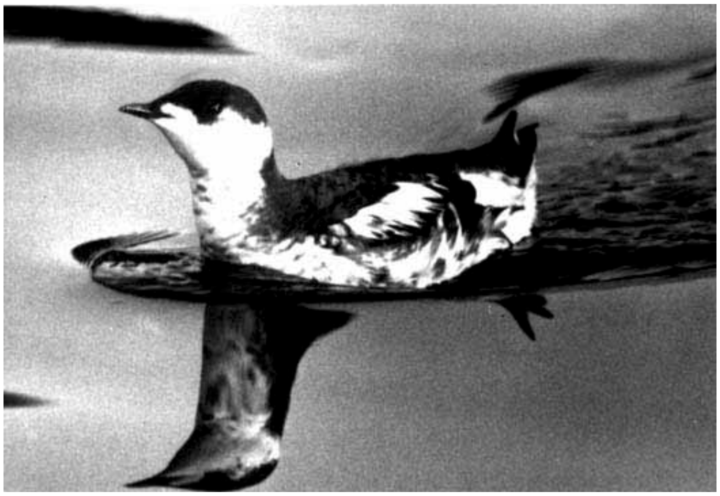
Habitat Requirements and Habitat Suitability Index for the Marbled Murrelet (*Brachyramphus marmoratus*) as a Management Target Species in the Ursus Valley, British Columbia.



Diplomarbeit am Fachbereich Biologie der Philipps-Universität Marburg

von Volker Bahn

Marburg, April 1998

“How do you know but ev’ry Bird that cuts the airy way, Is an immense world of delight, clos’d by your senses five?”

William Blake, Prophetic Books: The Marriage of Heaven and Hell, A Memorable Fancy (in Blake 1996)

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1. Introduction

The Primary coastal temperate rainforest is a unique and rare ecosystem. It originally covered only less than 0.2% of the world's land surface and, today, it is threatened by deforestation and conversion to managed forests. More than 50% of this rainforest world-wide has already been degraded (Bryant *et al.* 1997). This ecosystem is very productive and contributes largely to global biodiversity (Bunnell and Chan-McLeod 1997; Scientific Panel 1995a).

One quarter of the world's remaining old-growth temperate rainforest is in British Columbia (Bryant *et al.* 1997). 53% of British Columbia's and 70% of Vancouver Island's old-growth temperate rainforest has been logged already (Sierra Club of British Columbia 1997), and more than two-thirds of it in British Columbia has been degraded by logging or development (Bryant *et al.* 1997). Most of the remaining rainforest, except for protected areas, is slated to be logged in the next ten years (Bryant *et al.* 1997).

With increasing international awareness of the need to preserve biodiversity and ecosystem integrity, and growing protests from inside and outside the country, British Columbia initiated the development of a new policy towards resource and land management. Phrases such as sustainability, protection of biodiversity, and ecosystem integrity were quickly adopted. Means to reach these goals were initiated, such as the new Forest Practices Code of British Columbia Act (FPC), which is supposed to implement world class forestry standards, the Protected Area Strategy (PAS), which has the creation of protected areas equally representing all types of ecosystems encompassing 12% of British Columbia as goal, and the Commission on Resources and Environment (CORE), with the mandate to develop a provincial land use strategy with emphasis on economic, environmental, and social sustainability. Although a remarkable effort was put into these strategies, the results are not yet satisfactory.

- Only 6% of the low elevation old-growth rainforests in British Columbia are protected (Land Use Coordination Office 1996; Sierra Club of British Columbia 1997);
- 97% of the current logging in coastal temperate rain forests is done by clear-cutting (Sierra Legal Defence Fund 1997);
- the cutting of British Columbia's forests takes place at a rate approximately 20% above rate of regrowth (Sierra Legal Defence Fund 1996) not to mention ecological

sustainability;

- 10 % of the vertebrates and plants of British Columbia are threatened or endangered (British Columbia Ministry of Environment Reporting Office 1996).

Clayoquot Sound has the largest contiguous stretch of temperate rainforest on Vancouver Island (Figure 1 and Figure 2). It encompasses the southernmost multi-watershed complex of pristine rainforest in North America. Extensive protests against logging and recognition of the area's non-forestry related values have resulted in special planning efforts for this region. In the Land Use Decision of 1993, the government of British Columbia increased the number of protected areas in Clayoquot Sound and designated Special Management Areas (SMA). Furthermore, the Scientific Panel for Sustainable Forest Practices in Clayoquot Sound produced a large body of recommendations on planning processes, forest practices, and monitoring activities. Clayoquot Sound is supposed to become a model of sustainable forestry in a economical, social, and ecological sense.

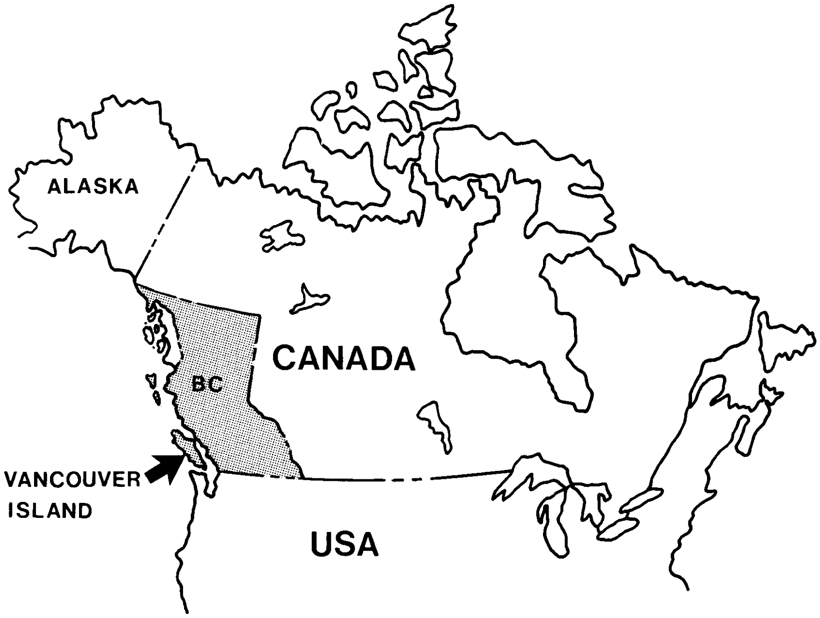

Figure 1: Map of Canada showing the location of Vancouver Island.

The Ursus Valley (see Figure 2, Figure 3, and Appendix III, Figure 1), one of the few remaining pristine watersheds > 5000 ha in size on Vancouver Island (Beebe 1990), has a unique status in Clayoquot Sound as it was designated as the only SMA with wildlife emphasis. The goal of planning in the Ursus is to accommodate the needs of wildlife before those of forestry. So far, the approach has been based on a relatively low number of vertebrate species.

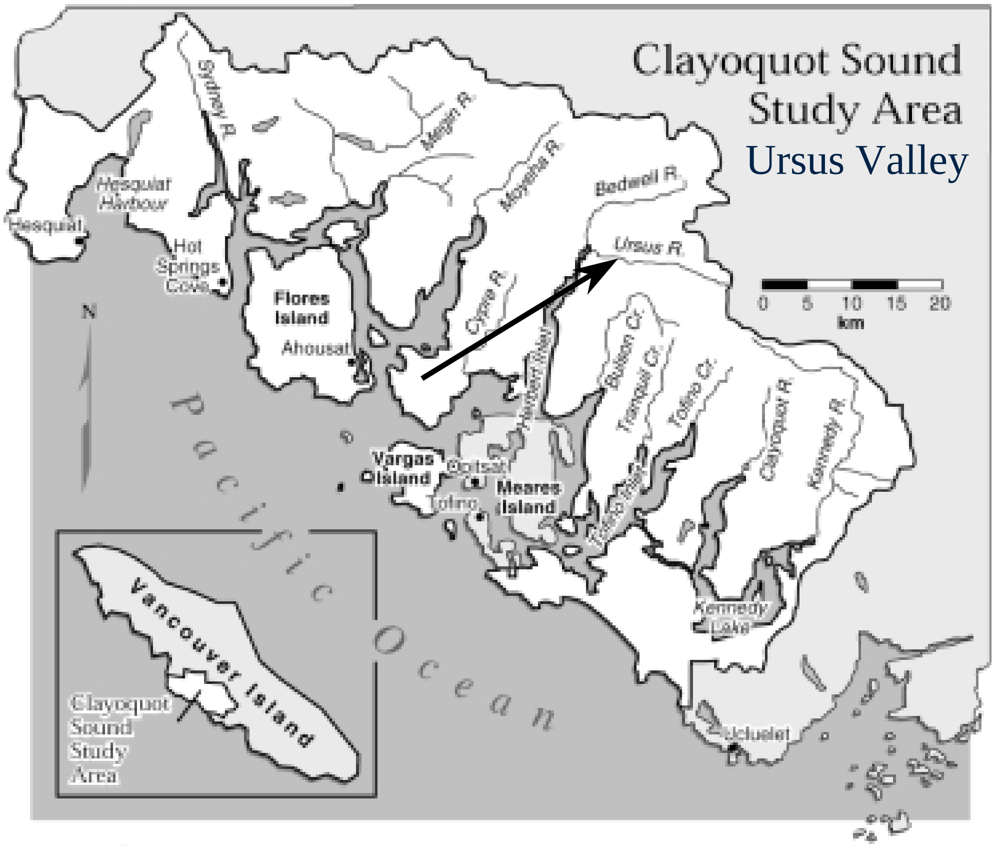

Figure 2: Location of the study area Ursus Valley in Clayoquot Sound, Vancouver Island (adapted from Scientific Panel 1995a).

