cal yr BP and had cooled off to 11.6 degrees C by 7,850 cal yr BP, which is still about 4 degrees C higher than today’s average July temperature in the North Cascades (Pellatt et al. 2000). Fire frequency increased rapidly between 14 to 10,000
cal yr BP, with a sharp increase in fire frequency at the cusp of the Holocene 11,600 cal yr BP (Marlon et al. 2006). Fire frequency increased concomitantly with temperature and as fuel accumulated from expanding forests. Yet, because dense forests had yet to build up, fire frequency was lowest during the Xerothermic than any other Holocene period (Prichard et al. 2009).

Pollen cores from across the Pacific Northwest reveal the Xerothermic as a time of rapid environmental change. As temperatures rose and glaciers receded pioneer plants settled the uncovered land. Open canopy forests first began developing during the late glacial period on coastal British Columbia (Galloway et al. 2007). These early forests consisted of a mix of wet adapted species: *Picea* (Spruce) and *Tsuga* (Hemlock), and dry adapted species: *Alnus* (Alder) and *Pseudotsuga* (Douglas Fir, see Table 4.1). On eastern and southern Vancouver island pine forests present from the late glacial period were superseded by *Alnus* and *Pseudotsuga* dominated open canopy forests by 11,400 cal yr BP, while moister conditions on the Pacific Coast enabled the establishment of closed canopy forests of *Tsuga* and *Picea* (Brown and Hebda 2002, Brown et al. 2008). In southwestern mainland British Columbia, *Picea* dominated open canopy forests with *Pinus* and *Alnus* covered the landscape from 10,000 to 7,000 cal yr BP (Pellat et al. 2000). At this time Washington’s North Cascades were covered by dry open canopy montane coniferous forests dominated by *Pinus contorta* (Prichard et al. 2009). During the Xerothermic, dry conditions encouraged the predominance of open canopy forests across much of the Pacific Northwest.

**Altithermal (7,000 to 3,800 cal yr BP)**

The transition from the Xerothermic to the Altithermal is variously placed between 8,000 cal yr BP to 6,000 cal yr BP with a transition to warmer and more humid conditions. Across North America the hottest average summer temperatures of the Holocene occurred between 6,000
and 3,000 cal yr BP (Viau et al 2006). In coastal northwestern North America increased humidity during the early Altithermal allowed the establishment of modern forests in some areas, but most areas maintained open canopy forests or parklands until 5,000 cal yr BP when humidity further increased (Moss et al. 2007). From 7,500 to 4,000 cal yr BP western red cedar expanded northward, growing first in the established coastal forests and other wet regions (Moss et al. 2007). This increased humidity caused glacial expansions in some mountains. Charcoal analysis shows that fires were common through the Altithermal (Enache and Cumming 2009, Sugimura et al. 2008). Although humidity increased from the Xerothermic, the Altithermal remained warmer and drier than modern conditions (Gajewski et al. 2000).

Table 4.2 Holocene Climate Periods with Characteristics.

<table>
<thead>
<tr>
<th>Climate Period</th>
<th>Time Range Calendar Years B.P.</th>
<th>Climate</th>
<th>Forest Cover</th>
<th>Fire</th>
<th>Glacial Advances</th>
</tr>
</thead>
<tbody>
<tr>
<td>Little Ice Age</td>
<td>500-150</td>
<td>Coldest, Wettest Wet Summers and Wet Winters</td>
<td>Heavier</td>
<td>Decreased Frequency</td>
<td>Maximum Advance</td>
</tr>
<tr>
<td>Medieval Warm Period</td>
<td>1,000-500</td>
<td>Hot, Dry Summers, Wet Winters</td>
<td>Lighter</td>
<td>Increased Frequency</td>
<td>Advance after 850 BP</td>
</tr>
<tr>
<td>First Millennium Advance</td>
<td>1,300-1,000</td>
<td>Cold, Wet</td>
<td>Heavier</td>
<td>Decreased Frequency</td>
<td>Advance from 1,300 to 1,000 BP</td>
</tr>
<tr>
<td>Fraser Valley Fire Period</td>
<td>2,000-1,300</td>
<td>Warm, Dry</td>
<td>Lighter</td>
<td>Increased Frequency</td>
<td>Retreat</td>
</tr>
<tr>
<td>Neoglacial</td>
<td>3,800-2,000</td>
<td>Cold, Wet</td>
<td>Heavier</td>
<td>Low Frequency</td>
<td>Advance from 3,800 to 2,000 BP</td>
</tr>
<tr>
<td>Altithermal</td>
<td>7,000-3,800</td>
<td>Hottest, Increasing Precipitation</td>
<td>Modern forests established in most areas by 5,000 BP</td>
<td>Highest Frequency</td>
<td>Retreat</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Advance from 7,300 to 5,800 BP</td>
</tr>
<tr>
<td>Xerothermic</td>
<td>11,500-7,000</td>
<td>Cold, Dry</td>
<td>Lightest</td>
<td>Lowest Frequency</td>
<td></td>
</tr>
</tbody>
</table>
In a few areas the increased humidity caused glacial expansion as more snow fell during winter months. On Mt. Baker the Coleman glacier expanded around 6,000 cal yr BP (Ryanne 2009). This is synchronous with glacial expansions at Garibaldi Park in southwestern British Columbia between 7300 and 5800 cal yr BP. This period of glacial advance was less extensive than the more recent advance of the Little Ice Age and was not measured in the Coast Mountains of British Columbia (Ryder and Thompson 1986).

The pollen core records of the early Altithermal vary significantly between localities yet all show that more plants adapted to hot and dry conditions lived in the area and forests were patchier than modern conditions. Using pollen records from across North America Viau et al. (2006) reconstructed average July temperatures across North America during the Holocene and found that July temperatures peaked around 6,000 and cooled off around 3,000 cal yr BP. In southern Puget Sound Hibbert (1979) found that summers were warm and dry 8,350 to 5,700 calendar years ago, while high amounts of Quercus spp. (Oak) pollen reveal the presence of oak savannas in warm open sites. Forest expansion is shown from the decline of Artemisia (sagebrush) and Pteridium (brake fern) while Tsuga heterophylla (western hemlock) and Pseudotsuga pollen increase (Hibbert 1979). Further north in the San Juan Islands, pollen core records indicate a landscape of open canopied forests interspersed with wet meadows maintained by frequent fires. This is shown from a large percentage of Cyperaceae (sedge) pollen, a small percentage of Tsuga pollen and high charcoal count (Sugimura 2008). In the North Cascades increased moisture between 8000 to 4500 cal yr BP caused mixed conifer forests to replace the earlier Pinus contorta forests, and fire frequency decreased. Further north in the southwestern British Columbian Cascades an increase of conifer, Cyperaceae pollen and charcoal indicate
warm wet climate conditions, increased fire frequency, and the establishment of dense modern forests (Pellatt et al. 2000).

By 5000 cal yr BP cool wet adapted forests with closed canopies began expanding in most regions through southwestern British Columbia and northwestern Washington. Near Mt Rainier after *Quercus* parkland was fully replaced after 5000 cal yr BP by the deeply shaded forests of *Pseudotsuga* and *Tsuga* (Hibbert 1979). In the Puget Sound at Mt. Constitution the onset of cooler and wetter conditions caused an increase of *Alnus* and *Pseudotsuga* with a concurrent decrease of *Pinus* after 5300 cal yr BP (Sugimura et al. 2008). In the North Cascades cooler and wetter conditions prevailed after 4500 cal yr BP. Here *Thuja plicata* and *Tsuga heterophylla* appear around 5000 cal yr BP and gradually create a dense closed canopy forest (Prichard et al. 2009). On Vancouver Island *Thuja plicata* is present by 8350 cal yr BP but does not attain their maximum coverage until 3750 cal yr BP (Brown and Hebda 2002). A shift in climate around 5000 cal yr BP increased moisture and started the development of wetlands and the expansion of closed canopy forests in moist and mountainous regions on Vancouver Island. However on the rain shadowed eastern site open canopy forests persisted (Brown et al. 2008). This expansion of forests around 5000 cal yr BP began the process of canopy closure which culminated in the Neoglacial.

The world wide cooling off at the end of the Altithermal marks the beginning of the late Holocene. This period is commonly referred to as the Neoglacial and it was originally thought to be climatically stable up to the present. However, recent research has found that this period was probably the most climatically volatile period of the Holocene. Because of this volatility the late Holocene has been split up into many small climate periods. The first is the Neoglacial followed
by the Fraser Valley Fire Period 1st Millennium Advance, Medieval Warm Period, and Little Ice Age (Table 4.2).

**Neoglacial (3,800 to 2,000 cal yr BP)**

Some consider the beginning of the Neoglacial to be around 5000 Cal. yr. BP when forests began expanding and glaciers advanced (Gajewski et al. 2000, Sugimura et al. 2008). However temperatures still remained higher than today’s average until 4000 to 3000 cal yr BP when temperatures dropped significantly and humidity continued to increase (Pellatt et al. 2000, Viau et al. 2006). Cool adapted trees increase in the pollen record and *Thuja plicata* attained their maximum range. Cooler and wetter conditions caused glacial advances and major forest expansion.

The records for Neoglacial glacial advances are roughly synchronous. In Canada’s southern Coast Mountains glaciers advanced at 3900 cal yr BP in Garibaldi Provincial Park and at 3650 cal yr BP nearby at Blowdown Lake. By 2400 cal yr BP there was a short glacial retreat followed by a second advance lasting until 1400 cal yr BP (Evans 1997). Closer to the coast in the same region the Tiedemann glacier advanced from 3500 to 1850 cal yr BP with a peak at 2350 cal yr BP (Arsenault et al. 2007). The Tiedemann glacier is the only one in the region to achieve its maximum Holocene extent during this period; most glaciers peaked later during the Little Ice Age (Ryder and Thompson 1986). Much further north on Alexander Island the Gilbert glacier advanced from 2250 to 1950 cal yr BP (Grove 2004). With temperatures cooling and humidity increasing to modern conditions, glaciers advanced throughout the Pacific Northwest.

Most areas had established a modern forest pattern before the Neoglacial, but a few held out until this period. Pollen records in southwestern British Columbia show cool wet adapted vegetation expanding at 4000 cal yr BP (Hebda 1995). By 3750 cal yr BP in Canada’s Cascade
Mountains decreasing temperatures and glacial advance established the modern biome of subalpine parkland (Pellatt et al. 2000). By 3400 cal yr BP all regions had established a modern cool wet adapted biome.

During the Neoglacial it is expected that fire frequency would decrease as it became cooler and wetter. There is much evidence to support this expectation; in the San Juan Islands fires were infrequent from 5300 cal yr BP to 2000 cal yr BP (Sugimura et al. 2008). In southwestern British Columbia fires were infrequent from 3500 to 2400 cal yr BP (Hallet et al. 2003). Much further north in central British Columbia, fire frequency decreased after 3500 cal yr BP and remained infrequent until 2300 cal yr BP (Enache and Cumming 2009). The charcoal analysis in this study used the charcoal-morphotype fire index which looks at the distribution of highly irregular and porous charcoal particles that are transported to lakes by wind instead of runoff. This method better reflects the fire regime of a region rather than just a locality so it is pertinent to the fire history of the Gulf of Georgia despite being outside the region. By 3500 cal yr BP most areas in the Pacific Northwest saw fires infrequently. Without fires to break up the canopy forests expanded resulting in a closed canopy homogenous conifer forest.

Yet in some areas fire frequency did not decrease during the Neoglacial. Although fires were rare on the west coast of Vancouver Island after 3650 cal yr BP, they remained frequent on the southeast and east sides of the island (Brown and Hebda 1999, 2002). Southeastern and eastern Vancouver Island lie within the rain shadow of the Vancouver Island Range and are much drier than the coast as a result and may explain the continuation of fires during this time. In the North Cascades of Washington fires are infrequent through the Altithermal but become frequent between 3000 and 2000 cal yr BP, this pattern of fire frequency is opposite to other areas (Prichard et al. 2009). Prichard et al. (2009) have many possible explanations for this pattern.
including fuel buildup created from denser forests, or higher humidity causing lightning, people causing fires, or summer drought despite higher total annual rainfall. Despite these exceptions, there is an overall trend of decreased fire frequency during the Neoglacial.

Other lines of evidence support the idea of a cool wet Neoglacial. In the Cascades of British Columbia Pellatt et al. (2000) found that July temperature dropped 4° C before 3750 cal yr BP from the Altithermal. Around 4400 cal yr BP there was a major die off of warm water chironomids, indicating a pronounced temperature decline. Further inland along the international border, Palmer et al. (2002) found that July temperature dropped 3° C by 5700 cal yr BP. On southern Vancouver Island, Zhang and Hebda (2005) measured symptoms of drought and stressful conditions for trees. They found the heaviest drought of the past 4000 years occurred at 3810 cal yr BP. This is synchronous with a dramatic shift in diatoms in central British Columbia at 3800 cal yr BP (Enache and Cumming 2009), and near the chironomid shift at 4400 cal yr BP. These studies all indicate a short period of instability in climate during a shift from warmer to cooler conditions. This shift to a cooler climate happened 1000 years earlier in the Pacific Northwest than the rest of North America where average summer temperatures remained high until 3000 cal yr BP (Viau et al. 2006).

The onset of modern climate conditions occurred in two phases: an early one between 7000 to 5000 cal yr BP, and a later one around 3800 cal yr BP. Increased precipitation caused glaciers in some areas to began advancing at 7000 cal yr BP, while cedar trees expanded their range northward so that by 5000 cal yr BP closed canopied forests had developed in most areas. Around 3800 cal yr BP there was a climatic flux when temperature decreased and precipitation increased sharply. After this flux there was a further episode of glacial expansion lasting until 2000 cal yr BP. Fire frequency decreased in most areas during this second cooling period and
remained low until around 2000 cal yr BP. The rest of the late Holocene had relatively short 
fluctuations in temperature and moisture that drove glacial expansions, fire regimes, and forest 
patterns.

**Fraser Valley Fire Period (2,000 to 1,300 cal yr BP)**

The Fraser Valley Fire Period was named such by Hallet and Lepofsky when they 
identified a period of increased fire frequency caused by prolonged summer drought from 2400 to 
1300 cal yr BP in southwestern British Columbia (Hallet et al. 2003). Many other studies in the 
same area have found a period of increased temperature and decreased moisture but none of them 
agree on their timing. Increased fires and decreased moisture during this period would cause 
forests to break up and meadows to expand (Lepofsky et al. 2005).

The makeup of the forest also supports the idea of a warm dry period around this time. 
Around 2000 cal yr BP there was a shift in the prevalence of tree species. In the SouthernC 
Mountains of British Columbia, *Pseudotsuga* increased as *Tsuga heterophylla* decreased 
(Arsenault et al. 2007). In the San Juans *Tsuga heterophylla* and *Alnus rubra* decreased as *Pinus* 
increased at 2000 cal yr BP (Sugimura et al. 2008). The increase of fire and drought tolerant 
species and decrease of shade tolerant species indicates warmer, drier conditions at this time. 
However in the North Cascade Mountains cool wet adapted *T. mertensia* and *Cupressus 
nootkatensis* (Yellow-cedar) both increased (Prichard et al. 2009). So everywhere there was a 
distinct shift in climate at 2000 cal yr BP, but it was not uniformly warmer and drier.

Analysis of charcoal from pollen cores supports the idea of a warm, dry Fraser Valley Fire 
Period but timing is mixed. In the same region as Hallet et al. (2003), Arsenault et al. (2007) 
found evidence of increased fire only from 1800 to 1350 cal yr BP. In central British Columbia, 
Enache and Cumming (2009) found increased fire frequency from 2300 to 1800 cal yr BP with a
decline following. In the San Juan Islands, Sugimura et al. (2008) charcoal levels after 2000 cal yr BP indicate an increased to one fire every 100-200 years. Prichard et al. (2009) in the North Cascades found the opposite of this pattern with fire frequency decreasing from 2000 to 1000 cal yr BP. Although some areas had increased fire frequency around 2400 cal yr BP, while other areas had increased fire later around 2000 BP, in all areas of the Pacific Northwest by 1300 cal yr BP fire frequency had declined.

There is no synchronicity to the behavior of Glaciers in the South Coast Mountains during this period. In this region Arsenault et al. (2007) found a glacial retreat from 1800 to 1350 cal yr BP, while the Tiedemann and Gilbert glaciers both receded until the Little Ice Age (Ryder and Thompson 1986). In the same region Evans (1997) found a glacial advance from 2400-1380 cal yr BP and a retreat from 1380 to 1100 cal yr BP. A glacial advance during this warm period may be due to a shift to a winter-wet summer dry precipitation regime that built up glaciers with increased winter precipitation.

The Fraser Valley Fire Period has been identified as a warm, dry, climate period with frequent fires from 2400 to 1300 cal yr BP (Lepofsky et al. 2005). However only two studies found evidence for warmer, drier conditions beginning around 2400 cal yr BP (Hallet et al. 2003, Enache and Cumming 2009). All other paleoclimatic studies showed that the climate shift occurred around 2000 cal yr BP. Yet not all areas showed evidence for a warmer, drier climate. In the Cascades of Washington and British Columbia this period saw glacial advances and denser forests (Evans 1997, Prichard et al. 2009). For the rest of the Pacific Northwest between 2000 and 1300 cal yr BP the climate was warmer and drier (Table 4.2).
1st Millennium AD Advance (1,300 to 1,000 cal yr BP)

Recently evidence of glacial advances was identified during the middle of the first millennium AD, revealing a period of renewed cool, wet conditions referred to as the First Millennium Advance (FMA) (Allen and Smith 2007). The FMA is also referred to as the littlest ice age because it is the smallest of the three late Holocene glacial advances (Grove 2004). The only evidence of a shift in vegetation during this period comes from pollen cores in the Coast Mountains that show shade tolerant *Tsuga heterophylla* displacing *Pseudotsuga* (Arsenault et al. 2007).

Unlike the pollen core data, there is extensive documentation of glacial advances during the FMA. Glacial advances during the FMA occurred in two separate stages: during the beginning of the first millennium and at the end of the first millennium. Between 200 and 700 AD (1750 to 1250 cal yr BP), 17 glaciers advanced in southeast Alaska and northern British Columbia (Reyes et al. 2006). During the FMA the Bridge Glacier in the southern Coast Mountains of British Columbia advanced at a rate of 1.8 meters per year from 540 to 968 AD (1400 to 1000 cal yr BP) (Allen and Smith 2007). While at the same time (1400 cal yr BP) the Sphinx glacier advanced in Garibaldi Provincial Park. Further east in the Coast Mountains, Evans (1997) places glacial advancement starting at 1100 cal yr BP, coinciding with decreased fire frequency after 1300 cal yr BP. In Southern Alaska the Tebenkof glacier advanced and started overriding trees at 700 AD (1250 cal yr BP) followed by tree recolonisation at 956 AD (994 cal yr BP, Barklay et al. 2009). Further away in Alaska and Lappland, glacial advances occurred at 1250 and 1050 cal yr BP (Grove 2004).

Although Reyes et al. (2006) place the FMA between 1750 to 1250 cal yr BP, evidence closer to the study area found the FMA beginning between 1400 and 1300 cal yr BP and lasting to
around 1000 cal yr BP. These glacial advances are likely triggered by a cooler, wetter climate which would encourage the growth of shade tolerant trees and along with decreased fire frequency would lead to closed canopy forests (Table 4.2).

**Medieval Warm Period (1,000 to 500 cal yr BP)**

The Medieval Warm Period (MWP) was first identified in Europe as a warm, dry period and is sometimes referred to as the Medieval Climactic Optimum, or the Medieval Climatic Anomaly; it has since been shown to have occurred across the Northern Hemisphere (Koch and Clague 2011). A proxy based global reconstruction of historic temperatures shows that the hottest pre-industrial period of the last 2,000 years occurred between 950 to 1100 AD (1000 to 850 cal yr BP) while after this warm spike temperatures dropped moderately to a plateau until 1450 AD (500 cal yr BP) when the Little Ice Age fully set in (Mann et al. 2008).

Worldwide, variation in precipitation drove fire frequency fluctuations for the last millennium. Fires were most frequent around 1100 AD (950 cal yr BP) coincident with the highest temperatures, and at 1500 AD (550 cal yr BP) when the Little Ice Age set in, with a drop in frequency around 1250 AD (800 Cal. yr. BP)(Pechony and Schindell 2010). In the northwestern United States, Marlon et al. (2006) found that fire frequency increased between 1200 to 900 cal yr BP followed by a decrease. Locally in the North Cascades, fires increased in frequency from 1000 to 500 cal yr BP (Prichard et al. 2009), while in central British Columbia, fire frequency increased from 1400 to 900 cal yr BP (Enache and Cumming 2009). The west coast of Vancouver shows the same pattern of increased fire with a sharp decrease at 850 cal yr BP (Gavin et al. 2003). This increase in fire frequency may have been partly driven by drier summers: on southern Vancouver Island a heavy drought occurred around 1200 cal yr BP (Zhang
and Hebda 2005). However, this is not supported by pollen cores taken from the Olympic Mountains, where from 1100 to 650 cal yr BP, Polygonum (a forb dependent on summer rain) increased while Cyperaceae (sedge) decreased (Gavin and Brubaker 1999). Cyperaceae decreased as warmer summers melted the snowpack that they depend on earlier in the year. Yet overall warmer and drier summers during the Medieval Warm Period increased fire frequency breaking up the closed canopy forests and creating patchier open canopy forests.

Although the climate was warmer and fires were more frequent, evidence from glacial moraines across the Pacific Northwest show glacial advances throughout the Medieval Warm Period. Between 800 and 1400 AD glaciers advanced across western Canada and Alaska, including the south Coast Mountains near the study site (Koch and Clague 2011). In the Coast Mountains of British Columbia the Klinaklini Glacier advanced at 800 cal yr BP and the Franklin Glacier began expanding around 800 cal yr BP (Ryder and Thompson 1986). Elsewhere in the Coast Mountains, the treeline retreated from the advance of glaciers starting at 1100 cal yr BP (Evans 1997). Across the border in Washington, the Coleman Glacier on Mt. Baker started advancing around 950 - 840 cal yr BP (Ryanne 2009). While other glaciers advanced the south coast of Alaska found glaciers retreating during the MWP by 956 AD (Barklay et al. 2009). Although the Medieval Warm Period was warmer and drier during the summer, increased precipitation during the winter could explain the widespread glacial advances (Koch and Clague 2011).

During the Medieval Warm Period, increased solar output drove climate conditions where summers were long and dry, winter were short and wet, and temperatures higher year round. Drier summers in mature closed canopy forests increased the severity and frequency of fires which worked to create patchier, open canopy forests. Wetter winters led to glacial advances in
mountains across the Pacific Northwest which pushed subalpine meadows downhill, breaking up forests and creating larger meadows in the mountains. These conditions peaked from 1000 to 850 cal yr BP and cooled off afterwards while still remaining significantly warmer than the Little Ice Age until around 500 cal yr BP.

**Little Ice Age (500 to 100 cal yr BP)**

Worldwide, the Little Ice Age was the coldest and wettest period since the early Holocene 6,000 years ago (Viau et al. 2006). Average summer temperatures dropped after 850 cal yr BP, then dropped further after 500 cal yr BP remaining very low until the 20th century (Mann et al. 2008). Almost all glaciers in the Pacific Northwest advanced and most achieved their greatest Holocene extent during the Little Ice Age (Ryder and Thompson 1986). Glaciers that began expanding in the Medieval Warm Period continued to do so through the Little Ice Age. On Mt. Baker, the Coleman Glacier had begun advancing during the Medieval Warm Period and continued to overrun forests between 800 to 525 cal yr BP (Grove 2004). Other glaciers such as the Easton Glacier on Mt. Baker only advanced during the height of the Little Ice Age between 520 to 320 cal yr BP (Ryanne 2009). Glaciers in the Coast Mountains of British Columbia followed the same pattern of continuing advances through the Little Ice Age. The Franklin and Klinaklini Glaciers were both advancing by 700 cal yr BP, and by 500 cal yr BP the Klinaklini had thickened by 130 meters, while the Tiedemann Glacier was advancing at least by 500 cal yr BP (Ryder and Thompson 1986). The Bridge Glacier rapidly advanced during the Little Ice Age with a maximum extension between 723 and 485 cal yr BP (Allen and Smith 2007). Further north in southern coastal Alaska, the Tebenkof glacier reached its maximum Holocene extent by 280 cal
yr BP (Barclay et al. 2009). No glaciers experienced recessions after this until the last century and most experienced their maximum Holocene extent during the Little Ice Age.

Cooler, wetter conditions during the Little Ice Age generally decreased the frequency of fires across the Pacific Northwest. Fire frequency declined after 900 cal yr BP, with a short increase at 500 cal yr BP followed by the largest dip at around 300 cal yr BP (Marlon et al. 2006). This pattern is supported locally in the North Cascades where fire frequency dropped after 500 cal yr BP (Prichard et al. 2009). There is some evidence of forests responding to the Little Ice Age, but the timing is widely varied. In Queets, WA shade tolerant Tsuga heterophylla increased at 1000 cal yr BP (Greenwald and Brubaker 2001), while in the San Juan Islands, Tsuga heterophylla became the dominant tree species around 200 years ago (Sugimura et al 2008). In the Olympic Mountains an increase of Cyperaceae after 600 cal yr BP shows that snowpack stayed longer through summer months (Gavin and Brubaker 1999). Cooling off from the Medieval Warm Period began in some areas as early as 1000 cal yr BP, but by 500 cal yr BP a further drop in temperature encouraged already expanding glaciers, and wetter summers decreased fire frequency and encouraged closed canopied forests to further develop.

Summary

The Holocene began after a large rise in global temperature which stabilized around 11,500 cal yr BP, yet climatic variability continued throughout the Holocene (Table 4.2). From 11,500 to 7,000 cal yr BP a warm, dry period known as the Xerothermic saw open canopy forests and low fire frequency. The Altithermal began around 7,000 cal yr BP as the climate became increasingly wet leading to glacial advances in some areas, while temperatures gradually rose to their highest Holocene levels. Modern closed canopy forests developed in most areas by 5,000 cal
yr BP, and along with high temperatures lead to increased fire frequency. By 3,800 cal yr BP the Neoglacial had set in with cooler temperatures and increased humidity leading to glacial advances and lower fire frequency. During the Fraser Valley Fire Period from 2000 to 1,300 cal yr BP, fire frequency increased as temperatures rose and humidity decreased, fires broke up the forests and created more open canopy forests. Glacial advances began again during the First Millennium Advance as the climate cooled and humidity increased; closed canopy forests expanded as fire frequency fell. During the Medieval Warm Period temperatures spiked from 1,000 to 850 cal yr BP while dry summers increased fire frequency which broke up closed canopy forests while wet winters continued the glacial advances that had started during the First Millennium Advance. The Little Ice Age began around 500 cal yr BP with the largest drop in temperature since the early Holocene and nearly all glaciers reached their Holocene maximum. During the Little Ice Age closed canopy forests expanded as humidity increased and fire frequency decreased.
Chapter 5. Stable Carbon & Nitrogen Isotopes


In Misarti et al. (2009) the carbon and nitrogen stable isotope signatures of six archaeological fish and sea mammal species were analyzed to determine changes through time in the marine ecosystem surrounding Sanak Island, Alaska over the last 4,500 years. Modern species were compared to their archaeological predecessors to determine whether shifts in trophic level and feeding location had occurred recently. They then compared stable isotope signatures from different climate regimes to determine whether diet changed in response to climate regime shifts. This was then related to other research in a larger project to understand the role of humans and climate in the structure of ecosystems surrounding Sanak Island (Maschner et al. 2009).

This study instead uses the carbon and nitrogen stable isotope signatures of wapiti (Cervus elaphus) from lowland northwestern Washington to determine changes through time in the
terrestrial ecosystem. Prehistoric Washington wapiti are compared to modern wapiti studied in North America and Europe (Drucker et al. 2008, Stevens et al 2006), and compares wapiti living during different climate regimes to determine how the environment and climate changed. There are many factors that affect $\delta^{13}C$ and $\delta^{15}N$ signatures of wapiti and plants, these factors will be discussed in the rest of this chapter.

**Stable Carbon Isotope Analysis**

Stable carbon isotope analysis measures the ratio of $^{13}C$ to $^{12}C$ in tissue samples, expressed in per mil (‰) and normalized by the equation:

$$\delta^{13}C = \frac{(^{13}C/^{12}C \text{ sample})}{(^{13}C/^{12}C \text{ standard}) - 1} \times 1000,$$

where $\delta^{13}C$ values are reported relative to the V-PDB standard, causing most results to be negative. The main source of the $\delta^{13}C$ ratio in plants is their carboxylation pathway type, the most common two types are C3 and C4. Plants with a C3 pathway discriminate for Carbon 12 over Carbon 13 and thus have lower $\delta^{13}C$ values with a $\delta^{13}C$ signature between -35 and -21‰ (Witt and Ayliffe 2001). C4 plants don’t regulate the amount of Carbon 13 they take in and thus have a higher $\delta^{13}C$ value usually between -9 and -16‰, closer to the atmospheric carbon isotope ratio of -8‰ (Klepinger 1984, O’Leary 1995). Smaller variations are caused by other factors including variation between plant species, dietary tissue type (such as leaf, stem, root ect.), and environmental conditions (such as light levels, humidity, temperature, and elevation).