The method of identifying the species by which the valley will be managed, and the management strategy itself, have not yet been explicitly outlined. I would like to put forward a target species strategy (Reck *et al.* 1994; Walter *et al.* 1998; Hansen *et al.* 1993), which gives concrete criteria on the selection of target species. Furthermore, I would like to give an example of what specific management goals for a target species could look like, using the Marbled Murrelet (*Brachyramphus marmoratus*).

The Marbled Murrelet was identified as one of the important species for ecosystem management decisions in the Ursus Valley. Therefore, the Ministry of Environment, Lands, and

Parks initiated an inventory of Marbled Murrelets there in 1995 and expanded the project over the next two years to include 14 watersheds across Clayoquot Sound. The Ursus Valley remained the most intensively surveyed watershed. I collected the data for this thesis during two of three years of the inventory.

Marbled Murrelet (*Brachyramphus marmoratus*) are sea birds belonging to the family Alcidae. Recently, the former two subspecies of the Marbled Murrelet, the Asian Long-billed Murrelet (*Brachyramphus marmoratus perdix*) and the North American Marbled Murrelet (*Brachyramphus marmoratus marmoratus*) have been recognised as separate species *Brachyramphus perdix* and *Brachyramphus marmoratus*, respectively (American Ornithologists' Union 1997).

Figure 3: From the centre of the Ursus Valley looking downstream towards the west.

Marbled Murrelet nesting habits are unique among members of the family Alcidae: they nest nearly exclusively in trees of old, coastal forests. The forests in which Marbled Murrelets breed are usually of high economic value and are easily accessible from the ocean. Therefore, they have been and still are heavily exploited by the logging industry. Removal of nesting habitat (i.e., large trees), among other threats such as gill-netting and oil spills, has reduced the numbers of Marbled Murrelets in North America and caused this species to be recognised as threatened in both Canada and the USA (Rodway 1990; U.S. Fish and Wildlife Service 1992).

Despite its threatened status and the interest of biologists in the elusive Marbled Murrelet, relatively little is known about important aspects of its biology, such as nest site selection, survival rates, longevity, and fecundity. Marbled Murrelets nest solitarily, hidden high up in large trees, and behave secretively in the inland breeding habitat. They fly inland mainly during dusk and dawn, at high speed, and, when approaching nest sites, below the canopy. The efforts of North American ornithologists to find a Marbled Murrelet nest were unsuccessful for more than a century, until 1974, when the first verified tree nest was found (Binford *et al.* 1975). Although more than 134 nests have been found since then (Nelson 1997), the elusiveness of Marbled Murrelets inland and the hidden nature of their nest sites still pose major difficulties in studying this bird and its breeding habitat associations. At sea censuses and research on life history parameters, necessary for the evaluation of population size changes, are also difficult to perform because Marbled Murrelets tend to change their location often, on both small (hours to days) and large (months to years) time scales. Movements have been partly interpreted as reactions to food and breeding habitat availability. Furthermore, mark-recapture studies have to deal with difficulties in capturing birds at sea and in using markers that are visible when the birds sit on the water (*e.g.*, nasal disks or wing markers) because regular markers around the feet can only be observed on captured birds.

Inland research efforts so far have concentrated on audio-visual surveys during dawn and dusk, when Marbled Murrelets visit forests for prospecting, incubating, parental care or other unknown reasons. The methods for these surveys are well established (Ralph *et al.* 1994), but the results are difficult to interpret and are laden with unwanted variability and biases. During audio-visual surveys, certain observed behaviours are interpreted as indicating nesting in the area around the survey station, which is then characterised by vegetation plots. This method has the advantage that it can cover relatively large areas with less effort than more direct methods such as tree climbing in search of nests.

In comparison to the USA, British Columbia has more remaining coastal old-growth forests, but fewer resources per unit area to study Marbled Murrelets intensively. Intensive, systematic studies with detailed habitat analysis have only been conducted in a few areas along the coast (Rodway *et al.* 1993a, 1993b, in Lagins Creek on the Queen Charlotte Islands; Manley *et al.* 1992 and Burger 1994 in the Carmanah and Walbran Valleys on the south-western coast of Vancouver Island; Manley *et al.* 1994 in the Megin Watershed in northern Clayoquot Sound; Beauchamp *et al.* 1998 and Drever *et al.* 1998 in Desolation Sound; and the ongoing study in Clayoquot Sound with special focus on the Ursus Valley, Burger *et al.* 1995 and 1997a, Beasley *et al.* 1997). Many more studies must be carried out to collect baseline data for the efficient landscape-level protection of the Marbled Murrelet breeding habitat. The forest industry makes up a significant part of British Columbia's gross domestic product (8%, Schwindt and Heaps 1996) and the pressure on the valuable coastal old-growth forests is high. Therefore, effective tools to determine areas of important Marbled Murrelet breeding habitat are urgently needed.

In addition to the inland studies of Marbled Murrelets in Clayoquot Sound, at sea censuses and radar counts at estuaries were conducted during the inventory. The at sea censuses were designed to get a general estimate of the population size in Clayoquot Sound, to monitor distribution and densities of Marbled Murrelets at sea, and to investigate juvenile recruitment. The radar counts helped to identify the relative importance of individual watersheds, to get an estimate of absolute numbers of Marbled Murrelets in Clayoquot Sound during the summer, to learn more about daily activity patterns of Marbled Murrelets and to evaluate the accuracy of audio-visual surveys in comparison to radar surveys (Burger 1997).

My objectives in this thesis were:

- to determine which parts of the Ursus watershed and which habitat characteristics are most important to Marbled Murrelets;
- to determine which habitat characteristics are best suited for the evaluation of potential Marbled Murrelet breeding habitat;
- to identify the main sources of unwanted variation and biases in the Marbled Murrelet activity data;
- to suggest refinements of field methods and analyses used in Marbled Murrelet research.

Additional objectives for the conservation section of this thesis were:

- to add conceptual depth and information on Marbled Murrelets as a conservation target species to the framework provided by the Scientific Panel;

- to discuss a conservation strategy for Clayoquot Sound based on the monitoring of an array of species which includes the Marbled Murrelet as a target species;
- to develop a standardised tool for habitat evaluation based on the habitat requirement information gained in this thesis;
- to supply concrete suggestions and methods for the consideration of the habitat requirements of the Marbled Murrelet in ecosystem management.

1.1 Background on Marbled Murrelets

1.1.1 Distribution

Marbled Murrelets are found exclusively along the North American Pacific shore. They range from the Aleutian Islands across Alaska, British Columbia, Washington, Oregon, to California. The present geographic centre of the population is in the northern part of south-east Alaska (Ralph *et al.* 1995).

Population sizes are comparably large from the Kodiak Islands in Alaska to the southern end of British Columbia. North and south of this stretch populations are smaller and further apart. The disjunct distribution in the southern portion of the range is thought to reflect fragmented breeding habitat (Ralph *et al.* 1995; Carter and Erikson 1992; Leschner and Cummins 1992a; Nelson *et al.* 1992). In those areas, Marbled Murrelets concentrate offshore of old-growth areas during the breeding season (April-August), when marine productivity is high (Ainley and Boekelheide 1990), but disperse when not breeding in response to more limited food availability during winter (Ralph *et al.* 1995; Nelson *et al.* 1992; Sowls *et al.* 1980). This indicates strongly that breeding habitat, and not food, is the limiting resource for Marbled Murrelet distribution.

The relationship between breeding habitat and Marbled Murrelet distribution at sea is less clear in British Columbia (Burger 1995a). The shorelines are more complex, the habitat fragments are larger and the survey effort has been less than in the USA. Burger (1994) found some evidence that Marbled Murrelets were aggregating in the segments of his survey transects that were located adjacent to the two largest tracts of old-growth forest remaining on a relatively straight 65 km stretch of shoreline off south-western Vancouver Island. Besides this example, no such relationship has been demonstrated in British Columbia.

More detailed accounts of Marbled Murrelet distribution in certain regions can be found in Kessel and Gibson (1978), Campbell *et al.* (1990), U.S. Fish and Wildlife Service (1992), Small (1994), Piatt and Naslund (1995), Burger (1995a), Speich and Wahl (1995), Varoujean and Williams (1995), Strong *et al.* (1995), Strong (1995), and Ralph and Miller (1995).

Current knowledge on Marbled Murrelet distribution inland relies on forest survey efforts and specimens, eggshells or other indicators of presence found inland. Records of Marbled Murrelets inland have been almost exclusively associated with old-growth forest stands (Burger 1995a; Grenier and Nelson 1995; Hamer 1995; Kuletz *et al.* 1995b; Paton and Ralph 1990; Rodway *et al.* 1993a). Vagrant birds have been found as far as 129 km inland (Nelson 1997) and a grounded juvenile 101 km inland (Rodway *et al.* 1992). The furthest inland nest found so far was 50 km from the Oregon shore (Nelson1997). Most Marbled Murrelets nest less than 30 km from the coast with distances between 30-60 km not being unusual (on average 6.4 km inland in Alaska) (Quinlan and Hughes 1990; Singer *et al.* 1991, 1995; Hamer and Nelson 1995b; Naslund *et al.* 1995, Nelson and Sealy 1995; Nelson 1997). A more detailed discussion of Marbled Murrelet breeding habitat and its attributes is the subject of this thesis (see discussion).

At sea Marbled Murrelets occur mostly in protected waters within 5 km of the shore (in Alaska within 50 km of the shore). They primarily forage in bays, fjords, and inlets, less often on the open ocean. They prefer to feed in water less than 60 m deep, but they have been observed in fjords deeper than 400 m and as far as 300 km offshore in Alaska. Preferred physical features of their feeding habitat are upwelling areas, strong tidal currents and rips, underwater sills, shelf edges, mouths of bays, narrow passages between islands, shallow banks, and kelp beds (Sealy 1975a, 1975c; Ainley *et al.* 1995; Burger 1995a; Piatt and Naslund 1995; Speich and Wahl 1995; Strachan *et al.* 1995; Strong *et al.* 1995; Speckman 1996; Nelson 1997). The most likely parameters influencing Marbled Murrelet distribution at sea are prey abundance, proximity to breeding habitat and environmental factors such as weather (Carter 1984; Carter and Sealy 1990; Kaiser *et al.* 1991; Mahon *et al.* 1992; Ainley *et al.* 1995; Nelson 1997). Carter and Sealy (1990) showed that Marbled Murrelets use some feeding areas consistently on a daily and yearly basis and (1986) that they occasionally feed on freshwater lakes, primarily in British Columbia and Alaska.

Marbled Murrelets have been shown to exhibit seasonal movements on a small scale in many parts of their range (Klosiewski and Laing 1994; Kuletz 1994, 1996; Piatt and Naslund

1995; Ralph and Miller 1995; Strachan *et al.* 1995; Strong *et al.* 1993; Rodway *et al* 1992). Burger (1995b) and Speich and Wahl (1995) showed that Marbled Murrelets move from the outer, exposed coasts of Vancouver Island and the Strait of Juan de Fuca into the sheltered and productive waters of northern and eastern Puget Sound in winter. Sealy (1975a) pointed out that Marbled Murrelets were absent from Langara Island in winter and early spring but returned in late April.

1.1.2 Physical Description

The Marbled Murrelet is a small diving seabird of the family Alcidae. The adult of the North American race is 24-25 cm long, weighs between 188-269 g and has a wing length of 122-149 mm (Nelson 1997). The wings are well adapted for diving and are longer, narrower and more pointed than those of most other alcids. Being adapted for diving and flying, the Marbled Murrelet has a high wing load and flies with rapid wing beats reaching speeds of up to 158 km/h (Burger 1997). It tends to fly in straight lines or wide circles and, combined with its speed, rapid wing beats, bent wings, and cigar shaped body, creates a distinctive appearance in flight.

The sexes do not differ in size, weight or appearance. However, alternate (breeding), basic (winter), and juvenile plumages are distinct (Carter and Stein 1995). Marbled Murrelets in basic plumage are dark brownish above, with bluish grey margins on back-feathers and largely white scapulars (Nelson 1997). They are white on the sides of their heads and around the neck, extending almost to the nape. The underparts are mostly white with occasionally persisting brown feathers sprinkled on flanks. The rectrices are uniformly blackish brown, the axillars and underwing-coverts are greyish brown, and the undertail-coverts are white. The alternate plumage features brownish black upperparts with rusty-buff margins on the back feathers. The underparts, the front and side of the neck and the sides the head to above the eye are mottled brown through white feathers with broad dark-brown margins. The rectrices and upperwing-coverts are dark-brown with occasional narrow white edges and brown spots on outer rectrices. The underwing-coverts and axillaries are brownish grey, the flanks are dark-brown, and the undertail-coverts are white.

Juvenile plumage undergoes a transition from newly-fledged to older juveniles, which are impossible to separate from adults in full basic plumage in the field (Carter and Stein 1995). The recently-fledged Marbled Murrelets have an overall darker appearance with uniform dark brownish above, except for the scapulars, and dark speckles on the sides of the head, the neck, the breast, and abdomen. The underwing-coverts are brownish grey with some white and the white collar is less distinct than on winter adults. Often dark-margined feathers form a neck-band, which disappears during the transition period (two weeks to two month after leaving the nest), as do the other differences from winter adults.

Nestlings are covered by a thick layer of natal down. They pick off the yellow-brown down just before fledging (Simons 1980; pers. observations). The cryptic nestling plumage is an adaptation to predation at old-growth forest nests (Binford *et al.* 1975).

During the two moult periods, the pre-basic and the pre-alternate moult, Marbled Murrelets are flightless. Therefore, they are unable to move further than swimming distance in search for prey and they are unable to breed. The timing of moult varies among years and different parts of the breeding range, in correspondence to variation in timing of breeding and variation in local prey resources (Ewins 1988, Emslie *et al.* 1990).

1.1.3 Ecology and Behaviour

1.1.3.1 Feeding

Marbled Murrelets forage by pursuit diving, using their wings under water (Ashmole 1971). They usually feed with rapid dives in relatively shallow water within 50 m of the surface (Sealy 1974, 1975c; Quinlan and Hughes 1984; Thoresen 1989; Kuletz 1991a; Sanger 1987b; Strachan *et al.* 1995). They mostly forage in pairs throughout the year, but are encountered individually or in groups as well. Pairs often dive simultaneously and communicate on the surface. Aggregations are more likely in the northern part of the range and in sheltered waters (Hunt 1995; Strachan *et al.* 1995). Hatch-year birds usually forage singly during the summer (Nelson 1997). In Alaska and British Columbia mixed-species feeding flocks were observed in sheltered waters (Chilton and Sealy 1987; Carter and Sealy 1990; Mahon *et al.* 1992; Hunt 1995; Strachan *et al.* 1995).

Marbled Murrelets forage day and night, the latter particularly while breeding (Carter and Sealy 1986; Nelson 1997). Congregations of Marbled Murrelets can be observed in predictable areas close to their breeding sites (Sealy 1975c; Carter and Sealy 1990; Strachan *et al.* 1995; Nelson 1997). Whereas adults eat abundant small fish, they feed their young larger, higher-quality prey, to minimise the number of trips to the nest necessary for high chick growth rates (Sealy 1975c; Carter and Sealy 1987a, 1990; Burkett 1995).

The main prey items of Marbled Murrelets vary with season, location, and prey availability. Furthermore, the diet differs among adults, nestlings and fledglings (Carter 1984; Mahon *et al.* 1992; Sealy 1975c). During the breeding period Marbled Murrelets have been shown to prey particularly on small schooling fish including Pacific sand lance (*Ammodytes hexapterus*), northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea harengus*), capelin (*Mallotus villosus*), surf smelt (*Hypomesus sp*.) and viviparous seaperch (*Cymatogaster aggregata*). In winter and spring their focus shifts to invertebrates such as euphausiids, mysids, and gammarid amphipods, combined with some of the schooling fish, capelin, smelt, and herring. They have also been shown to consume Pacific sardine (*Sardinops sagax*), walleye pollock (*Theragra chalcogramma*), Pacific sandfish (*Trichodon trichodon*), rockfishes (*Scorpaenidae*), codfishes (*Gadidae*), pricklebacks (*Stichaeidae*), squid (*e.g., Loligo opalescens*) and shrimp (*e.g., Pandalus borealis*) (Sealy 1975c; Ainley and Sanger 1979; Krasnow and Sanger 1982; Sanger 1983, 1987b; Carter 1984; Vermeer 1992; Ewins *et al.* 1993; Burkett 1995; Nelson 1997). Furthermore, Carter and Sealy (1986) found Marbled Murrelets preying on sockeye and Kokanee salmon (*Oncorhynchus nerka* and *O. n. kennerlyi*) on coastal freshwater lakes. Most of the data cited stems from Alaska and British Columbia; prey items in the USA are not well known. Marbled Murrelets are opportunistic feeders, which are able to change their prey consumption in accordance with prey availability. Especially in winter and spring, when pelagic fishes are less abundant, an optional switch to demersal crustaceans may enhance survival (Sanger 1987a).