The $\delta^{13}C$ signatures of animal tissue are helpful in revealing dietary and environmental shifts and reflect protein sources in the animal’s diet. Hair, hoof, tooth enamel, muscle, feces and bone are all frequently used in stable isotope analyses, and retain the isotopic signature of the animal’s diet over the time the tissue grows. Because of this time averaging, slow growing tissues like bone and enamel are preferred for long term studies as seasonal variation is averaged out.
(Maschner et al. 2009). In archaeological contexts, bone and teeth are usually the only surviving tissues but enamel collagen is 14‰ higher than dietary δ^{13}C values while bone collagen is lower by 5.1‰ (Drucker et. al 2008, Garcia et al 2009). In adolescent mammals, bone collagen retains the isotopic signature of drinking milk for the first few years, which is 3-4‰ lower than full adults (Witt and Ayliffe 2001).

Variations in collagen stable carbon isotopes due to climate have been studied for a long time, but some studies have only seen differences in areas that have plants with C3 and C4 pathways (Heaton et al 1986, Cormie and Schwarcz 1996, France 2007). C4 plants are xeric tropical grasses that prefer hotter, drier conditions to C3 plants. In a single plant species, variation causes as much as a 3‰ δ^{13}C variation (Heaton et al 1986), whereas herbivores on a strict C4 plant diet have δ^{13}C values 14‰ higher than herbivores on a strict C3 diet (France 2007). Because of the large difference in stable isotopic signature between C3 and C4 plants, studies in regions that have a mix of these plants will only discern the relative amounts that C3 and C4 plants contribute to the diet.

In areas with only C3 plants climatic differences in temperature, and humidity can be discerned in δ^{13}C variation (Table 5.1; Heaton 1999, Hedges et al 2004, Van Klinken et al. 2000, Stevens et al 2006, West et al 2006). Hotter temperatures increase δ^{13}C by about 0.03‰ for every degree Celsius and decrease 0.1‰ for each 1% increase in relative humidity (Heaton 1999). In response to hot, dry conditions plants close their stomata to conserve water and internal CO2 decreases. This forces plants to fix more ^{13}C causing a more positive δ^{13}C signature. In response to cool, wet conditions plants open their stomata and internal CO2 increases causing less ^{13}C to fix and a more negative δ^{13}C signature (Van Klinken et al. 2000). These changes are passed on
from plants to their consumers so we would expect wapiti in warmer, drier conditions to have higher $\delta^{13}C$ signatures compared to individuals that live in cooler, wetter conditions.

**Table 5.1. Factors Influencing $\delta^{13}C$ (adapted from Heaton 1999).**

<table>
<thead>
<tr>
<th>$\delta^{13}C$</th>
<th>Decreased $^{13}C$</th>
<th>Increased $^{13}C$</th>
<th>Difference $\delta^{13}C$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Branch Length</strong></td>
<td>Shorter</td>
<td>Longer</td>
<td>1.5‰</td>
</tr>
<tr>
<td><strong>Canopy</strong></td>
<td>Closed</td>
<td>Open</td>
<td>2‰</td>
</tr>
<tr>
<td><strong>Plant Type</strong></td>
<td>Herbaceous</td>
<td>Woody</td>
<td>2‰</td>
</tr>
<tr>
<td><strong>Temperature</strong></td>
<td>Colder</td>
<td>Hotter</td>
<td>0.3‰/°C</td>
</tr>
<tr>
<td><strong>Aridity</strong></td>
<td>Wetter</td>
<td>Drier</td>
<td>0.1‰/%r.h.</td>
</tr>
<tr>
<td><strong>Elevation</strong></td>
<td>Lower</td>
<td>Higher</td>
<td>1‰/1km</td>
</tr>
</tbody>
</table>

**Canopy Effect**

Along with temperature and humidity, light also affects the $\delta^{13}C$ values of plants. More sunshine increases carboxylation, causing increased $^{13}C$ fixation in plants and higher $\delta^{13}C$ values (Van Klinken et al. 1994, Heaton 1999, Hedges et al. 2004). Light levels vary in the same region between the perpetual twilight of a mature closed canopy forest and a sunny open prairie. Low light levels in forests causes litter decomposition and soil respiration to release $^{13}C$ depleted CO2. While dense foliage in closed forests limit air circulation causing the depleted CO2 to be absorbed by plants in the understory and passed on to the consumers, resulting in a lower $\delta^{13}C$ signature referred to as the canopy effect (France 1996).

The canopy effect is strongest in dark, dense canopied forests such as tropical rainforests (Merwe and Medina 1991, Sandberg et al 2011). Other studies have tested for it in temperate and boreal forests with varying success (France 1996, Stevens et al 2005, Garcia et al. 2009, Drucker et al. 2008, 2010). Drucker et al. (2010) found caribou foraging in boreal forests had significantly
lower δ\textsuperscript{13}C values relative to those foraging in open tundra. Similarly, France (1996) found foliage in a closed canopy spruce forest had δ\textsuperscript{13}C values 1.2‰ lower than foliage in nearby open areas, and 2‰ lower than canopy foliage (France 1996). However, no difference in δ\textsuperscript{13}C was found between open areas and open canopied pine/birch plantations. This shows that in temperate regions only densely canopied forests have a discernable canopy effect.

Paleontologists have noted decreasing δ\textsuperscript{13}C values in large herbivores during the transition from the Pleistocene to the Holocene and attributed it to either an increase in atmospheric CO2 concentrations, or the widespread growth of forests in the northern hemisphere (Hedges et al. 2004, Bump et al. 2007, Drucker et al. 2008). Worldwide atmospheric CO2 concentrations increased from the Pleistocene to the Holocene from approx. 190 to 250 ppmv, lowering atmospheric δ\textsuperscript{13}C by about 0.5‰ (Van Klinken et al. 1994). At the same time open tundra was replaced by forests, which also lowers δ\textsuperscript{13}C. In Europe, Hedges et al. (2004) measured a decrease of 3‰ in δ\textsuperscript{13}C signatures of large herbivores during the early Holocene. This was interpreted as resulting from increasing CO2 because all the animals in their study showed the same depletion despite varying habitats and foraging behavior. In contrast Drucker et al. (2008) found the same decrease in δ\textsuperscript{13}C signatures of large herbivores consistent with a canopy effect. Bump et al. (2007) found North American mammalian δ\textsuperscript{13}C signatures decreased by 1‰ during the Pleistocene Holocene transition. The δ\textsuperscript{13}C signatures of mammals in Europe and North America both decrease more than the increase of atmospheric CO2 could cause and it likely that the decrease in δ\textsuperscript{13}C during the Holocene transition was due to a canopy effect from the growth of forests in northern latitudes.
Stable Nitrogen Isotope Analysis

Stable nitrogen isotope analysis measures the ratio of $^{15}$N to $^{14}$N in tissue samples and are expressed in per mil (‰) and normalized by the equation $\delta^{15}N = \left( \frac{^{15}N/^{14}N_{sample}}{^{15}N/^{14}N_{standard}} - 1 \right) \times 1000$. The main cause in variation in $\delta^{15}N$ ratios is the method of nitrogen absorption in the plant (Amudson et al. 2003). Nitrogen fixers take N2 from the air and have an average $\delta^{15}N$ value 4‰ lower than non-nitrogen fixers that take nitrogen from the soil (Rodiere et al. 1996). Other sources of nitrogen variation in plants include protein content, soil nitrogen levels and climatic factors (Table 5.2; Amudson et al. 2003).

The $\delta^{15}N$ signature of plants is affected by differences in temperature and humidity (Amudson et al. 2003, Hedges et al. 2004, Stevens et al. 2006, Craine et al. 2009). In warmer drier conditions $\delta^{15}N$ increases in soil and plants while in cooler wetter conditions it decreases, but temperature affects $\delta^{15}N$ more than humidity. Thus the most $^{15}N$ depleted soils are in the arctic and the most enriched soils are in the tropics, and vary globally between -5‰ to 3‰ (Amudson et al. 2003). As soil $\delta^{15}N$ increases plant $\delta^{15}N$ increases at a faster rate than soil $\delta^{15}N$. Foliar $\delta^{15}N$ increased at a rate of 0.23‰ per degree Cellcius and decreases by 2.6‰ for every order of magnitude increase in mean annual precipitation (Craine et al. 2009). These changes in $\delta^{15}N$ are passed on to herbivores, thus herbivores in warmer drier conditions should have higher $\delta^{15}N$ values than those in cooler wetter conditions.

Within plants, $^{15}N:^{14}N$ ratios are further altered after nitrogen uptake from the soil. Plants with higher levels of protein show higher $\delta^{15}N$ signatures (Table 5.2). Walter and Leslie (2009) found higher $\delta^{15}N$ values in the livers of deer foraging in recently burned areas due to the increase in protein. On the central coast of British Columbia, Darimont et al. (2007) found that deer preferred foraging in the protein rich cedar forests and exhibited higher $\delta^{15}N$ values relative to
deer feeding in other forest types. Mycelium absorbs nitrogen from trees and shrubs, which as a result have less protein than plants without mycelium relationships such as forbs and grass (Michelson et al. 1998). The anti-fungal properties of cedar prevent these mycorrhisal relationships from forming which allows cedar forests to have higher protein levels and higher δ¹⁵N signatures than other forest types.

Table 5.2. Factors Influencing δ¹⁵N.

<table>
<thead>
<tr>
<th>δ¹⁵N</th>
<th>Lower</th>
<th>Higher</th>
<th>Span of δ¹⁵N</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil Humidity</td>
<td>Wetter Colder</td>
<td>Drier Hotter</td>
<td>8‰</td>
<td>Amudson et al. 2003</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plant Humidity</td>
<td>Wetter Colder</td>
<td>Drier Hotter</td>
<td>5‰</td>
<td>Craine et al. 2009</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td>4‰</td>
<td></td>
</tr>
<tr>
<td>N₂ Absorption</td>
<td>Fixer</td>
<td>Absorber</td>
<td>4‰</td>
<td>Rodiere et al. 1996</td>
</tr>
<tr>
<td>Protein</td>
<td>High Protein Forage</td>
<td>Low Protein Forage</td>
<td>3‰</td>
<td>Walter and Leslie 2009</td>
</tr>
<tr>
<td>Mycorrhizal</td>
<td>Present</td>
<td>Absent</td>
<td>3.5 - 7.7‰</td>
<td>Michelson et al. 1998</td>
</tr>
<tr>
<td>Marine Input</td>
<td>No Salmon</td>
<td>Lots of Salmon</td>
<td>5‰</td>
<td>Hocking and Remchen 2009</td>
</tr>
</tbody>
</table>

Expectations for Stable Isotope Analysis of Wapiti Bones

A canopy effect is indicated by depleted mammalian δ¹³C values evident during the early Holocene when forests replaced open tundra. However, no one has attempted the measurement of late Holocene fluctuations in canopy cover from stable isotope analysis. The canopy effect should be very pronounced in mature temperate rainforests that are comparable to tropical rainforests in low understory light levels and poor ventilation. Darimont et al. (2007) demonstrated this by using δ¹³C values to discriminate deer foraging in logged habitats relative to deer foraging in unlogged forests in the temperate coastal rainforest of central British Columbia.
Differences in wapiti foraging behavior should be discernible from changes in stable isotope signatures between warm dry periods and cool wet periods during the last 5,000 years. Temperature and humidity directly affect the stable isotope signatures of plants and also favor different plant types with varying stable isotope signatures. There are many factors that would affect the stable isotope signature of wapiti, but overall cool wet climate regimes result in a depleted wapiti stable isotope signature relative to wapiti in a warm, dry climate regime (Tables 5.3 and 5.4).

Table 5.3. Major Factors Influencing Wapiti Stable Isotope Signatures During Cool and Wet Climate Regimes.

<table>
<thead>
<tr>
<th>Colder &amp; Wetter Climate</th>
<th>Lower δ¹³C</th>
<th>Higher δ¹³C</th>
<th>Lower δ¹⁵N</th>
<th>Higher δ¹⁵N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Decreased Temperature¹</td>
<td>More Trees &amp; Shrubs⁴</td>
<td>Decreased Temperature²</td>
<td>Increased Salmon Derived Nitrogen⁵</td>
</tr>
<tr>
<td></td>
<td>Increased Humidity¹</td>
<td></td>
<td>Increased Humidity²</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Denser Forest Canopy, More Forest⁶</td>
<td></td>
<td>More Trees &amp; Shrubs³</td>
<td></td>
</tr>
</tbody>
</table>

### Table 5.4. Major Factors Influencing Wapiti Stable Isotope Signatures During Warm and Dry Climate Regimes.

<table>
<thead>
<tr>
<th>Warmer &amp; Drier Climate</th>
<th>Lower $\delta^{13}$C</th>
<th>Higher $\delta^{13}$C</th>
<th>Lower $\delta^{15}$N</th>
<th>Higher $\delta^{15}$N</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>More Grass &amp; Forbs$^4$</td>
<td>Increased Temperature$^1$</td>
<td>Decreased Salmon Derived Nitrogen$^5$</td>
<td>Increased Temperature$^2$</td>
</tr>
<tr>
<td></td>
<td>Decreased Humidity$^1$</td>
<td></td>
<td></td>
<td>Decreased Humidity$^2$</td>
</tr>
<tr>
<td></td>
<td>More Open Canopy and Fewer Forests$^6$</td>
<td></td>
<td></td>
<td>More Grass &amp; Forbs$^3$</td>
</tr>
</tbody>
</table>


Cooler, wetter conditions directly deplete $\delta^{13}$C and $\delta^{15}$N in plants, and favor mesic plants and late seral stage habitats (Table 5.3). This would increase the development of denser forest canopies and the expansion of forest resulting in an increased Canopy Effect decrease in $\delta^{13}$C. Increased forest cover would result in wapiti consuming more trees and shrubs which have higher $\delta^{13}$C and $\delta^{15}$N values relative to grass and forbs. Cooler, wetter conditions favor salmon runs and result in riparian vegetation absorbing more marine derived nitrogen, high in $^{15}$N (Lepofsky et al. 2005, Bartz and Naiman 2005). Salmon derived nitrogen also favor the development of thicker canopies which would further increase the Canopy Effect (Bartz and Naiman 2005). It is unknown what the relative strength of these factors are in influencing wapiti stable isotope signatures, however the strongest factor is the decreased $\delta^{13}$C and $\delta^{15}$N from a cooler wetter climate.