1.1.3.2 Breeding

Courtship behaviour of Marbled Murrelets has been observed mostly during spring but also during summer and winter (Nelson and Hamer 1995a). They are thought to form year-round pairs as other alcids do (Harris and Birkhead 1985). Copulations have been rarely observed, both in trees and on the water (Strachan *et al.* 1995; Nelson and Hamer 1995a; Speckman 1996; Nelson 1997). It is possible that they mostly take place at the breeding sites (trees), as in other alcid species (Sealy 1975a). More support for copulation at breeding sites comes from observations of pairs of Marbled Murrelets in the forest year-round, not only during breeding season. These forests visits could be interpreted as pair-bonding, sexual behaviour and prospecting for nest sites. Birds were seen landing in trees several times without nesting in that particular tree (pers. observations), while in Oregon Nelson and Hamer (1995a) observed a pair of birds landing on a platform for three mornings in early May, two weeks prior to laying an egg at the same site.

The timing of breeding is likely affected by food availability and variability in the environment; *e.g.*, there are some indications that Marbled Murrelets nest later or not at all in years of lower food abundance (*e.g.*, during El Niño years; Speckman 1996; Nelson 1997). Latitude may also play a role (Hamer and Nelson 1995a). In British Columbia, the egg-laying and incubation period starts in early May and ends in early July with the last birds fledging at the end of August (Sealy 1974; Carter and Sealy 1987b; Rodway *et al.* 1992; Hamer and Nelson 1995a). In the southern portion of the Marbled Murrelet range the breeding season is longer and sometimes double peaked, indicating that Marbled Murrelets try to lay a second clutch or try to renest after nesting failure (Hamer and Nelson 1995a). Drever *et al.* (1998) observed Marbled Murrelets trying to renest after nest failure in Desolation Sound. Some ledge-nesting alcids regularly replace lost eggs (Johnsgard 1987) and the shorter incubation and nestling periods of the Marbled Murrelet may make double brooding more feasible (Hamer and Nelson 1995a). Overall the breeding period is much longer and less synchronous than in other alcids (Hamer and Nelson 1995a).

Many aspects of Marbled Murrelets breeding ecology are comparable to those of other alcids. They lay one egg per clutch, share all duties of incubation and chick rearing with their mates, and probably exhibit mate and breeding area fidelity (Simons 1980; Birkhead 1985; Ewins *et al.* 1993; Nelson *et al.* 1994; Divoky and Horton 1995; Strong *et al.* 1995). However, unlike other alcids, they do not nest colonially, do not have nest site fidelity, and do not nest on the ground or in burrows except for a small proportion of the population in Alaska (Marshall 1988a; Hamer and Nelson 1995b). The closest relative to the Marbled Murrelet, the Kittlitz's Murrelet (*Brachyramphus brevirostris*), is the only auk known to nest solitarily (Day *et al.* 1983; Birkhead 1985; Naslund *et al.* 1994). Marbled Murrelets probably nest solitarily (Gaston 1985) or in loose aggregations (Divoky and Horton 1995).

Marbled Murrelet young are semi-precocial, as are many other alcids. However, they hatch from relatively large eggs, which are nearly as big as those of precocial alcids. The chick is able to thermoregulate at an early age and grows more rapidly than other alcids (Simons 1980; Hamer and Cummins 1991; De Santo and Nelson 1995). They have a 30-day incubation period and 28-day nestling period (Sealy 1974; Simons 1980; Hirsch *et al.* 1981).

It is estimated that Marbled Murrelets breed after they reach 2-4 years of age; however, the frequency with which they breed after that is unknown (De Santo and Nelson 1995;

Beissinger 1995). The incubation shifts are usually 24h, with exchange of adults usually occurring during the pre-dawn hours (Sealy 1974; Carter 1984; Hirsch *et al.* 1981; Naslund 1993a; Nelson and Hamer 1995a; Nelson and Peck 1995). Eggs can be left unattended for up to one day (Simons 1980).

The hatching and fledging success of Marbled Murrelets is remarkably lower than in other alcids (hatching: 67% compared to a mean of 70% ± 13% (SD), $n = 18$; fledging: 45% compared to a mean of 78% ± 10% (SD) in the other alcids, $n = 16$) (De Santo and Nelson 1995). Nelson and Hamer (1995b) found that only 28% of 32 observed nests were successful. Most nest failures (43%) were due to egg and chick predation. In addition, Marbled Murrelet fledglings experience some mortality on their way from the nest tree to the ocean (Nelson and Hamer 1995b); however, these numbers are mostly derived from years with El Niño effects, when ocean temperatures are unusually high and productivity is low (Ainley 1990), and reproductive success could be higher in regular years.

1.1.4 Population Status and Threats of the Marbled Murrelet in North America

The Marbled Murrelet is listed as threatened in Washington, Oregon, and federally in the USA, and as endangered in California. In Canada, it is nationally listed as threatened (Rodway 1990) and is listed as endangered in British Columbia. However, only the federal listing in the USA is legislated, the other listings are conventions produced by experts without legal consequences. Its numbers are declining throughout its range (Ralph *et al.* 1995).

Ralph *et al.* (1995) estimates the population of the Marbled Murrelet to be 300 000 individuals, but other estimates vary widely. Nelson (1997) gives a range of 263 000 - 841 000. Her estimate is a conglomerate of numbers published by:

- Piatt and Ford (1993) and Agler *et al.* (in press): 200 000 - 758 000 in Alaska equals 67 - 90% of the whole population;
- Rodway *et al.* (1992): 45 000-50 000 in British Columbia;
- Speich and Wahl (1995) and Varoujean and Williams (1995): 5 000-6 500 in Washington;
- Strong *et al.* (1995) and Varoujean and Williams (1995) with 6 600-20 000 for Oregon;
- Ralph and Miller (1995): 6 450 in California.

Population trends: The historical evidence for changes in population abundances of Marbled Murrelets in North America are limited to anecdotal accounts of biologists. Brooks (1926b) mentioned a strong decline in Marbled Murrelets in the Strait of Georgia in 1925-26 compared to observations in 1920 and earlier, and Pearse (1946) reported a decrease in numbers of Marbled Murrelets on the east coast of Vancouver Island, attributing it to removal of old-growth forests. Surveys conducted in 1979 and 1992-93 in Barkley and Clayoquot Sounds suggested that densities of Marbled Murrelets decreased by 20-60% over that period (Burger 1995b; Kelson *et al.* 1995). Populations in the Gulf of Alaska have declined by 50-73% over the last 20 years (Piatt and Naslund 1995; Nelson 1997). It is likely that Marbled Murrelets were historically as abundant all along the North American coast (even at locations where they sustain relatively small numbers now) as they currently are in parts of Alaska (Ralph *et al.* 1995). Declines and population trends have been discussed by several authors (Sealy and Carter 1984; Marshall 1988a; Carter and Erickson 1992; Nelson *et al.* 1992; Ralph 1994; Nelson 1997). Beissinger (1995) estimated based on a demographic model that the annual decline in Marbled Murrelet numbers is 4-6% per year throughout its range but could conceivably be twice as high. The model was based on rates of fecundity as estimated by juvenile to adult ratios counted on the ocean after the breeding season and annual survivorship was estimated based on allometric relationships found in alcids. In any scenario tested by Beissinger (1995) Marbled Murrelet populations declined throughout its range. It is necessary to note that much of the research recently done on population declines (*e.g.*, Kelson *et al.* 1995; Piatt and Naslund 1995; Beissinger 1995) is based on data that was influenced by El Niño effects, which were shown to reduce reproductive success in other alcids (Boekelheide *et al.* 1990) and some of the declines may possibly stem from this source (Burger 1995b; Ralph *et al.* 1995).