In hot, dry periods increased temperature and decreased humidity cause higher $\delta^{13}$C and $\delta^{15}$N isotopic signatures in plants, and along with increased fire frequency favor more xeric plants.
and early seral stage habitats (Table 4.4). These factors would break up forests and favor more open landscapes resulting in a weaker Canopy Effect, and increase the proportion of wapiti diet consisting of forbs and grasses that have lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values relative to browse. Increased fire frequency would also raise protein levels in plants, further increasing wapiti $\delta^{15}\text{N}$ values (Walter and Leslie 2009). Overall, the strong effect of increased temperature and decreased humidity should result in higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of wapiti from warm, dry climate periods.
Chapter 6. Methods

Relative wapiti abundance was determined for dated components at six sites in northwestern Washington State and stable isotope analysis of carbon and nitrogen was conducted on bone collage extracted from selected wapiti bones in order to trace variations in diet, environment, and climate regimes. Wapiti (*Cervus elaphus*) was chosen because of its ubiquity in archaeological sites, and its economic importance to prehistoric societies. Because wapiti is a top ranked prey, it was assumed that people always hunted wapiti whenever encountered, so the abundance of wapiti remains relative to other mammals should reflect their relative abundance on the landscape. Wapiti samples came from levels closely associated with radiocarbon dates from six sites in western Whatcom County (Figure 6.1). The sites had calibrated radiocarbon dates ranging from 300 to 5300 cal yr BP. By choosing coastal shell midden sites within the same modern vegetation zone, variation in $\delta^{13}$C and $\delta^{15}$N due to elevation, soil salinity, soil PH, and environment was minimized.
Stable Isotope Analysis

Carbon and Nitrogen stable isotope analysis was conducted on twenty eight wapiti bone collagen samples associated with radiocarbon dates. Wapiti were identified at Western Washington University, and then corroborated at the Burke Museum by comparison with complete adult and immature modern wapiti skeletons, and modern deer (*Odocoileus sp.*) skeletons in their large collection. The samples were identified to element then weighed, measured, and photographed before destructive isotope analysis was conducted.

Samples were analyzed at the CAMAS stable isotope laboratory at Idaho State University following their research protocols (Misarti 2009), while some initial processing steps were completed at Western Washington University. Samples were cut into approximately three, 1.0 g pieces using a rock saw at Western Washington University’s Geology Department. The outer
surfaces of the samples were sanded off using a Dremel rotary sander to remove bone cortex and

dirt. Then for each sample roughly equal sized chunks with a combined weight of between 0.2
and 0.3 grams were cut using a low-speed diamond cutting wheel.

Further preparation and analysis at the CAMAS lab was accomplished by Kelli Barnes
using the following procedures. Samples were cleaned with mechanical means and in a ultrasonic
bath. Samples were air dried completely, then a 2:1 solution of chloroform:methanol was applied
for eight hours for lipid extraction. The chloroform:methanol was poured off, and the remainder
was allowed to evaporate completely from the bone. 5 ml water was added to the test tube with
the sample, then 6N HCl was added dropwise. Samples, water and acid were kept chilled at all
times during the acid treatment and the solution was poured off when needed. Following
neutralization, 3 drops of 5% KOH solution added to 4 ml water was applied for eight hours for
humic acid extraction, with additional treatments as needed. Once neutralized, samples were
gelatinized with a weak HCL treatment, and vigorous vortexing at 60C with N gas (an inert gas)
filling the remainder of the test tubes. Finally, collagen was filtered through .45micron inert filters
and the liquid was collected, frozen, and then freeze dried.

Sample FS 14 was removed from the analysis prior to beginning the chemical treatment
because it was very crumbly and appeared degraded. Sample FS 204 did not survive chemical
treatment and was discarded. Sample AT 375 had a poor C:N ratio indicating the collagen may
have degraded, making the δ^{15}N signature suspect; however this should not affect the δ^{13}C
signature. An additional two pared δ^{13}C and δ^{15}N values from AMS dated wapiti bone collagen
samples taken by Dubeau (2012) and Palmer (2012; Appendix A) to more accurately date site
components at the Cherry Point site 45WH1.
Relative Wapiti Abundance

A measure of the percentage of mammal remains identifiable as wapiti was used in order to compare the relative abundance of wapiti through time (Appendix B). Mammal remains from levels associated with a radiocarbon date mammal remains were identified and mammal NISP (number of identified specimens) was calculated, then wapiti remains were identified and wapiti NISP was calculated. The relative abundance of wapiti was determined by dividing wapiti NISP by mammal NISP and converting into a percentage for each radiocarbon date, and for each climate period. Included in these counts are unidentifiable mammal remains, rodents, and teeth, while antler and artifacts were not included. Identification of faunal material was determined by comparison with the faunal collection at the anthropology department in Western Washington University.

Radiocarbon Dates

Radiocarbon dates from shell were calibrated at 2σ with the program CALIB 6.01 using the Marine09 radiocarbon age calibration (Reimer et al. 2009). The local marine reservoir correction (ΔR) was adjusted following Deo et al. (2004) who suggests a ΔR value of 401 years for the period of 0-500 \(^{14}\)C BP and 1200-3000 \(^{14}\)C BP, and a ΔR value of 0 for 500-1200 \(^{14}\)C BP. All non-shell radiocarbon dates were calibrated 2σ with the program CALIB 6.01 using the IntCal09 radiocarbon age calibration (Reimer et al. 2009).
Stratigraphic Analysis

Thirty-one excavation units (the term “cut” is used in the field report and field notes) from six sites were analyzed to determine what levels were closely associated with the radiocarbon dates. To determine what levels were closely associated with radiocarbon dates, field reports, excavation unit profiles, maps, field notes, and descriptions on bags were studied and compared. For some excavation units, these reference materials were missing and it was only possible to include mammal remains from the level at the depth of the radiocarbon date. In other excavation units a detailed analysis of the stratigraphy was possible and more excavated levels and/or excavation units could be included.

Semiahmoo 45WH17

The Semiahmoo site is located on the northwestern tip of Drayton Harbor at the base of a large sand spit (Figure 6.1). It was excavated during a field school run by Garland Grabert in 1974 and again in 1977 for a contract project (Grabert et al. 1978, Montgomery 1979). The 1973 excavation used 20 cm arbitrary levels, while the 1977 excavation used 10 cm arbitrary levels except for a few excavation units that were excavated on natural levels; both years used ¼” mesh screens (Figure 6.2).
Excavation Unit S5E1: This excavation unit is part of the 1973 excavation. A charcoal sample from a strata of charcoal stained beach pebbles near the bottom of the excavation unit yielded a conventional radiocarbon date of 2875±65 BP (UW332, see Appendix X for details on radiocarbon dates) during the early Neoglacial Period. Lying directly above this is a strata of burnt shell and ash with a hearth feature cut into it consisting of crushed clam, humus, some charcoal and FBR from 80 to 120 cm (Figure 6.3). Above 90 cm this layers becomes mixed with other strata. To exclude these other strata only 100 to 120 cm was used, it contained four mammal bones including one complete wapiti astragalus (AT146, see Appendix A for list of isotope samples) selected for isotope analysis.
Figure 6.3. Profile of S5 E1 West Wall (adapted from original profile).

Excavation Unit S6W4: This excavation unit is part of the 1977 excavation and the excavation unit profile was not located. A charcoal sample from 100 to 104 cm in units B and resulted in a conventional date of $580\pm60$ (UW462) and a calibrated date range of 518 to 661 cal yr BP. This date falls at the end of the Medieval Warm Period. This charcoal sample came from a feature consisting of a cluster of FCR, ash, charcoal, and mussel. Levels between 70 cm and 100 cm are considered associated with the radiocarbon date. Within these levels are eight wapiti fragments including an axis, cervical vertebral fragments, and long bone fragments. The axis (AT277) and a cervical vertebral fragment (AT279) were sent in for isotope analysis.
**Excavation Unit S17 W5:** A charcoal sample from Feature 15, in unit G at 164 to 167 cm below the surface yielded a conventional radiocarbon date of 830±60 BP (UW458) within the Medieval Warm Period. Feature 15 is a hearth within Stratum #10 the deepest cultural stratum. It is made of dark red humic silt and gravel on top of basal spit gravels and lenses of clay (Figure 6.4). The three strata above this are all comprised by crushed shells including blue mussel. Above this is a layer of gravel at 95 cmbs above which a deposit of mostly whole shell marks a distinct shift in deposition. This implies that above 100 cm is from a later time and levels 100 cm to the base are considered associated with the radiocarbon date.

*Figure 6.4.* North Profile of S17 W5 (adapted from Figure 4 in Grabert et al. 1978:44).
Excavation Unit S18 E7 and S18 E6: These excavation units are two halves of a trench measuring 6 meters by 2 meters. The trench was excavated in natural rather than arbitrary levels. Several human burials were found in the upper levels of this trench; human remains were not included in the counts of mammal remains. The radiocarbon date comes from an amalgamation of two charcoal samples both from a large hearth (Feature #38) at 198-210 cm below surface, in the deepest Stratum of Excavation Unit S18 E7 subunits C and D (Figure 6.5). The samples yielded a conventional radiocarbon date of 2715±55 BP (UW463) which falls in the middle of the Neoglacial period. The hearth lies in a stratum composed of decayed blue mussel, fragmented clams, gravel, humus, and charred mammal bone. Strata considered associated with the radiocarbon date are 11B, 11C, 7A, 7B, and 7C (Appendix D). This is about 180 cm to base in S18 E7 and 140 cm to base in S18E6. Strata 7A and 11B are crushed and whole shell with pebbles from 180 cm to 235 cm in S18 E7 and 110 cm to 150 cm in S18 E6. Strata 7B and 7C are humus, pebbles, and crushed shell from 180 to 240 cm in S18 E7 and 155 to 230 cm in S18 E6. Strata is 11 C is crushed shell with blue mussel from 170 to 190 in S18 E7. Six wapiti bone fragments came from these excavation units including three metapodial fragments that refit, two phalange fragments, one rib fragments, and one longbone fragment. A metapodial (AT310) and a phalange fragment (AT127) were sent in for isotope analysis.
Figure 6.5. North Profiles of S18E7 and S18 E6 (adapted from Figure 4 in Grabert et al. 1978:44).
Excavation Unit S28 W10: Four vertebrae were selected by Ellen Kendall in 2005 for radiocarbon dating from Faunal Feature #24 at 95 to 105 cm. They were selected because of their association with dog burial #7 which came from between 100 and 170 cm below surface. The vertebrae yielded a conventional date of 930±70 BP (GX323130), and a calibrated range of 699 to 961 cal yr BP which lies near the beginning of the Medieval Warm Period. The depth of 95 to 105 cm below surface includes strata of fine crushed shell with humus and FBR’s, a band of fine crushed blue mussel with humitic sand, and sterile clay bands. Because the fine crushed shell strata begins at 80 cm and the dog burial is between 100 and 170 cm, all levels between 80 cm and 170 cm are considered associated with the radiocarbon date. This includes 28 wapiti bones of which samples from a radius (AT150) and a cervical vertebrae (AT159) were sent in for isotope analysis.

There was a major discrepancy in the identification of mammal bones from Faunal Feature #24. The report identified all of them as from a single subadult wapiti, but comparing them to collections at the Burke Museum revealed that the vertebrae, ribs, and sternum at 95-100 cm were Northern fur seal (*Callorhinus ursinus*). Faunal Feature 24 seems to be part of Feature 25, described on pp.96-98 of Grabert et al. (1978). The report also suggests that because both are covered with a layer of beach cobbles that these deposits are “continuous” with Faunal Features #13 and 14 in excavation unit S26 W7. These excavation units lie 10 meters apart so it is unlikely that they are continuous. However a radiocarbon dated *Clinocardium nuttallii* valve from S26 W7 at 70 to 80 cm yielded a calibrated date range of 514 to 817 cal yr BP which is close to the date in S28 W10.
Excavation Unit S26 W7: This dated valve came from a layer of nearly whole valves, most of which were *Clinocardium nuttallii*. It yielded a conventional radiocarbon date of 1550+/-40 (B292827). Calibration using the Deo et al. (2004) reservoir correction resulted in a calibrated date range of 634 to 780 cal yr BP, within the Medieval Warm Period. The sample was chosen for this study because it lies in between four wapiti bones in Faunal Features #13 (65 and 67 cm) and #14 (84, 87 cm) along with one other at 78 cm. The dated level of 70-80 cm encompasses the stratum of whole shells, as well as a stratum of broken shell with sand above and a stratum of humus, sand and gravel below. Expanding the sample 10 cm above and below the dated level adds no new strata so levels 60 to 90 cm are considered associated with the radiocarbon date. Within these three levels 11 wapiti bone fragments were found including a thoracic vertebrae (AT427) and a rib (AT429) that were sent in for isotope analysis.
Excavation Unit S28 E9: Two samples were radiocarbon dated from this excavation unit and date to the middle of the Neoglacial Period. The higher charcoal sample at 295 to 300 cm below surface yielded a date of $2830 \pm 65$ BP (UW459). It lies 15 cm above Feature 27, a 50X50 cm hearth in Unit B at 315 to 320 cmbs in stratum #9 which consists of a decomposed shell and mussel matrix. The lower charcoal sample at 323 cmbs yielded a conventional radiocarbon date of $3015 \pm 65$ BP (UW460). It lies 25 cm below feature 27 within Stratum #14 consisting of a dark humic matrix with sand/clay, and compact pebbles and above a sterile paleosol of basal gravel. Stratum #8 is thin and lies just above the higher date. It consists of compact shell and fine crushed mussel with a charcoal stain. Stratum #7 is over 60 cm at its thickest and consists of loose whole shell with blue mussel lenses and fine humitic sands. Stratum #8 is considered associated with the radiocarbon samples because it is so similar to Stratum #9 and there is only a 200 year difference between Stratum #14 and #9. Stratum #7 is not included because it is very different and could be
much younger. Levels from 270 cm to the base were considered associated with the radiocarbon dates. A single wapiti bone was found in these levels: a whole calcaneous (AT375) which was sent in for isotope analysis.

Figure 6.8. North Wall of S28 E9 (adapted from Figure 12 in Grabert et al. 1978:84).
Excavation Unit S40 W17: A charcoal sample from 100 cm below surface yielded a conventional radiocarbon date of 350±50 BP (UW461). This excavation unit is typified by layers of shell separated by layers of ashy sand. The charcoal sample came from Feature 43, a hearth 90 - 100 cm deep within the deepest ash zone above a layer of shell. The sterile layer was reached below this layer of shell. The sterile layer varies greatly in depth between 40 cm in the southwest corner to 140 cm below surface in the northeast corner. This means any arbitrary levels will cut through many different strata, making it difficult to prescribe any level to this date. Luckily the radiocarbon date lies during the most recent climate period, the Little Ice Age. So all levels above and including the dated level are considered part of the Little Ice Age, excluding surface finds (110 cm to 0 cm). Two hundred and eighty-eight mammal bones are in these levels including forty-four wapiti remains. Two wapiti bone samples were sent in for carbon isotope analysis: a right distal humerus (AT92) and a cervical vertebra (AT409).
Figure 6.9. North Wall of S40 W17 (adapted from Figure 8 in Grabert et al. 1978:66).

Cherry Point Site 45WH1

The Cherry Point site is a traditional reef net fishing camp on a small point overlooking the Strait of Georgia. Garland Grabert conducted excavations at this site out of Western Washington University in six field seasons starting in 1969 and ending in 1986 (Markham 1993). The site was excavated in 20 centimeter arbitrary levels and screened through ¼ inch mesh. Some of the areas of this site were excavated with adjoining excavation units making it possible to correlate levels from multiple excavation units to one radiocarbon date. Two faunal analyses were conducted at this site: Hanson and van Gaalen (1994) analyzed the southeastern portion of the site
and identified all faunal material, while Dubeau (2012) analyzed the mammalian faunal remains for most of the site and includes a more recent stratigraphic analysis.

Figure 6.10. Map of Cherry Point site 45WH1.

**Excavation Unit N3 W9:** An AMS date from a wapiti femur fragment at 36 cm below surface yielded a date of 2420±30 BP (B292828) with a calibrated range of 2350 to 2690 cal yr BP during the Neoglacial Period (Palmer 2012). No profiles of this excavation unit are available
so only mammal remains from the 20 to 40 cm level were counted towards this date. There are 35 mammal remains in this level including two wapiti longbone fragments.

**Trench S1W4 to S5W4:** Five excavation units form a continuous trench: S1W4, S2W4, S3W4, S4W4, and S5W4. Two radiocarbon dated samples come from this trench. During the excavation a charcoal sample (ID#1149) was taken from S3W4, 72 cm below surface at the bottom of an intrusive fire pit (Blodgett 1976:34). It yielded a conventional radiocarbon date of 1300±200 BP Excavation unit S3W4 contains two large intrusive pits and the excavation did not separate faunal remains by Feature. Because of this, it cannot be determined what levels are associated with this date and this excavation unit is not included. More recently a marine shell sample was retrieved from the 40 to 60 cm level bag of S4W4. It yielded a conventional radiocarbon date of 3710±60 BP (B279606) and a calibrated date range of 2940 to 3350 cal yr BP. This level contains a layer of dense shell that is continuous through the entire trench, and it is most likely that the marine shell sample came from this stratum. Below this stratum is grey to brown pebbly soil which is continuous through the trench. Artifacts from this stratum are typical to the Locarno Beach period which began around 3500 BP. The dense shell stratum and the grey to brown pebbly Stratum are considered associated with the radiocarbon date. In excavation units S5W4, S4W4, and S2W4 this is everything below 40 cm, in S1W4 everything 35 cm and below. Eighty-eight mammal remains are in these levels, two of which are wapiti. One is part of a right femur from excavation unit S1W4 level 55 to 75 (MD25), and the other is part of a metapodial from excavation unit S2W4 40-60 cm (MD54). Samples from these two wapiti bones were sent in for isotope analysis.

**Excavation Unit S1 W10:** A marine shell sample (UGAMS03342) from 60 to 80 cm below surface yielded a conventional radiocarbon date of 1470±25 BP (Rorabaugh 2009). This
date was corrected using the Deo et al. (2004) local marine reservoir which resulted in a calibrated date range of 562 to 680 cal yr BP, during the Medieval Warm Period. The sample came from an intrusive fire pit feature in the southern portion of the excavation unit in a layer of gray soil, sparse shell, and small pebbles. The 60 to 80 cm level cuts through two stratigraphic levels (Rorabaugh 2009:153), so it is not included in this analysis. The 40 to 60 cm level contains only the top layer of gray soil and is considered most directly associated with the radiocarbon date. Sixty seven mammal bones were counted in this level but no wapiti remains were identified.

Figure 6.11. West Wall Profile of S1 W10 (Figure 6.4 in Rorabaugh 2009:153).

Excavation Units S7E8, S8E8, S7E9, and S8E9: These four excavation units next to each other joined north to south with a 1 meter bulk separating the excavation units east to west; each excavation unit measures 3 by 2 meters. Two radiocarbon dates come from these cuts. A charcoal sample (RL272) from S7E8 at 160 to 175 cm below surface yielded a radiocarbon date
of 2630±240 with a calibrated date range of 2152 to 3338 cal yr BP. This sample came from a layer of coarse brown sand in the deepest level of excavation (Blodgett 1976). The only level with mammal bone in it associated with this date is 140 to 160 cm in S8E8, which contains seven mammal remains, none of which are identifiable as wapiti.

An additional date was obtained more recently by Aubrey Steingraber to better date fish bone deposits for a study on salmonid species identification (Aubrey Steingraber, personal communication 2012). The marine shell sample (B298339) from the 80-100 cm level of S8E8 yielded a radiocarbon date of 1280±40 with a calibrated date range of 427 to 561 cal yr BP during the end of the medieval Warm Period. This is the lowest layer that contains shell and it is easily traceable through all four of these cuts. It lies above a thick stratum of dark clay with pebbles and below a complex of features in shell midden. The interface between the bottom of the shell midden and the top of the dark clay layer is considered associated with this radiocarbon date. In S7E8, S8E8, and S7E9 this includes levels 60-100, in S8E9 this includes level 120-140. There are 146 mammal bones from these levels including 15 wapiti bones.

**Excavation Unit S24 E29:** A wood sample (B292829) from a hearth 60 to 80 cm below surface yielded a conventional radiocarbon date of 1230±40 BP and a calibrated range of 1064 to 1266 (Palmer 2012). The sample was identified as arrow-wood (*Holodiscus discolor*). This is the only excavation unit in this study with a radiocarbon date during the brief First Millennium Advance, a brief cool wet period from 1000 to 1300 BP. There are 139 mammal bones from the 60 to 80 cm level of which 19 were identified as wapiti. A sample of wapiti vertebra (AT497) was sent in for stable isotope analysis.
Ferndale Site 45WH34

Western Washington University field school students excavated the Ferndale site located in Ferndale, Washington in 1972 under the guidance of Garland Grabert (Figure 5.12). The site was excavated in 20 centimeter arbitrary levels and screened through \( \frac{1}{4} \) inch mesh (Nokes 2004). The entire Ferndale site dates to the hot, dry Altithermal climate period with 10 of 15 calibrated dates ranging from 4400 to 5300 cal yr BP. Five dates ranging from 1,300 to 150 cal yr BP are inconsistent with stratigraphic evidence, and are believed to be from intrusive wood (Gillis 2007:58). Nokes (2004) identified the mammal bones within this site in 2002 and 2003 for his thesis, and found 161 wapiti remains out of 4896 mammal remains. Stratigraphy was analyzed by Gillis (2007) and is not repeated here. Based on her analysis, it is reasonable to treat the site as a single component site, thus I consider the whole mammalian assemblage to be associated with the date range of 4400 to 5300. Seven wapiti bone samples from this site were sent in for isotope analysis (see Appendix A).
Figure 6.12. Map of Ferndale Site 45WH34 showing calibrated radiocarbon date ranges (Gillis 2007:54).
Birch Bay Site 45WH9

This site is located on Birch Bay on the eastern side of the Strait of Georgia (Figure 5.1). Gaston and Grabert (1975) monitored trench excavations while a sewer line was installed. A few test cuts were excavated in 20 cm arbitrary levels and screened through 1/4 inch mesh. In Test Cut A, a charcoal sample 165 cm deep yielded a conventional radiocarbon date of 848±108 BP with a calibrated range of 671 to 965 cal yr BP (UW343), falling during the Medieval Warm Period. Levels from 120 to 160 cm are associated with this date and contain 20 mammal bones including 1 wapiti long bone fragment. In 2010 the sewer line was replaced and Drayton Archaeology monitored utility trench excavation. A wapiti rib (BS8) sent in for stable isotope analysis, was recovered from Feature 5 in the trench 50 cm horizontal from a charcoal sample (also within Feature 5) that yielded two radiocarbon dates (B278907, B278908) that yielded conventional dates of 530±40 BP and 640±40 BP (Baldwin et al. 2011:90).

Figure 6.13. South Wall of Test Cut A, 45WH9 (adapted From Gaston and Grabert 1975:57).
Lummi Peninsula Sites

These sites all lie on the Lummi Peninsula, a large stabilized spit west of Bellingham. Grabert and Griffin (1983) monitored utility trench excavations and oversaw the excavation of test cuts in arbitrary 20 cm levels. Screen size was not stated but Dr. Grabert usually used ¼” screens.

45WH100 Test Cut 5: A charcoal sample taken from Stratum 2 (Feature 6) at a depth of 145 cm resulted in a conventional 14C date of 2410±60 BP (B4109) with a calibrated range of 2344 to 2706 during the Neoglacial Period. Feature 6 is described as a heap of shell lying on top of the sterile layer lying at 160 to 180 cm within Stratum 4 (Feature 4) and below Stratum 5 (Feature 5). Stratum 4 is described as a denser and darker stained midden earth with shell containing 50% 2 cm size pebbles, 35% whole to half shell in slightly stained charcoal matrix at a depth of 120 to 180 cm (Grabert and Griffin 1983:55). Stratum 4 lies above the sterile layer and below Stratum 6 a thin layer of light brown sand described as an ancient ground level. Stratum 5 also lies within Stratum 4 and is described as a baked clay hearth comprised of burnt shell fragments in sandy-clay matrix with 77 associated mammal bones at a depth of 130 to 140 cm and a lens at 150 to 160 cm. There is a discrepancy between the depth of the radiocarbon date listed in the report as 145 cm deep and lying within Stratum 2 with a depth listed as 160 to 180 cm. Both of these depths lie within Stratum 4 (120 to 180 cm). All levels below 120 cm to sterile at 180 cm were considered associated with the radiocarbon dated sample; this includes Features 4, 5 and 6. There were 48 mammal bone fragments within these levels that included two wapiti fragments.
45WH111 Test Cut 3: A charcoal sample (B4105) lying at 110 cm within Feature 25 (Stratum 1) in the basal clay layer at the base of the excavation, and yielded a convention 14C date of 460± 50 BP with a calibrated date range of 326-626 cal yr BP. This falls during the beginning of the Little Ice Age but extending into the Medieval Warm Period. The whole excavation unit above this dated level then lies within the Little Ice Age, but levels 80 to 140 are most closely associated to the radiocarbon date. Between 20 and 50 cm there are 10 wapiti fragments identified to element and 25 wapiti fragments in the whole unit, all above 90 cm. A wapiti humerus fragment (AT39.1) and a unciform (AT39.2) were sent to Idaho State University for stable isotope analysis.
Figure 6.15. Profile of 45WH111 Test Cut 3 east wall (adapted from Grabert and Griffin 1983:88).
Chapter 7. Results

The data from this study support the hypothesis laid out by Broughton et al. (2008) that wapiti populations decline during warm, dry and highly seasonal climate periods. The relative wapiti abundance is significantly lower during the warm dry Altithermal and Medieval Warm Periods, and significantly higher during two of the three cool, wet periods. Stable isotope analysis revealed significantly higher $\delta^{15}$N values in wapiti remains during the Medieval Warm Period than any other period, suggesting xeric conditions. High variability in the stable isotope signatures of wapiti from Semiahmoo suggests that wapiti were hunted in many different environments.

Wapiti Abundance

Relative wapiti abundance was calculated by dividing wapiti NISP by mammal NISP and converting into a percentage. Excluding Ferndale which was analyzed separately, the entire sample consists of 1,863 mammal remains, 170 of which were identified as wapiti remains (Table 7.1). Over half the sample comes from Semiahmoo (45WH17), most of which falls during the date range of 300 to 1000 cal yr BP during the Little Ice Age (LIA) and Medieval Warm Period (MWP). Cherry Point (45WH1) contributes about ¼ of the total sample, most of which comes from the date range of 427-1270 cal yr BP during the Little Ice Age, Medieval Warm Period and First Millennium Advance (FMA). A comparatively small proportion of the sample is from 45WH9, 45WH100, and 45WH111. The Ferndale (45WH34) assemblage was analyzed separately by Nokes (2004) and should be compared cautiously to sites in this study due to differences in methodology and sample size. Ferndale
is much larger with a total mammal NISP of 4896, 169 of which are identified as wapiti. It is also over 1000 years earlier than the next oldest site component, and believed to be predominately a single component dating between 4,400 and 5,300 cal yr BP (see Gillis 2007 for a discussion of this).

<table>
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<th>Site Number</th>
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<th>#^{14}C Dates</th>
<th>Cal. Date Range</th>
<th>Climate Period(^1)</th>
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<th>Wapiti NISP</th>
<th>Relative Wapiti Abundance(^2)</th>
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\(^1\)LIA: Little Ice Age, MWP: Medieval Warm Period, FMA: First Millennium Advance, NG: Neoglacial, ALT: Altithermal. \(^2\)Relative Wapiti Abundance = wapiti NISP/ mammal NISP * 100%.

A dynamic pattern of relative wapiti abundance is revealed by grouping wapiti abundance by site and separating by climate period (Figure 7.1). Overall the highest wapiti abundance during each climate period is at Semiahmoo, and the highest three wapiti abundances are found during the three colder periods. The Neoglacial have contradictory
wapiti abundance measures where Cherry Point (45WH1) and 45WH100 have low wapiti percentages while Semiahmoo (45WH17) has a much higher percentage of wapiti. Site assemblages dating to the Medieval Warm Period all have low relative wapiti abundances, however Birch Bay has a very low sample size. The Cherry Point wapiti abundance does not appear on the graph because out of 67 mammal remains dating to this period none were identified as wapiti. When samples are grouped into climate period and inter-site variation is averaged out (Figure 7.2), there is a pattern of increasing wapiti abundance in each cool period, and a decrease in the Medieval Warm Period.

Figure 7.1. Relative wapiti abundance by site and climate period.
Figure 7.2. Wapiti abundance per climate period.

Table 7.2. Wapiti and Mammal NISP per Climate Period.