Predators are the main cause of nest failure of Marbled Murrelets. Nelson and Hamer (1995b) found that 43% of 32 nests and Manley (in Nelson 1997) found that 71% of 14 nests were preyed upon. Known avian predators at nest sites and in the forest are: Common Raven (*Corvus corax*), Stellar's Jay (*Cyanocitta stelleri*), Sharp-shinned Hawk (*Accipiter striatus*), Peregrine Falcon (*Falco peregrinus*), and Northern Goshawk (*Accipiter gentilis*; Singer *et al.*1991; Marks and Naslund 1994; Nelson and Hamer 1995b; Nelson 1997); suspected predators are: Gray Jay (*Perisoreus canadensis*), Great-horned Owl (*Bubo virginianus*), and Cooper's Hawk (*Accipiter cooperii*; Nelson 1997); predators at sea are: Peregrine Falcon (*Falco* *peregrinus*), Bald Eagle (*Haliaeetus leucocephalus*), Western Gull (*Larus occidentalis*), and northern fur seal (*Callorhinus ursinus*; Campbell *et al.* 1977; Vermeer *et al.* 1989; Rodway *et al.* 1992; Nelson 1997). Predation rates are suspected to be higher in or near fragmented habitats (Nelson and Hamer 1995b). More edge in the forest not only makes nests more conspicuous but is also associated with increased densities of Marbled Murrelet predators.

Oil threats to Marbled Murrelets come from catastrophic, large spills and chronic small-volume spills (Burger 1992; Vermeer and Vermeer 1975). King and Sanger (1979) rated the Marbled Murrelet as one of the most vulnerable species to oil pollution because it feeds close to shore.

The *Exxon Valdez* oil spill in Prince William Sound killed at least 8400 *Brachyramphus* murrelets, most of them *B. marmoratus* (Carter and Kuletz 1995; Kuletz 1996). That is 3.4% of the Alaskan population and 6-7% of the population in the spill zone. On top of direct mortality by oil pollution, it has sublethal, physiological, and reproductive consequences that affect local populations. For example the *Exxon Valdez* oil spill appears to have reduced breeding rates at Naked Islands as expressed in a lower ratio of hatch-year birds to after hatch-year birds in the post spill years (Kuletz 1996).

The Nestucca oil spill killed about 143 Marbled Murrelets off Vancouver Island (Burger 1993). The risk of oil spills killing many birds is high in the inshore areas off south-western Vancouver Island, the southern Strait of Georgia, and the Puget Sound, where high densities of Marbled Murrelets and a large volume of tanker traffic coincide (Burger 1992, 1995a).

Numerous other oil spills documented in the last 25 years have killed smaller numbers of Marbled Murrelets along the shore of North America (Fry 1995; Carter and Kuletz 1995; Nelson 1997). The total effect of oil spills on local populations is hard to estimate because of the low recovery of oiled carcasses, but especially fragmented and otherwise stressed populations will potentially become extirpated by future oil spills (Carter and Kuletz 1995).

Among other pollutants, Fry (1995) identified pulp mill discharges containing polychlorinated dibenzo-dioxins (PCDD) and polychlorinated dibenzo-furans (PCDF) as the biggest threat to Marbled Murrelets. They have been shown to accumulate in sediments, fish populations and fish-eating birds, causing reproductive impairments and malformations in bird populations (Bellward *et al.* 1990; Elliott *et al.* 1989). Although no specific studies have been done on Marbled Murrelets, the highest level of dioxins in a study by Whitehead *et al.* (1991)

were found in Western Grebes, which have a prey base similar to that of the Marbled Murrelet. Therefore, it is very likely that Marbled Murrelets foraging in the proximity of pulp mill effluents accumulate high amounts of PCDD’s and PCDF’s as well (Fry 1995). Fimreite *et al.* (1971) found the highest concentration of mercury of all seabird species collected at Horseshoe Bay in Marbled Murrelets.

Another major threat to Marbled Murrelets is the gill-net fishery. Carter *et al.* (1995) estimated that annually tens to hundreds of murrelets in Washington, hundreds to thousands of murrelets in British Columbia, and several thousands to tens of thousands of murrelets in Alaska drown in gill-nets. More specifically, Wynne *et al.* (1991, 1992) estimated that 1424 Marbled Murrelets drowned in gill-nets in Prince William Sound in 1990. Extrapolating from that, Piatt and Naslund estimated that as many as 3300 Marbled Murrelets (2940 adults, 360 juveniles) die every year in gill-nets in Alaska. That means that as much as 1.5% of the population of adult Marbled Murrelets of Alaska could die yearly in gill-nets. In Barkley Sound, British Columbia, Carter and Sealy (1984) estimated a minimum of 175-250 Marbled Murrelets killed in gill-nets in 1980. That represents 6.2% of the breeding population or 7.8% of the expected fall population plus nestlings dying due to lack of care. Marbled Murrelets also suffer mortality from sports fishing with brilliantly coloured lures (Campbell 1967).

According to population models, the survivorship of reproductive adults is crucial for species with low reproductive rates such as the Marbled Murrelet (Boulanger *et al.* unpubl.). Therefore, the effects of the above sources of Marbled Murrelet mortality on the future of the Marbled Murrelet population should not be underestimated.

However, the largest threat of all is undoubtedly the loss of breeding habitat (Rodway 1990; USFWS 1992; Ralph *et al.* 1995; Nelson 1997). Large portions of coastal temperate rain forests have been removed during this century. The breeding habitat of the Marbled Murrelet, large trees at low elevations, close to the ocean, are of especially high economic value and have therefore been exploited most heavily. In addition to the direct loss of nesting habitat, the remaining habitat has become fragmented. The increased edge effect in the fragments likely increases the rates of predation on nests (Paton 1994; Bryant 1994; Yahner and Scott 1988) and influences other parameters such as epiphyte distribution, which is important for Marbled Murrelet nesting (Nelson and Hamer 1995b). Nelson and Hamer (1995b) found that successful nests (*n* = 9) were significantly further away from the forest edge than nests that failed (*n* = 8), and failure was mostly due to predation.

Other threats to Marbled Murrelets include fish farms, which can potentially displace Marbled Murrelets, contaminate their food with antifoulants and antibiotics, and directly compete for food by harvesting euphausiids for fish food (Rodway 1990). Recreational boating and other activities in the feeding habitats of Marbled Murrelets can potentially decrease the quality of the habitat for Marbled Murrelets (Rodway 1990). Some Marbled Murrelets have been killed by cars and during the felling of trees (Nelson 1997). There is no evidence that direct disturbance by humans at the nest has had effects on Marbled Murrelet breeding success but I observed a feeding parent at a nest not moving for more than 45 min after landing possibly because I was in a neighbouring tree installing a video camera. After I left the tree the parent carried on feeding the chick and the chick fledged successfully.

El Niño effects (unusually high ocean temperatures cause low productivity) should not bother Marbled Murrelets as a single factor but can become important in combination with other pressures (Burkett 1995). The juxtaposition of feeding and nesting areas is critical in years of low prey abundance because of the energy demands of multiple trips to nests, further distances for adults and therefore on reproductive success.

The abundance and distribution of sand lance might influence reproductive success. Monoaghan *et al.* (1989) have shown a correlation between the number of tern chicks available for banding and the recruitment of sand lance. Sand lance populations might need active management attention (Auster and Stewart 1986; Nakata *et al.* 1991; Pinto *et al.* 1984)

1.1.5 Conservation of the Marbled Murrelet

The dependence of the Marbled Murrelet on coastal old-growth forests, specifically on the trees that are of highest economic value, and its very low reproductive rate, pose a large threat to the survival of the species. As Marbled Murrelets probably survive to a relatively high age (Common Murres (*Uria aalge*) live up to 32 years (De Santo and Nelson 1995)), damage done to populations in the form of reduced recruitment will show with a considerable time lag. In addition, at sea censuses of Marbled Murrelets are loaded with uncontrollable variation, partly due to small and large-scale movements of Marbled Murrelets in the range of hours to years, but also attributable to other effects such as El Niño. Therefore, many years of research will be necessary to determine existing trends in population sizes. This information is required in the assessment of the effects of breeding habitat loss on Marbled Murrelet populations and to answer the question of how much habitat the Marbled Murrelet needs to sustain viable populations.

The decline in populations and breeding habitat of the Marbled Murrelet has caused conservation initiatives in Canada. In 1990 the Marbled Murrelet was designated threatened by COSEWIC (Council on the Status of Endangered Wildlife in Canada), following a report by Rodway (1990). It was included as endangered in the British Columbia Red List in 1996. (The Red list includes any species being considered for the more formal designation of Extirpated, Endangered or Threatened under the British Columbia Wildlife Act. It also includes species already designated in those categories.). At this point both listings are merely conventions produced by experts and are not legally binding.

Under the Forest Practices Code of British Columbia (FPC), Marbled Murrelets are designated as an ”Identified Wildlife Species” (IWS). The IWS’s will be considered in the Identified Wildlife Management Strategy (IWMS), which is a supplement to the FPC. The IWMS is still in the draft stage, although the planning process began three years ago.