<table>
<thead>
<tr>
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<th>First Millennium Advance</th>
<th>Early Neoglacial</th>
<th>Late Altithermal</th>
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Pearson's Chi Squared Test for Independence was implemented to test what factors relative wapiti abundance is dependent on. Wapiti NISP was compared to Mammal NISP, and separated by, sites, cultural phase, climate periods, and combined Warm and cool climate periods. Table 7.3 shows an example of this statistical test where Wapiti NISP was compared to Mammal NISP and separated by cultural phases. Expected values were derived by adding up each column total, multiplying by the row total, and dividing by the grand total. The observed $\chi^2$ was calculated where $\chi^2 = \sum_{i=1}^{n} \frac{(Observed_i-Expected_i)^2}{Expected_i}$ and relative wapiti abundance was found to be associated with climate period ($\chi^2 = 102, df = 4, P < 0.01$).
For cultural periods, the LIA, MWP, and FMA were combined into the Gulf of Georgia Phase, while the NG and ALT remain separate as the Locarno Beach and St. Mungo Phase, while for sites the wapiti and mammal NISP was separated for each site (see Table 7.1). Relative wapiti abundance was found to be associated with climate period, combined warm vs cool periods, cultural period and sites while Cramer’s Phi suggests the strongest association is with climate period (Table 7.4). When the Ferndale assemblage is removed from the analysis, wapiti abundance is no longer dependant on site or cultural period, which shows that the Ferndale site is causing the outcome in these two tests. The Ferndale site mammal assemblage is unique from other sites in this study in that it occurs entirely within the Altithermal climate period and the St. Mungo cultural period, and also has a much larger sample size. When excluding the Ferndale assemblage, wapiti abundance is still significantly different between climate periods ($\chi^2 = 13, df = 3, P < 0.01$), and when comparing the Medieval Warm Period to the combined cool periods ($\chi^2 = 7.65, df = 1, P < 0.01$).

Table 7.3 Contingency Table for Relative Wapiti Abundance Vs. Climate Periods.

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<th>LIA</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Expected</strong></td>
<td>241.90</td>
<td>10.98</td>
<td>7.55</td>
<td>39.98</td>
<td>38.59</td>
</tr>
<tr>
<td><strong>Wapiti</strong></td>
<td>4823.10</td>
<td>219.02</td>
<td>150.45</td>
<td>797.03</td>
<td>769.41</td>
</tr>
<tr>
<td><strong>Mammal</strong></td>
<td>4823.10</td>
<td>219.02</td>
<td>150.45</td>
<td>797.03</td>
<td>769.41</td>
</tr>
</tbody>
</table>
Table 7.4. Contingency Tables of Relative Wapiti Abundance.

<table>
<thead>
<tr>
<th>Including Ferndale Site 45WH34</th>
</tr>
</thead>
<tbody>
<tr>
<td>Method</td>
</tr>
<tr>
<td>DF</td>
</tr>
<tr>
<td>Probability</td>
</tr>
<tr>
<td>Cramer's Phi</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Excluding Ferndale 45WH34</th>
</tr>
</thead>
<tbody>
<tr>
<td>Method</td>
</tr>
<tr>
<td>DF</td>
</tr>
<tr>
<td>Probability</td>
</tr>
<tr>
<td>Cramer's Phi</td>
</tr>
</tbody>
</table>

The previous tests showed that wapiti abundance is significantly different between climate periods, but we do not know which individual periods are significantly different from each other. To test for significant difference in wapiti abundance between individual climate periods a 2x2 contingency table was used with Yules Q showing the strength of the association (Table 7.4). Two pairs of climate periods were not significantly different: the Neoglacial and Medieval Warm Period, and the First Millennium Advance and Little Ice Age. Yules Q is negative in nearly all cases showing that wapiti abundance increases in each later period, except between the First Millennium Advance and Medieval Warm Period. The Altithermal is significantly different from all periods below the 0.01 level, while the Medieval Warm Period and Little Ice Age are the only other pair significantly different below the 0.01 level. Yule’s Q shows that the strength of the association is strongest between the Altithermal and First Millennium Advance and weakest between the Medieval Warm Period and Little Ice Age, while all other Q values are similar.
The analysis of relative wapiti abundance revealed a statistically significant association with climate period, and a significant difference between warm and cool climate periods, with higher abundance in cool periods, and lower abundance in warm periods. Two of the cool periods, the First Millennium Advance and Little Ice Age are not significantly different from each other, while the Neoglacial has significantly smaller relative wapiti abundance than other cool periods. The relatively low abundance of wapiti during the Medieval Warm Period is further validated of all three sites occurring then having separately low abundances. It is likely that long dry summers and short spring plant growth seasons depressed the population of wapiti during the Medieval Warm Period.

Wapiti Stable Isotope Analysis

The stable isotope $\delta^{13}C$ and $\delta^{15}N$ analysis resulted in 29 samples with $\delta^{13}C$ values ranging from -20.79 to -25.68, and $\delta^{15}N$ values ranging from 1.98 to 5.56 (Figure 7.3). The wapiti bone collagen samples have a mean $\delta^{13}C$ value of -23.55 with a standard deviation of 1.07, a mean $\delta^{15}N$ value of 3.54 and standard deviation of 0.81. One of these samples had a poor C:N ratio reflecting possible collagen degradation so the $\delta^{15}N$ value is not reliable and is
not included, however the $\delta^{13}$C value is considered good and is included (Bruce Finney personal communication 2012).

Wapiti from the Semiahmoo site (45WH17) have a far more variable isotopic signature that wapiti at any other site, with the two highest $\delta^{13}$C and $\delta^{15}$N values and each of the lowest $\delta^{13}$C and $\delta^{15}$N values. The $\delta^{13}$C enriched values around -21‰ are likely from wapiti eating aquatic lake plants that are enriched in $\delta^{13}$C and $\delta^{15}$N relative to terrestrial plants (Drucker et al. 2010). Samples low in $\delta^{13}$C and high in $\delta^{15}$N are likely from wapiti feeding in riparian zones heavily fertilized by salmon, as the transfer of large amounts of marine nitrogen from decaying salmon has been shown to raise the $\delta^{15}$N values of understory plants, and increase the density of the riparian forest canopy (Bartz and Naiman 2005, Hocking and Reimchen 2009), which would lower the $\delta^{13}$C values of understory plants.
Figure 7.3. Paired $\delta^{13}$C and $\delta^{15}$N values of wapiti by site. Red triangles are from 45WH17, blue diamonds are from 45WH1, yellow squares are from 45WH34, purple rectangles are from 45WH111 and the green circle is from 45WH9.

The $\delta^{13}$C values of wapiti from this study are depleted relative to modern wapiti from other studied regions worldwide (Figure 7.4). Wapiti from open landscapes such as the Cis-Baikal steppe and Scottish Moors are enriched 1 to 3‰ in $\delta^{13}$C relative to wapiti from densely forested regions. Wapiti from prehistoric Washington are depleted 1.5‰ relative to modern forested regions, showing an extreme example of the canopy effect. This is consistent with paleoenvironmental reconstructions of Washington covered by dense, late seral temperate rainforest by 5000 cal yr BP (Sugimura et al. 2008, Prichard et al. 2009).
Figure 7.4. Worldwide modern δ^{13}C values of wapiti showing median and standard error. Samples were corrected to show bone collagen δ^{13}C values. The δ^{13}C values from the Saskatchewan boreal forest, Polish old growth forest, and Cis-Baikal steppe are from Drucker et al. (2008). The δ^{13}C values from the English woodland, polish mixed forest, Scottish plantation, and moors are from Stevens et al. (2005). The δ^{13}C values from NE Oregon forest/meadow are from Starkey et al. (2003) and only show the mean for their 29 samples. This study is represented as the Washington rainforest and was corrected for the -1.5‰ δ^{13}C depletion from fossil fuel burning.

Temporal Trends in Isotope Values

The samples are not temporally continuous, instead there are three time periods represented: 300 to 1300, 2300 to 3300 and 4400 to 5300 cal yr BP (Figure 7.5). The earliest period is represented solely by Ferndale (45WH34) and is centered around 4800 cal yr BP during the late Altithermal. The last 1300 years have more variability than earlier periods, which includes most of the Semiahmoo wapiti. This is also the longest continuous time span and includes three climate periods: the First Millennium Advance, the Medieval Warm
Period, and the Little Ice Age. No significant difference was found between the stable isotope values after 1300 and before 2300 cal yr BP for $\delta^{13}$C (Mann–Whitney U-test, $U = 98, p = 0.77$) or $\delta^{15}$N (Mann–Whitney U-test, $U = 84, p = 0.55$). This suggests that overall the climate and environment remained fairly stable through time.
When separating stable isotope samples by climate periods a trend emerges of slightly higher $\delta^{13}C$ and $\delta^{15}N$ in warm, dry periods followed by slightly lower $\delta^{13}C$ and $\delta^{15}N$ in cool, wet periods (Table 7.5, Figure 7.6). Four of the five climate periods have roughly equal sample sizes with seven in the Little Ice Age (LIA) and Neoglacial (NG), and six in the
Medieval Warm Period (MWP) and Altithermal (ALT). The First Millennium Advance (FMA) has only two samples so it is not included as a separate climate period in statistical tests. The warm, dry periods have higher mean $\delta^{15}$N values than the cool wet periods and lower mean $\delta^{13}$C values (Table 7.6). The Medieval Warm Period is unique with the highest maximum and minimum $\delta^{15}$N values, and the highest average $\delta^{15}$N values (Table 7.5), so any significant differences are likely to be with this period.

**Table 7.6.** Descriptive Statistics for Climate Period $\delta^{15}$N.

<table>
<thead>
<tr>
<th>$\delta^{15}$N</th>
<th>LIA</th>
<th>MWP</th>
<th>NG</th>
<th>ALT</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>Min</td>
<td>1.98</td>
<td>3.44</td>
<td>2.26</td>
<td>2.67</td>
</tr>
<tr>
<td>Max</td>
<td>4.85</td>
<td>5.56</td>
<td>4.4</td>
<td>4.91</td>
</tr>
<tr>
<td>Mean</td>
<td>3.367</td>
<td>4.195</td>
<td>3.382</td>
<td>3.46</td>
</tr>
<tr>
<td>Median</td>
<td>3.22</td>
<td>3.705</td>
<td>3.465</td>
<td>3.36</td>
</tr>
<tr>
<td>Stand. dev</td>
<td>0.861</td>
<td>0.906</td>
<td>0.754</td>
<td>0.698</td>
</tr>
</tbody>
</table>

**Table 7.7.** Descriptive Statistics for Climate Period $\delta^{13}$C.

<table>
<thead>
<tr>
<th>$\delta^{13}$C</th>
<th>LIA</th>
<th>MWP</th>
<th>NG</th>
<th>ALT</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>7</td>
<td>6</td>
<td>7</td>
<td>7</td>
</tr>
<tr>
<td>Min</td>
<td>-25.68</td>
<td>-24.81</td>
<td>-24.8</td>
<td>-24.31</td>
</tr>
<tr>
<td>Max</td>
<td>-21.05</td>
<td>-20.79</td>
<td>-22.95</td>
<td>-22.06</td>
</tr>
<tr>
<td>Mean</td>
<td>-23.573</td>
<td>-23.385</td>
<td>-23.844</td>
<td>-23.216</td>
</tr>
<tr>
<td>Median</td>
<td>-23.75</td>
<td>-23.675</td>
<td>-24.02</td>
<td>-23.21</td>
</tr>
<tr>
<td>Stand. dev</td>
<td>1.433</td>
<td>1.418</td>
<td>0.654</td>
<td>0.866</td>
</tr>
</tbody>
</table>

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Figure 7.6. Wapiti $\delta^{13}$C and $\delta^{15}$N separated by climate period. Cool, wet periods are marked in blue while warm, dry periods are marked in red.

The Kruskal-Wallis test did not reveal a significant difference between the medians of the climate periods for $\delta^{13}$C ($p=0.762$) or $\delta^{15}$N ($p=0.196$, Table 7.7). When comparing combining cold periods and combined warm periods the Mann-Whitney test showed no significant difference for $\delta^{13}$C ($p=0.409$) or $\delta^{15}$N ($p=0.182$). To see if any individual climate periods are significantly different, Mann-Whitney tests were run between each climate period. The only significant difference occurs between the Medieval Warm Period and the Altithermal $\delta^{15}$N values ($p=0.027$), while no significant difference exists between the $\delta^{13}$C values of any climate periods. To see whether the Medieval Warm Period or Altithermal is responsible for the significant difference $\delta^{15}$N values for each were tested against all other $\delta^{15}$N values, and against combined cold period $\delta^{15}$N values using the Mann-Whitney U-test. The only significant difference occurs between Medieval Warm Period $\delta^{15}$N values and all other stable isotope values ($p=0.023$), while $\delta^{15}$N values approach significance between the Medieval Warm Period and combined cold periods ($p=0.063$). These tests show that $\delta^{13}$C
values remain stable through time, while during the Medieval Warm Period $\delta^{15}\text{N}$ values increase significantly.

**Table 7.8.** Statistical tests on stable carbon and nitrogen isotopes.

<table>
<thead>
<tr>
<th>Statistical Tests</th>
<th>$\delta^{13}\text{C}$ Probability</th>
<th>$\delta^{15}\text{N}$ Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kruskal-Wallis</td>
<td>0.762</td>
<td>0.196</td>
</tr>
<tr>
<td>Climate Periods</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mann-Whitney U-test</td>
<td>0.409</td>
<td>0.182</td>
</tr>
<tr>
<td>Warm v Cold</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mann-Whitney U-test</td>
<td>Between Climate Periods:</td>
<td></td>
</tr>
<tr>
<td>MWP v ALT</td>
<td>0.617</td>
<td>0.027*</td>
</tr>
<tr>
<td>MWP v LIA</td>
<td>0.886</td>
<td>0.100</td>
</tr>
<tr>
<td>MWP v NG</td>
<td>0.830</td>
<td>0.379</td>
</tr>
<tr>
<td>ALT v LIA</td>
<td>0.523</td>
<td>0.898</td>
</tr>
<tr>
<td>ALT v NG</td>
<td>0.318</td>
<td>0.943</td>
</tr>
<tr>
<td>LIA v NG</td>
<td>0.805</td>
<td>0.977</td>
</tr>
<tr>
<td>Mann-Whitney U-test</td>
<td>MWP and ALT $\delta^{15}\text{N}$ values:</td>
<td></td>
</tr>
<tr>
<td>MWP v All Others</td>
<td>0.023*</td>
<td></td>
</tr>
<tr>
<td>MWP v Cold</td>
<td>0.063</td>
<td></td>
</tr>
<tr>
<td>ALT v All Others</td>
<td>0.595</td>
<td></td>
</tr>
<tr>
<td>ALT v Cold</td>
<td>0.718</td>
<td></td>
</tr>
</tbody>
</table>

*Significantly different at the 0.05 level.