IWS’s will be protected in Wildlife Habitat Areas (WHA’s), which will have to meet certain criteria outlined in the draft. However, there is a limit to how much impact the protection granted by the IWMS can have on timber supply in British Columbia: 1% of the annual allowable cut of 1995. The degree of protection provided by the strategy does not depend on the species needs but on what the government decided to be an acceptable level of impact on timber supply. Therefore, the IWMS is not a wildlife management strategy, but rather a timber supply management strategy with wildlife considerations.

In the IWMS draft, protection of Marbled Murrelet habitat specifically is not allowed to have any impact on timber supply additional to the 11-13% of old seral stage forest retained under the recommendations for the low biodiversity option in the Biodiversity Guidebook (FPC 1995). However, this retention level is meant to manage forests in a way that is somewhat similar to their natural disturbance regimes and has to accommodate all species and considerations not covered by the IWMS. The Biodiversity Guidebook (FPC 1995) states that:

> ”The lower biodiversity emphasis option may be appropriate for areas where other social and economic demands, such as timber supply, are the primary management objectives. This option will provide habitat for a wide range of native species, but

> the pattern of natural biodiversity will be significantly altered, and the risk of some native species being unable to survive in the area will be relatively high."

The Marbled Murrelet, having high structural and spatial demands on its breeding habitat is clearly a candidate to be unable to survive under the lower biodiversity emphasis management option. In addition, the lower biodiversity emphasis option was not intended to be applied to the whole area of British Columbia but to about 45% of it.

The conservation of the Marbled Murrelet is not legally supported in British Columbia right now. Although various conservation efforts exist (*e.g.*, the Marbled Murrelet Recovery Team) the protection of the Marbled Murrelet will remain weak once the IWMS has been implemented. For the reasons explained above the number of WHA's specifically designated for Marbled Murrelets will be very limited. The future of the Marbled Murrelet in British Columbia will likely remain uncertain under this strategy.

1.2 Background on the Coastal Temperate Rainforest of North America

Coastal temperate rainforest only occurs in moderate climates with few temperature extremes, high frequency of clouds and fog, and high amounts of precipitation (>1920 mm/year) (Redmond and Taylor 1997; Kellogg 1992). Typically these conditions exist where mountain ranges directly border the ocean between 32 and 60 degrees latitude, with high amounts of precipitation as a consequence of clouds being pushed up into cooler air. Precipitation data from Clayoquot Lake, which is approximately 6 km away from the Ursus Creek, indicate annual means of well above 5000 mm per year (5641.6 mm in 1994 and 6560 mm in 1995; Clayoquot Biosphere Project, unpublished data).

The intensity of precipitation varies considerably locally and seasonally, and increases with elevation (Scientific Panel 1995a). Winter storms deliver large amounts of rain in short periods of time (up to 222.8 mm in 24 hours, measured in Carnation Creek in February 1986, in Scientific Panel 1995a) accompanied by strong winds. The summers are considerably drier with only 15% of the yearly precipitation during the months June - September. The relative shortage of water during the period of highest light intensity and temperature explains the dominance of conifers in the coastal temperate rainforest.

The climate is oceanic with cool summers and mild winters. Snowfall is rare at sea level and widely fluctuating at higher altitudes. Heavy winter rain, especially when falling on melting snow, creates the highest stream discharges.

A considerable amount of the precipitation is intercepted by vegetation, especially epiphytes (mosses and lichens), and evaporates back into the air (Franklin 1988). However, most of the water is absorbed by and passes through the highly permeable soil (Scientific Panel 1995a). The ability of the soil to transport water through pores and channels formed by old root channels, animal burrows and other openings is crucial to slope stability (Tsukamoto *et al.* 1982; Sidle *et al.* 1985). Timber extraction and disturbance (*e.g.*, compaction) of soil during road construction lead to higher rates of annual runoff of water and, in many instances, to alterations in timing and peaks of storm runoff (Hetherington 1982). Increased peak discharges can lead to higher sediment loads, streambed erosion and land slides (Simenstad *et al.* 1997).

Important characteristics of a climax ecosystem are the natural renewing processes or the natural disturbance regime. In the west coast portion of the coastal temperate rainforest large disturbances are uncommon (Kellogg 1992). Windthrow is the principle agent of disturbance, assisted by infrequent landslides and occasionally by small fires (Scientific Panel 1995a). Natural openings resulting from disturbances are generally less than two tree lengths in diameter in these forests (Meidinger and Pojar 1991).

The long intervals between disturbances result in a diverse forest ecosystem in many senses. Most stands are dominated by large old trees of species that are among the largest and most long-lived trees in the world (Pojar and MacKinnon 1994). In the gaps that result from dying and falling ”giants” young trees regenerate in a well-developed understory layer. Therefore, the age distribution ranges from saplings to more than 1000 years old trees, and sizes vary greatly from seedlings to giants more than 80 m high and 3 m in diameter. In this way, all trees are eventually replaced without a major disturbance in the rest of the stand. The estimate for a complete ”turn over” by gap-phase replacement is 300 to 1000 years for sites in Clayoquot Sound (Lertzman and Krebs 1991).

The Scientific Panel (1995a) differentiates two phases in the submontane very wet maritime coastal western hemlock variant: the Hemlock-Amabilis Fir (HA) and the Cedar-Hemlock (CH) phases, associated with different disturbance regimes. The HA-phase, on the one hand, is characterised by regular blowdowns of patches of forest ranging from a few trees to several hectares. The stand structure following such a windthrow (uniform trees, dense canopies, shallow rooting) makes the forest susceptible to further windfall. Therefore, this disturbance regime appears to be, to a certain degree, self-perpetuating. Examples of sites in the Ursus that could fit this category are UFH and UBB. However, this phase is rarely found in the relatively sheltered Ursus watershed. The CH-phase, on the other hand, has a more open stand structure, often with spike-topped, firm-rooting western redcedars. The canopy offers less resistance to wind and it is mostly isolated individuals that are blown down.

The podzolic soils and the long and wet growing periods support productive old growth forests with a very high accumulated biomass (600-900 m^3/ha of standing trees and 70-400 m^3/ha of downed wood in the CWH zone; Scientific Panel 1995a; Harcombe and Oswald 1990). With up to 3500 t/ha they accumulated about seven times as much organic material as the tropical rainforests (Kelly and Braasch 1988). The large amount of standing and fallen dead wood provides microhabitats for a great variety of organisms, especially fungi, plants and invertebrates (Harmon *et al.* 1986; Franklin 1988; Scientific Panel 1995a; Winchester 1997a).

The unique small-scale mosaic of structures and climates in the temperate old-growth rainforests in the Pacific Northwest makes these forests home to numerous specialised species that are highly dependent on them and account for the large contribution of these forests to global biodiversity (Franklin 1988; Fenger and Harcombe 1989; Bunnell 1990; Pojar *et al.* 1990; Winchester and Ring 1996a, 1996b; Winchester 1997a). Large old trees, gaps in the canopy, and standing dead trees are important structural features of Marbled Murrelet habitat. Uneven canopies are associated with well-developed understory vegetation, which is more productive than that of adjacent closed-canopy areas (Alaback 1984; Inselberg 1993).

Especially worth mentioning are the rich non-vascular flora, the numerous specialised invertebrate species and the birds of Clayoquot Sound. Unfortunately, not many studies have been done on the non-vascular flora. However, the ecological importance of the abundant mosses, lichens and fungi in this area of large climatic moisture surpluses and high productivity is evident (Pojar *et al.* 1990). Mosses and lichens have a high capability to retain water and are important pioneer colonisers and soil builders. They create important microhabitats for the germination of other plants and for invertebrate animals (Scientific Panel 1995a). Marbled Murrelets often use moss-covered platforms as nest sites. Fungi are essential partners in mycorrhizae and facilitate decomposition and nutrient cycling.

The diversity of (micro-) habitats in the ancient rainforest provide for the faunal species richness of Clayoquot Sound. In particular, structurally complex trees and dynamic, open areas such as bogs and hydroriparian areas provide required habitats for a wide range of organisms. Although, as elsewhere, invertebrates have key roles in ecosystem functions and contribute most to biodiversity (Asquith *et al.* 1990; Mattson and Addy 1975; O'Neill 1976), there are very few studies done on this part of the animal community in Clayoquot Sound. Studies in the canopy of Carmanah Valley, which is south of Clayoquot Sound on the west coast of Vancouver Island and has similar vegetation, have revealed many insect and spider species formerly unknown to science (Winchester and Ring 1996a, 1996b; Winchester 1997a, 1997b).

The vertebrate fauna of Clayoquot Sound is better known. Although bats have not yet been studied in all areas, 297 vertebrate species have been recorded in Clayoquot Sound, which is 81% of the 368 species known to occur in the region of the coastal temperate rainforest between Alaska and Oregon (Table 1). However, because of their isolation on Vancouver Island, Clayoquot Sound's forests are devoid of some of the species occurring in comparable forests on the mainland. Most (62%) of the vertebrate species recorded in Clayoquot Sound are forest-dwelling. Many of those species (46%) breed in older forests (>140 years) using downed wood (43%) and/or cavities (32%). Many animals make significant use of riparian areas (76%) and edge habitat, choosing more protective forest habitat for breeding and hibernating (Scientific Panel 1995a).

Among the numerous important and interesting habitats in the temperate rainforest, the hydroriparian ecosystems deserve special attention. They are an important area of activity for a large portion of all fauna and contain the most diverse flora in a watershed (Scientific Panel 1995a). In addition, many terrestrial and all aquatic organisms use them as travel corridors.

Hydroriparian zones are adversely affected by logging and road building (Hartman and Scrivener 1990). Their integrity is important to many species, such as the economically important salmonids (salmon and trout), as well to slope stability and peak flow mitigation. For Marbled Murrelets streams may be important landmarks for orientation and flight paths (Nelson and Hamer 1995a; Singer *et al.* 1991, 1995; pers. observations), and the integrity of the hydroriparian zone helps prevent breeding habitat loss caused by landslides and bank erosion. The input of sediments and other effects of logging could influence the abundance of Marbled Murrelet prey species in fjords and sounds (*e.g.*, herring spawning; Scientific Panel 1995a).

Table 1: Number of native land-dwelling vertebrates in Clayoquot Sound region and related forest types (from Scientific Panel 1995a).

Zone	Amphibians	Reptiles	Birds	Mammals	Total
Forests of Coastal Western Hemlock Zone (CWH) [1]	11	6	138	64	219
Forests of Mountain Hemlock Zone (MH) [1]	7	4	69	58	138
Coastal temperate rainforest (Alaska to Oregon) [2]	24	6	259	79	368
Clayoquot Sound:					
all species [3]	7	3	258	29	297
blue-listed species [4]	-	-	31	3	34
red-listed species [5]	-	-	8	3	11

[1] Breeding species only. Includes mainland British Columbia as well. All but eight species in the MH zone are also found in the CWH zone.
[2] Includes non-breeding species.
[3] Includes non-breeding species; many birds use the area primarily during migration.
[4] Species considered to be vulnerable or sensitive.
[5] Species that are candidates for designation as endangered or threatened.

1.3 Study Area

The study area was the Ursus Valley, which drains into the lower Bedwell River in Clayoquot Sound, Vancouver Island, British Columbia, Canada (see Figure 1, Figure 2, and Appendix III, Figure 1). The UTM co-ordinates of the valley are 305 000m.E. and 5473 000m.N. (Universal Transversal Mercator Grid). The 7,342 ha large watershed lies in the transition zone between the coastal plains and the inland mountains. It is a deep glacially eroded trough and is surrounded by peaks higher than 1000m and ridges higher than 500m. The east-west orientation, which is unusual for a valley in Clayoquot Sound, results in distinctly south- and north-facing slopes.

The main valley is dominated by steep rock and colluvial slopes, while the lower slopes are characterised by colluvial fans and cones, and some morainal benches (Clement 1995). The valley floor is a relative flat floodplain, becoming confined and steep in the east.

Almost all of the Ursus is covered with temperate rainforest. Dominant tree species in low elevation forests are western hemlock (*Tsuga heterophylla*) and amabilis fir (*Abies amabilis*), with conspicuous stands of red alder (*Alnus rubra*) and Sitka spruce (*Picea sitchensis*) and scattered western redcedar (*Thuja plicata*). At medium elevations, yellow cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) occur in mixed stands with amabilis fir and western hemlock. Yellow cedar, mountain hemlock and amabilis fir dominate the subalpine forests.

The Ursus is an essentially pristine valley without any known major disturbances. 98.5% of its forests are in age classes 8 and 9 (older than 141 years) (Scientific Panel 1995a). Some small clearcuts, dating from 1952 and 1966, exist at the entrance of the valley towards the Bedwell River. There were some mining assessments in the Ursus Valley during the early 20's and the 60's, resulting in mining claims, which never have been used but are still considered for exploitation on a small scale today.

The valley has been traditionally used by the Ahousaht First Nation for many thousands of years. No major alterations in the ecosystem are known to have resulted from aboriginal use. The hereditary chiefs are attempting to regain control of their traditional territory and to re-establish their traditional system of stewardship in the Ursus. The Ahousaht First Nation has cooperated with the Western Canada Wilderness Committee on a study of cultural modified trees (CMT's) in the Ursus Valley, to increase the knowledge of the traditional use of the valley and to support their land claims.

The Ursus has received attention during the ongoing Clayoquot Sound debate over the future of the region and timber extraction issues. It was designated a Special Management Area with an emphasis on wildlife in the Clayoquot Sound Land Use Decision, in 1993. Background for this decision was sign of Roosevelt elk found in the valley. This species was then selected as an important one for old-growth management; however, follow-up studies did not find enough elk activity to support management based on this species. But, as the elk researchers observed high Marbled Murrelet activity in the valley the focus shifted to this species as prime management indicator. Management decisions on forestry and other resource extraction in the Ursus will depend on the results of wildlife inventory studies on selected species or guilds (*e.g.*, black bears, Roosevelt elk, Goshawks, song birds, Marbled Murrelets) and other resource values (*e.g.*, scenic value for tourism).

1.3.1 Land-Shaping Processes

The land-shaping processes in the Ursus, mainly slope processes, stream erosion and deposition, are driven by the passage of water through the landscape. The intense winter rains and snowmelt are the strongest forces in these processes.

Slope processes are primarily debris slides and debris flows. They occur when shallow subsurface waters saturate the lowest soil layers, reducing the soil strength enough to make the overlaying soil and vegetation slip downhill (O'Loughlin 1968; Buchanan and Savigny 1989).

Frequently, debris slides result in a significant loss of soil and vegetation cover and expose unweathered material such as bedrock or till. They often accumulate material as they go downhill and turn into debris flows, which are highly viscous accumulations of saturated soil, stones, and vegetation cover. Both debris slides and flows commonly enter steep water courses where they are augmented by stream flow. They can also start in steep stream channels during peak discharges when dams of woody debris fail and sediments accumulated behind them start flowing downhill. Slide events in the Ursus Valley have a high probability of terminating directly in stream channels, because of the valley's steep slopes, narrow valley flats and high drainage density. There they can cause severe damage to the hydroriparian zone (Anon.1996).

Natural causes for debris slides and associated flows are heavy rainfall on ground already saturated by rain (Church and Miles 1987), tree blow down and wind stress transmitted by trees (Chatwin *et al.* 1991), other downhill movements such as rockfall or snow avalanches, and seismic vibrations. Anthropological causes of landslides are typically clearcutting and road building (Scientific Panel 1995a, O’Loughlin 1968; Sidle *et al.* 1985; Howes 1987). In particular, decreased soil strength due to root decay (Buchanan and Savigny 1989), soil disturbance associated with yarding, wind throw on edges of cut blocks, loading of steep slopes with sidecast material during road construction, and interception and redirection of shallow subsurface water by roads can contribute to slope instability.

Stream processes occur wherever surface water runs off. The characteristics of the stream channels are determined by the amount and frequency of water, sediment, and organic debris input and by the material and morphology of the landscape. In the steep hillsides of the Ursus the dominant stream process is downcutting, which results in deep gullies and bedrock canyons. In the lower slopes with less gradient, streams and sediment flows deposit sediment, building alluvial fans just before reaching the main channel of the Ursus. The mainstream of the Ursus has a diverse system of main and side channels and large organic debris deposits (i.e., log jams) on an active floodplain on alluvial valley fill. The accumulations of large wood pieces in the channel regulate the movement of sediments and smaller organic debris (Beschta 1979; Bilby 1981; Naiman and Anderson 1997).

All three stream channel types are relatively sensitive to direct disturbances or changes in sediment or peak flows that might result from road building and extractive activities (Anon.1996). The drainage function of the upper gullies might become compromised by additional debris or direct disturbance by forestry activities. The reduced flow-off can result in catastrophic discharge events with deleterious effects for the lower stream system. The fans are mostly formed by irregular, sudden, catastrophic debris flow events and their multiple channels change their position often. Therefore, the fans are unstable and very sensitive to disturbance (Anon.1996). In the main channel of the Ursus higher frequency or size of peak discharges might lead to channel bed and bank erosion. Higher loads of sediment and nutrients have been shown to be harmful to the sensitive aquatic habitats (Scientific Panel 1995a).