Stable carbon and nitrogen isotope valued from Semiahmoo wapiti show the widest range in stable isotope values, with $\delta^{13}\text{C}$ signatures varying by as much as 4.5‰ in wapiti from the same time (Figure 7.7). Three stable isotope values date to 2700-3200 cal yr BP, while 10 date to 300-1000 cal yr. BP. The standard deviation of the $\delta^{15}\text{N}$ values don’t change much, while $\delta^{13}\text{C}$ standard deviation increases from 0.44 to 1.53, in the later period (Table 7.8). Semiahmoo is also unique in having the highest relative wapiti abundance during the early Neoglacial and Little Ice Age. This is consistent with Montgomery’s (1979) faunal analysis that showed a higher proportion of wapiti at Semiamoo than at other contemporary
sites. Semiahmoo hunters may have specialized in wapiti and intensified wapiti hunting by increasing the number of habitat types exploited.

**Table 7.9.** Descriptive Statistics for Semiahmoo $\delta^{13}C$ and $\delta^{15}N$ Values.

<table>
<thead>
<tr>
<th></th>
<th>$\delta^{15}N$ Early$^1$</th>
<th>$\delta^{15}N$ Late$^2$</th>
<th>$\delta^{13}C$ Early$^1$</th>
<th>$\delta^{13}C$ Late$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>4</td>
<td>10</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Min</td>
<td>1.93</td>
<td>1.98</td>
<td>-24.02</td>
<td>-25.68</td>
</tr>
<tr>
<td>Max</td>
<td>4.4</td>
<td>5.56</td>
<td>-23.14</td>
<td>-20.79</td>
</tr>
<tr>
<td>Mean</td>
<td>3.11</td>
<td>3.69</td>
<td>-23.59</td>
<td>-23.32</td>
</tr>
<tr>
<td>Median</td>
<td>3.06</td>
<td>3.54</td>
<td>-23.6</td>
<td>-23.36</td>
</tr>
<tr>
<td>Stand. dev</td>
<td>1.06</td>
<td>1.01</td>
<td>0.44</td>
<td>1.53</td>
</tr>
</tbody>
</table>

1: 2700-3200 BP, 2: 300-1000 BP

**Figure 7.7.** Semiahmoo wapiti $\delta^{13}C$ and $\delta^{15}N$ values.

**Summary**

This study found significantly higher $\delta^{15}N$ values of wapiti bone collagen during the Medieval Warm Period than other late Holocene climate periods, while $\delta^{13}C$ values remained stable throughout. The significantly higher $\delta^{15}N$ signatures during the Medieval Warm Period
suggest that the hottest driest conditions of the late Holocene occurred at that time. The $\delta^{13}C$ values do not significantly change over time and suggests that dense canopied, late seral coniferous forests covered northwestern Washington by 5,300 cal yr BP and varied little through late Holocene climate periods. The relative abundance of wapiti was found to be dependent on climate period and was significantly smaller during the hot, dry Medieval Warm Period and Altithermal than during colder, wetter periods. All site components dating to the Medieval Warm Period have similarly low wapiti abundance, further suggesting that adverse climate conditions during this period caused depressed wapiti abundance.
Chapter 8. Discussion

Lepofsky et al. (2005:278) argues that the abundance of cervids would increase in periods of long summer drought as a result of increased fire frequency breaking up forests and increasing the productivity of meadows and food wapiti rely on. This study found the opposite of this prediction, with significantly lower relative abundance of wapiti during the Altithermal and the Medieval Warm Period, when long summer droughts were common. There may have been increased meadow productivity, but δ\textsuperscript{13}C values of wapiti suggest that overall the environment remained heavily forested. Instead, decreased relative wapiti abundance during hot dry conditions fits Broughton et al.’s (2008) model where a shift in precipitation regime increases winter precipitation and decreases spring precipitation hindering plant growth and lowering the survival rate of large game. Paleoclimate reconstructions of the Medieval Warm Period reveal a pattern of heavy winter, and light summer precipitation with higher temperatures, increased fire frequency and continued glacial advances (Marlon et al. 2006, Mann et al. 2008, Koch and Clague 2011). This shift to drier conditions in the Medieval Warm Period is reflected in significantly higher δ\textsuperscript{15}N values in wapiti from this study.

Broughton et al. (2008) suggests that large game would be less abundant during the Altithermal on the Northwest Coast due to seasonal extremes of long summer droughts and strong winter precipitation. This is supported by the significantly lower wapiti abundance found in this study from 4,400 to 5,300 cal yr BP during the Altithermal than all later climate periods, suggesting that wapiti populations were depressed due to the adverse climate
conditions. However $\delta^{13}$C and $\delta^{15}$N values of wapiti dating to the Altithermal are not significantly different than later climate periods measured in this study. This fits with local paleoenvironmental evidence that suggests the Altithermal began cooling off and becoming increasingly wet between 4,500 and 5,300 cal yr BP, leading to the establishment of modern coniferous forests in many regions (Hibbert 1979, Sugimura et al. 2008, Brown et al. 2008, Prichard et al. 2009).

Despite questioning Lepofsky et al.’s (2005) prediction of wapiti response to long summer drought, their overall model is a good description of cultural and environmental response to climate change. Their model predicts a regional decline in salmon abundance and predictability due to high atmospheric temperature increasing water temperature, lower stream water levels, and high fire frequency increasing river siltation. The large water volume of rivers would moderate these effects while smaller streams would be more greatly affected. During the fall salmon mill around the mouths of streams waiting for winter rain to flood, increasing the amount of salmon at the deltas of the largest rivers such as the Fraser and the Nooksack relative to salmon along the coast and smaller streams. Leposfsky et al. (2005:282) predict that cultures would respond by strengthening connections to villages at these larger deltas to ensure access to the more abundant salmon, while people already at these deltas would benefit from more prestige.

Although Lepofsky et al. (2005) refer specifically to the Fraser Valley Fire Period, the Medieval Warm Period shares many of the environmental characteristics such as long warm summer droughts and increased fire frequency and predictions can be equally applied. During the Medieval Warm Period rising sea surface temperature and decreased upwelling caused decreased marine resource productivity (Daniels 2009), causing declines in salmon
productivity. This added to the depression of wapiti and other Cervid populations would further motivate people to access deltaic resources, and other areas that moderate climate effects.

Upland resources may have become more productive during the Medieval Warm Period and other winter-wet summer-dry periods. Broughton et al. (2008:1919) notes that increased winter precipitation would increase the snowpack, shielding alpine plants from the negative effects of summer drought with snowmelt. High winter snowfall depresses tree growth in high altitudes and expands subalpine meadows which feed water from melting snowpack in the summer (Burchard 2003:42), while increased fire frequency would further break up forests and likely lead to much larger subalpine meadows than modern conditions (Lepofsky et al. 2005:279). Subalpine meadows are very productive habitat for cervids, supplying them with abundant forbs, grasses and small bushes. They were also important to local societies for their abundance of berries, grouse and cervids (Burtchard et al. 2003:42). Increased productivity of upland resources coinciding with decreased lowland productivity would further increase their importance to local societies and would see increased use by people during this time.

**Intensification of Wapiti**

Decreased abundance of large prey animals is often seen as evidence for human driven resource depression as predicted by the Prey Choice Model (Grayson 2001). Synchronous decline in the relative abundance of wapiti and δ^{15}N enrichment of wapiti during the Medieval Warm Period strongly suggests that climate was the cause rather than
hunting pressure. However Ames and Maschner (1999:54) note that a peak in human population may have occurred around 1000 years ago, which could increase hunting pressure. It is not impossible to rule out increased hunting pressure from an expanded human population as a possible cause for decreased wapiti abundance, but I argue that the evidence for climate causation is stronger.

Data from stable isotope analysis and relative abundance of wapiti suggest that Semiahmoo hunters specialized in wapiti and intensified wapiti hunting by increasing the number of habitats exploited. During the early Neoglacial and Little Ice Age the relative abundance of wapiti is higher at Semiahmoo than at other sites. This is consistent with Montgomery’s (1979) faunal analysis that showed a higher proportion of wapiti at Semiamoo than at other contemporary sites. The standard deviation of δ¹³C values is greater during 300-1000 cal yr BP than 2700-3200 cal yr BP and suggests that beginning sometime between these dates Semiahmoo hunters intensified wapiti hunting by traveling further and increasing the number of habitat types exploited.

**Future Research Possibilities**

Several avenues for further work are suggested by the research presented here. Increasing the sample size of wapiti from each of the late Holocene climate periods tested in this study would allow a more detailed examination of the timing of climate periods and their relative strength. The Fraser Valley Fire Period was not included in this study but should be added to allow testing of whether wapiti populations responded similarly during hot, dry periods. The Garibaldi Park Glacial advance from 7300 – 5800 cal yr BP during the
Altithermal is similar to the Medieval Warm Period in that they both show higher temperatures, high fire frequency, and increased winter precipitation. It would be a good candidate for inclusion to see if wapiti relative abundance and stable carbon and nitrogen values are similar to those found in the Medieval Warm Period; however faunal remains from this period are quite rare. Including more δ^{13}C and δ^{15}N signatures of wapiti from the Altithermal would help to further refine when closed canopied temperate rainforests were established; important to many models of cultural change on the Northwest Coast.

Conducting a similar δ^{13}C and δ^{15}N isotope analysis of other animal bones could show how animals respond differently to climate shifts and how the ecosystem responds as a whole. Including more herbivore species that respond differently to shifts in environmental variables could serve as an important contrast and allow a greater ability to distinguish changes in diet from changes in humidity and temperature. Bump et al. (2007) argues that δ^{13}C signatures from top level predators better reflect climate conditions than other animals, as variations are averaged out as they pass up the food chain. Mammalian carnivores other than dogs are relatively rare in archaeological faunal assemblages, so it would be difficult to get a large enough sample size of a single species.

It might be possible to learn more about the diversity of habitats exploited and thus the hunting ranges and territory of people associated with different sites by studying the variation in isotope values in wapiti bones. A study on modern deer in coastal British Columbia was able to differentiate the primary habitats exploited by deer by comparing hair stable isotope values to average stable isotope values of pellets in different habitats (Darimont et al. 2007). If the same methods were used for modern wapiti in a coastal temperate rainforest it would be possible to find temporal and spatial patterning in the
primary habitats exploited by people. Results of this study found that Semiahmoo hunters were hunting or trading for wapiti from many different habitats including wetlands and riparian forests. Modern analogues would allow more precision in determining foraging habitats.
Chapter 9. Conclusion

Paleoclimate records suggest that seasonal extremes in temperature and humidity peaked during the Medieval Warm Period in the Gulf of Georgia Region and followed a winter-wet, summer-dry precipitation pattern. My results suggest that increased seasonality decreased the quality and quantity of spring and summer vegetation, decreased the duration of the spring plant growth period and increased the variability of its timing. Warmer and drier spring-summer conditions in the Medieval Warm Period resulted in significantly higher $\delta^{15}$N values in wapiti collagen. These adverse climate conditions would have lowered the survival rate of wapiti and decreased the encounter rate for hunters who increased their hunting of smaller prey. This decreased wapiti encounter rate was reflected in archaeological faunal assemblages from the lower Fraser River Delta region as significantly decreased relative wapiti abundance during the Medieval Warm Period. During the Little Ice Age moderated precipitation seasonality increased spring-summer precipitation and wapiti populations recovered.

The $\delta^{13}$C signatures of wapiti in my samples are heavily depleted relative to modern populations of wapiti from both open and forested environments reflecting a strong and continuous canopy effect over the last 5,300 calendar years. This suggests that old growth temperate rainforests were established before this time and covered the region without major interruption. Roosevelt wapiti are particularly well adapted to old growth forests, which moderate climate extremes and offer stable resources. The expansive presence of old growth
temperate rainforests on the coastal Pacific Northwest may have promoted large populations of wapiti.
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Coupland, Gary  

Cormie, A.B. and H.P Schawrcz  

Creel, Scott and Michael Creel

Croes, Dale R.

Daniels, Phoebe S.

Darimont C.T, P. C. Paquet And T. E. Reimchen

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Leopold, A

Lepofsky, Dana, Ken Lertzman, Douglas Hallett, and Rolf Mathewes

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McNamara, K.

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Zhang, Qi-Bin, and Richard J. Hebda
Appendix A: Raw Data for Stable Isotope Analysis, Relative Wapiti Abundance, and Radiocarbon Dates.
Table A.1. δ^{13}C and δ^{15}N Values of Wapiti Collagen.

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<th>Isotope Analysis No.</th>
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<th>Depth (cm)</th>
<th>Excavation Unit</th>
<th>Site</th>
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<th>δ^{15}N</th>
<th>δ^{13}C</th>
<th>Comments</th>
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<td>$\delta^{13}$C</td>
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$^1$LIA: Little Ice Age, MWP: Medieval Warm Period, FMA: First Millennium Advance, NG: Neoglacial, ALT: Altithermal.
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<td>45WH17</td>
<td>S5E1</td>
<td>100-120</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>2940-3350</td>
<td>3710 +/- 60</td>
<td>NG</td>
<td>45WH1</td>
<td>S1W4</td>
<td>35-75</td>
<td>11</td>
<td>1</td>
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<td>2940-3350</td>
<td>3710 +/- 60</td>
<td>NG</td>
<td>45WH1</td>
<td>S2W4</td>
<td>40-60</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>2940-3350</td>
<td>3710 +/- 60</td>
<td>NG</td>
<td>45WH1</td>
<td>S4W4</td>
<td>40-80</td>
<td>18</td>
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<td>2940-3350</td>
<td>3710 +/- 60</td>
<td>NG</td>
<td>45WH1</td>
<td>S5W4</td>
<td>40-60</td>
<td>26</td>
<td>0</td>
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<tr>
<td>4400-5300</td>
<td>Many $^2$</td>
<td>ALT</td>
<td>45WH34</td>
<td>All $^c$</td>
<td>All $^c$</td>
<td>4896</td>
<td>161</td>
</tr>
</tbody>
</table>

$^1$LIA: Little Ice Age, MWP: Medieval Warm Period, FMA: First Millennium Advance, NG: Neoglacial, ALT: Altithermal. $^2$45WH34 is considered a single component site within a single climate period so faunal abundance was not separated by radiocarbon dates.
Table A.3. Radiocarbon Dates.

<table>
<thead>
<tr>
<th>Site</th>
<th>Cut</th>
<th>Depth (cm)</th>
<th>Sample#</th>
<th>Lab #</th>
<th>Type</th>
<th>Conventional $^{14}$C Date</th>
<th>Details</th>
</tr>
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<tbody>
<tr>
<td>45WH1</td>
<td>N3W9</td>
<td>36</td>
<td>45WH1N3W936cm</td>
<td>B292828</td>
<td>Bone</td>
<td>2420 +/-30</td>
<td>Wapiti Femur$^2$</td>
</tr>
<tr>
<td>45WH1</td>
<td>S1E1</td>
<td>60-80</td>
<td>Cat # 633</td>
<td>None</td>
<td>Charcoal</td>
<td>2340 +/-200</td>
<td>2 S, 0.5 E Base of Shell Horizon$^3$.</td>
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<tr>
<td>45WH1</td>
<td>S1W10</td>
<td>80-100</td>
<td>45WH1 S1W10 80-100</td>
<td>UGAMS4047</td>
<td>Shell</td>
<td>3340 +/-30</td>
<td>Level Bag$^{1,4}$</td>
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<td>S1W10</td>
<td>60-80</td>
<td>45WH1 S1W10 60-80</td>
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<td>Shell</td>
<td>1470 +/-25</td>
<td>Level Bag$^4$</td>
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<td>45WH1</td>
<td>S21E29</td>
<td>80-100</td>
<td>45WH1S21W2980</td>
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<td>Bone</td>
<td>1140 +/-30</td>
<td>Wapiti Cervical Vertebra$^5$</td>
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<td>45WH1</td>
<td>S24E29</td>
<td>70</td>
<td>45WH1S24E2970cm</td>
<td>B292829</td>
<td>Wood</td>
<td>1230 +/-40</td>
<td>Holodiscus discolor from a hearth$^2$.</td>
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<td>45WH1</td>
<td>S3W4</td>
<td>72</td>
<td>Cat # 1149</td>
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<td>Charcoal</td>
<td>1300 +/-200</td>
<td>Unit B, 6.85 to 6.93 S, 10.16 W$^3$</td>
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<td>45WH1</td>
<td>S4W4</td>
<td>40-60</td>
<td>45WH1S4W450c</td>
<td>B279606</td>
<td>Shell</td>
<td>3710 +/-60</td>
<td>40-60 Level Bag$^5$</td>
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<td>S7E8</td>
<td>160-175</td>
<td>Cat # 1597</td>
<td>RL272</td>
<td>Charcoal</td>
<td>2630 +/-240</td>
<td>Unit B, 19.1 to 19.8 S, 22.15 to 22.4 E in the sandy layer$^3$</td>
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<tr>
<td>45WH1</td>
<td>S8E8</td>
<td>80-100</td>
<td>WH1S8E880100</td>
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<td>Shell</td>
<td>1280 +/-40</td>
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<td>45WH9</td>
<td>TCA</td>
<td>165</td>
<td>None</td>
<td>UW343</td>
<td>Wood</td>
<td>848 +/-108</td>
<td>Possibly Charcoal$^6$</td>
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<tr>
<td>Site</td>
<td>Cut</td>
<td>Depth (cm)</td>
<td>Sample#</td>
<td>Lab #</td>
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<td>Conventional 14C Date</td>
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<td>45WH9</td>
<td>Utility Trench</td>
<td>30-125</td>
<td>Cat #7</td>
<td>B278907, B278908</td>
<td>Charcoal</td>
<td>690 +/- 40, 520 +/- 40</td>
<td>Feature 5&lt;sup&gt;7&lt;/sup&gt;</td>
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<tr>
<td>45WH17</td>
<td>S17W5</td>
<td>170</td>
<td>Cat # 840</td>
<td>UW458</td>
<td>Charcoal</td>
<td>830 +/- 60</td>
<td>Unit G, 50.3 S, 14.25 W, Feature 15, Stratum 10&lt;sup&gt;8&lt;/sup&gt;</td>
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<tr>
<td>45WH17</td>
<td>S18E7</td>
<td>194-196</td>
<td>Cat # 1569 &amp; 1577</td>
<td>UW463</td>
<td>Charcoal</td>
<td>2715 +/- 55</td>
<td>Units C D, amalgamated samples from Feature 38. Associated strata: 11B, 11C, 7A-C&lt;sup&gt;8&lt;/sup&gt;</td>
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<tr>
<td>45WH17</td>
<td>S26W7</td>
<td>70-80</td>
<td>WH17S26W770C</td>
<td>B292827</td>
<td>Shell</td>
<td>1550 +/- 40</td>
<td>Clinocardium valve from level bag, assoc. w/Faunal Features 13, 14&lt;sup&gt;9&lt;/sup&gt;.</td>
</tr>
<tr>
<td>45WH17</td>
<td>S28E9</td>
<td>295-300</td>
<td>Cat # 1076</td>
<td>UW459</td>
<td>Charcoal</td>
<td>2830 +/- 65</td>
<td>Unit E, 15 cm above Feature 27, in stratum 9&lt;sup&gt;9&lt;/sup&gt;.</td>
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<tr>
<td>45WH17</td>
<td>S28E9</td>
<td>323</td>
<td>Cat # 1215</td>
<td>UW460</td>
<td>Charcoal</td>
<td>3015 +/- 65</td>
<td>Unit C, 82 S, 26 E 25cm below Feature 27, Stratum 14&lt;sup&gt;8&lt;/sup&gt;</td>
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<tr>
<td>45WH17</td>
<td>S28W10</td>
<td>95-105</td>
<td>None</td>
<td>GX323130</td>
<td>Bone</td>
<td>930 +/- 70</td>
<td>Northern Fur Seal, assoc. w/Dog Burial No. 7, Faunal Feature 24&lt;sup&gt;10&lt;/sup&gt;</td>
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<tr>
<td>45WH17</td>
<td>S40W17</td>
<td>100</td>
<td>Cat # 1302</td>
<td>UW461</td>
<td>Charcoal</td>
<td>350 +/- 50</td>
<td>Unit F, 120.88-121.28 S, 48.55-48.60 W, Feature 43&lt;sup&gt;9&lt;/sup&gt;</td>
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<td>45WH17</td>
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<td>Cat # 1215</td>
<td>UW332</td>
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<td>From charcoal stained beach gravel&lt;sup&gt;8&lt;/sup&gt;.</td>
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<td>Charcoal</td>
<td>580 +/- 60</td>
<td>Units B C, 15.6-15.82 S, 9.86-10.15 W, Feature 43&lt;sup&gt;8&lt;/sup&gt;</td>
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<td>Cat # 219</td>
<td>B187078</td>
<td>Shell</td>
<td>4960 +/- 70</td>
<td>Subunit 3 Level Bag&lt;sup&gt;10&lt;/sup&gt;</td>
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<tr>
<td>45WH34</td>
<td>N2W4</td>
<td>41-44</td>
<td>Cat # 465</td>
<td>B176490</td>
<td>Charcoal</td>
<td>4000 +/- 40</td>
<td>Mature Red Cedar Feature 17&lt;sup&gt;10&lt;/sup&gt;</td>
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<td>Site Code</td>
<td>Feature</td>
<td>Cat #</td>
<td>Material</td>
<td>Age</td>
<td>Age Error</td>
<td>Notes</td>
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<td>117</td>
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<td>4370 +/-90</td>
<td>Bark and Branches Feature 11</td>
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<td>130</td>
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<td>4220 +/-40</td>
<td>Birch Bark Feature 11</td>
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<td>None</td>
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<td>Feature 11</td>
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<td>40-60</td>
<td>39</td>
<td>B187079</td>
<td>Shell</td>
<td>4850 +/-80</td>
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<td>40-60</td>
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<td>B192797</td>
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<td>4230 +/-70</td>
<td>Unidentified Mammal Level Bag</td>
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<tr>
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<td>1082</td>
<td>B187080</td>
<td>Shell</td>
<td>4970 +/-80</td>
<td>Subunit 3 Feature 14</td>
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<td>B192796</td>
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<tr>
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<td>145</td>
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<td>B4109</td>
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<td>Stratum 2, Feature 6</td>
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<td>45WH11</td>
<td>TC3</td>
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<td>22</td>
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<td>16</td>
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<td>Wood</td>
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<td>Feature 13, Stratum 14</td>
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<td>TC1</td>
<td>123</td>
<td>5</td>
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<td>Wood</td>
<td>2040 +/-190</td>
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<td>45WH43</td>
<td>TC2</td>
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<td>6</td>
<td>B4104</td>
<td>Charcoal</td>
<td>280 +/-50</td>
<td>Feature 3, Stratum 2</td>
</tr>
</tbody>
</table>

1 Not used in this study; 2 Palmer (2012); 3 Blodgett (1975); 4 Rorabaugh (2009); 5 Dubeau (2012); 6 Gaston and Grabert (1975:59); 7 Baldwin et al. (2012); 8 Grabert, et al. (1978:202-210), Montgomery (1979:54), Gaston (1975:71); 9 See Appendix B; 10 Gillis (2007); 11 Grabert & Griffin (1983:31); 12 Dates on file at Department of Anthropology, Western Washington University.
March 2, 2011

Mr. Angus Tierney
Western Washington University
Department of Anthropology MS9083
516 High Street
Bellingham, WA 98225
USA

RE: Radiocarbon Dating Result For Sample WH17S26W770C

Dear Mr. Tierney:

Enclosed is the radiocarbon dating result for one sample recently sent to us. It provided plenty of carbon for an accurate measurement and the analysis proceeded normally. The report sheet contains the method used, material type, and applied pretreatments and, where applicable, the two-sigma calendar calibration range.

This report has been both mailed and sent electronically. All results (excluding some inappropriate material types) which are less than about 20,000 years BP and more than about ~250 BP include a calendar calibration page (also digitally available in Windows metafile (.wmf) format upon request). Calibration is calculated using the newest (2004) calibration database with references quoted on the bottom of the page. Multiple probability ranges may appear in some cases, due to short-term variations in the atmospheric 14C contents at certain time periods. Examining the calibration graph will help you understand this phenomenon. Don't hesitate to contact us if you have questions about calibration.

We analyzed this sample on a sole priority basis. No students or intern researchers who would necessarily be distracted with other obligations and priorities were used in the analysis. We analyzed it with the combined attention of our entire professional staff.

Information pages are also enclosed with the mailed copy of this report. If you have any specific questions about the analysis, please do not hesitate to contact us. Someone is always available to answer your questions.

The cost of the analysis was charged to the VISA card provided. As always, if you have any questions or would like to discuss the results, don't hesitate to contact me.

Sincerely,

[Signature]

Page 1 of 3
Mr. Angus Tierney  
Western Washington University

<table>
<thead>
<tr>
<th>Sample Data</th>
<th>Measured Radiocarbon Age</th>
<th>13C/12C Ratio</th>
<th>Conventional Radiocarbon Age(*)</th>
</tr>
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<tbody>
<tr>
<td>Beta-292827</td>
<td>1180 ±40 BP</td>
<td>-2.2 o/oo</td>
<td>1550 ±40 BP</td>
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</table>

SAMPLE: WH17836W770C  
ANALYSIS: Radiometric-Standard delivery  
MATERIAL/PRETREATMENT: (shell); acid etch  
2 SIGMA CALIBRATION: Cal AD 1160 to 1420 (Cal BP 790 to 530)
CALIBRATION OF RADIOCARBON AGE TO CALENDAR YEARS

(Variables: C13/C12=-2.2; Delta-R=454±73; Glob res=-200 to 500; lab. mult=1)

Laboratory number: Beta-292827

Conventional radiocarbon age: 1550±40 BP
(1100±80 adjusted for local reservoir correction)

2 Sigma calibrated result: Cal AD 1160 to 1420 (Cal BP 790 to 530)
(95% probability)

Intercept data

Intercept of radiocarbon age
with calibration curve: Cal AD 1290 (Cal BP 660)

1 Sigma calibrated result: Cal AD 1240 to 1330 (Cal BP 720 to 620)
(68% probability)

References:
- Database used: MARINE98
- Calibration Database: INTCAL04 Radiocarbon Age Calibration
- Mathematica: A Simplified Approach to Calibrating C14 Dates

Beta Analytic Radiocarbon Dating Laboratory
4985 S.W. 74th Court, Miami, Florida 33155 • Tel: (305) 667-5167 • Fax: (305) 663-5964 • E-Mail: beta@radiocarbon.com
Appendix C. Analyzed Excavation Units Not Used In This Study.
In my initial search for radiocarbon dated contexts, I found three other radiocarbon dates from other local sites, and I analyzed the stratigraphy of the associated cuts. When I examined the associated faunal material the sample sizes were too small to be usefully included in this analysis. They are included here to aid others who may be interested in researching the stratigraphy of these sites.

**45WH43 Test Cut 2:** A charcoal sample within Feature 3 (Stratum 2) yielded a conventional 14C date of 280±50 BP (B4104). Feature 3 is a charcoal stained sandy clay with a dense rock cluster mostly in the east side of Unit A. This stratum lies above the sterile level and no artifacts or bone were found in this Stratum. All levels within this shallow unit were considered associated with the radiocarbon dated sample. Six mammal fragments were recorded within this unit; none of which were identified as wapiti.

**45WH111 Test Cut 1:** Sample # 16 lying at 131 cm and associated with Feature 15 (Stratum 14) resulted in a conventional 14C date of 1590±60 BP. Feature 15 is described as 90% whole shell in a clean and fine-grained sand matrix between 120 and 150 cm deep. Feature 13 (Stratum 13) is intrusive into Feature 15 and Feature 11 (Stratum 12) and is a hearth with FMR and post molds. I treated all levels between 120 and 150 cm as associated with the radiocarbon dated sample. This includes strata 12 through 15 and Features 11, 13, 15, and 16. Strata 12 and 15 contain no bone so they will not influence the results. Only 4 mammal fragments lie at this depth, none of which are considered to be wapiti.

**45WH114 Test Cut 1:** A charcoal sample from the southern margin of Unit B at a depth of 123 cm within Feature 6 yielded a conventional 14C date of 2040±190 BP and a calibrated
range of 1500 to 2500 BP (B4108). Feature 6 is a ridge of clay from a hearth at a depth of 119 to
124 cm within Stratum 1. Stratum 1 is 90% shell at a depth of about 105 to the base of test cut 1
at 130 cm. Levels between 100 and 130 are considered associated with the radiocarbon dated
sample. This includes Features 4, 5, 6, and 8 along with all of Stratum 1 and parts of strata 2 and
3. Strata 2 and 3 are composed of clay and sand Feature 4 is a brown silt/sand from 115 to 123 cm
that is contiguous with Features 5 and 6. Feature 5 is composed of shell at a depth of 115 to 120
cm. Feature 8 is a lens of ash and FMR related to the Feature 6 hearth. The date of 2040±190 BP
lies at the cusp between the end of the Neoglacial and beginning of the Fraser Valley Fire Period.
Twelve mammal fragments lie within these levels including one wapiti incisor and one other
wapiti fragment. This excavation unit was not included because the calibrated date range spans a
significant part of two climate periods.