The steep slopes (55% of the watershed has slopes of 60% or greater) and the intense winter precipitation account for the high natural instability of the Ursus. The number of natural landslides as detected from air photos (32, with 23 ending in a stream channel) is an indicator of the instability and sensitivity of the steep hillsides. As forestry development under similar conditions has shown in the past, landslides would become very likely with any kind of resource exploitation (Anon.1996).

1.3.2 Geology and Soils

Underlying rocks in Clayoquot Sound are mostly coarse crystalline metamorphic and intrusive rocks and less commonly older volcanic and sedimentary rocks (Jungen and Lewis 1978). The resulting soils are mainly ferro-humic podzols, with minor occurrences of folisols and gleysols (Jungen 1985; Jungen and Lewis 1978).

Podzols are formed on coarse textured and well-drained parent materials, in areas of high precipitation. They contain much silica and few bases such as calcium or magnesium carbonate. Decomposing organic matter releases iron and aluminium, which is washed out of the A- into the B-horizon by the large amounts of water moving through the porous parent materials. This process of leaching also moves nutrients and organic matter from Ae-horizons into Bhf-horizons. Therefore, podzols have low levels of nutrient cations. Iron and aluminium oxides accumulate in lower layers of the podzol and often form cemented layers of low permeability, hindering drainage even in materials with initially high permeability (AG Boden 1994; Jedicke 1989). The relative acidity of the soil somewhat inhibits the breaking down of the organic layer which has important functions on podzols. It contains most of the nutrients available to plants, supports a high diversity of life and prevents soil erosion. In addition, podzols strongly retain phosphorus and therefore keep nutrients level in groundwater and streams low, which limits the primary production in west coast streams (Mundie *et al.* 1991).

Folisols consist of the organic layers (L-, F-, and H-horizons) only and rest directly on bedrock. They mostly occur in rocky terrain of the higher slopes. Both types of soils are sensitive to disturbance of the top layers, which contain virtually all of the available nutrients, have high water-absorbing and -retaining capability, and protect mineral soil from surface erosion (Scientific Panel 1995a).

1.3.3 Biogeoclimatic Classification

Under the provincial Ecoregion Classification System (Table 2) the Ursus Valley lies within the Coast and Mountains Ecoprovince, the Western Vancouver Island Ecoregion, and the Windward Island Mountains (WIM) Ecosection (Demarchi 1993). In terms of the Biogeoclimatic Ecosystem Classification System the Valley is dominated by the Coastal Western Hemlock Biogeoclimatic Zone (CWH) with minor components of the higher elevation Mountain Hemlock Biogeoclimatic Zone (Mh) and the Alpine Tundra (AT) Biogeoclimatic Zone. Most of the survey stations were within the submontane very wet maritime coastal western hemlock variant (CWHvm1, $n = 41$) but some stations were in the montane very wet maritime coastal western hemlock variant (CWHvm2, $n = 19$) and the windward moist Maritime mountain hemlock variant (Mhmm1, $n = 2$) (Green and Klinka 1994). The finest scale of biogeoclimatic units used in the study was site series (16 different site series were identified in vegetation plots at survey stations). They are based on plant species composition, nutrient regime, and moisture regime.

Clement (1995) mapped vegetation units based on site series for the Ursus Valley and found a total of 20 different biogeoclimatic vegetation types. He classified the habitat polygons, as identified from aerial photographs, into primary (represents 40-100% of a polygon), secondary (10-50%), and tertiary (10-30%) site series. He labelled site series or groups of site series with names including the characteristic species (*e.g.*, CWHvm1/09 = Sitka spruce - Salmonberry) (see Clement 1995 for details). With regard to the suitability of vegetation as Marbled Murrelet habitat, it is important to note that the mapping relates to the potential climax and not the actual state of the vegetation.

Table 2: Biogeoclimatic Ecosystem Classification Hierarchy with consideration of the Ursus Valley.

Classification Hierarchy	Classification Unit	Ursus Valley
Regional Classification	Ecoprovince	Coast and Mountains
	Ecoregion	Western Vancouver Island
	Ecosection	Windward Island Mountains
Zonal Classification	Biogeoclimatic Zone	Coastal Western Hemlock (CWH), 0 - 900 m; Mountain Hemlock (Mh), 700 - 1200m; Alpine Tundra (AT), >1200 m
	Biogeoclimatic Subzone	Very Wet Maritime (vm); Moist Maritime (mm); Alpine Tundra
	Biogeoclimatic Variant	Submontane / Montane (vm1 / vm2), 0-600m / 600-900m; Windward (mm1); Alpine Tundra
Site Classification	Site Association	not available
	Site Series	*e.g.*, CWHvm1/09: Sitka spruce - Salmonberry
	Site Type	not available

1.4 The Clayoquot Sound Planning Process and the Involved Decisions and Institutions

Most of the unlogged watersheds on the west coast of Vancouver Island are in Clayoquot Sound. Even in relation to the whole west coast of British Columbia, Clayoquot Sound has a substantial proportion of the unlogged watersheds (Moore 1991). It still offers abundant breeding habitat for Marbled Murrelets and is therefore of greatest significance to them in British Columbia and North America (Sealy and Carter 1984, Rodway *et al.* 1992, Burger 1995b, Kelson *et al.* 1995).

In the early 1990's public attention was drawn to Clayoquot Sound as environmentalists tried to stop logging activity in this pristine area of high aboriginal, wilderness conservation, and economic value. Protests were not addressed and subsequently turned into blockades against forest workers and many people were arrested. With growing public attention the pressure on politicians to deal with this unique area increased and led to special planning efforts.

The Clayoquot Sound Sustainable Development Committee was established, whose recommendations guided the Clayoquot Land Use Decision, April 1993. It was followed by an agreement between the First Nations and government, concerning the role of First Nations in the planning process until a final treaty is signed, which will clarify the extent of land and control the First Nations will regain in the area. To enhance the planning process and to make the forest practices in Clayoquot Sound ”the best in the world” (Premier Harcourt cited in Scientific Panel 1995a), the government established a Scientific Panel for Sustainable Forest Practices in Clayoquot Sound. The efforts of the panel culminated in three detailed reports, which guide research, planning efforts, forest practices, and First Nation’s involvement in Clayoquot Sound right now.

In the following chapters I would like to introduce the important decisions, agreements, laws, and institutions relating to this issue, to clarify the framework in which Marbled Murrelet protection takes place now and will take place in the future in Clayoquot Sound.

1.4.1 Clayoquot Land Use Decision, April 1993

The Clayoquot Land Use Decision was made by the government of British Columbia, in April 1993, following the draft report of the Clayoquot Sound Sustainable Development Committee (Government of British Columbia 1993). It established Protected Areas (87 600 ha, 33.4% of Clayoquot Sound total land area) and Integrated Resource Management Areas (IRMA’s; 163 900 ha, 62.3%). These IRMA’s were intended to combine sustainable forestry and long-term employment with the requirements of wildlife, fisheries, tourism, and recreation. A sub-category of the IRMA’s are the Special Management Areas (SMA’s; 46 500 ha, 17.6%). In the SMA’s forestry activity has to meet specific recreation, wildlife, or scenic values objectives. The Ursus Valley was designated an SMA with an emphasis on wildlife.

1.4.2 Interim Measures Agreement, March 19, 1994 (IMA, 1994)

Under the acceptance of the 1991 recommendations of the British Columbia land claims Task Force and the August 20, 1993 protocol Respecting the Government -to- Government Relationship between the First Nations Summit and the Government of British Columbia, the Interim Measures Agreement has been ratified between the Hawiih (hereditary chiefs) of the five First Nations having territory in the Clayoquot Sound (Tla-o-qui-aht, Ahousaht, Hesquiaht, Toquaht and Ucluelet) and the Province of British Columbia. Its main goal is to identify areas for First Nations land, areas for joint management and areas for development. The agreement includes the establishment of a Central Region Board (CRB), which has the responsibility to review all plans in Clayoquot Sound (IMA Section 7 (h)) and the authority to examine all applications, permits, decisions, reports, or recommendations related to land management (IMA, Section 7 (f) (ii)). The goals of the CRB are:

- to provide opportunities for First Nations consistent with aboriginal resource uses and heritage, and to consider options for treaty settlement;
- to conserve resources in Clayoquot Sound and to promote resource use that supports sustainability, economic diversification, and ecological integrity;
- to encourage dialogue within and between communities and to reconcile diverse interests (Central Region Board 1997)

In 1996, the Nuu-Chah-Nulth Central Region Chiefs and the provincial government signed the Interim Measures Extension Agreement (IMEA), which confirmed the continuation of the CRB in the planning process. (The Nuu-Chah-Nulth is a group, traditionally based on language, of 14 west-coast bands on Vancouver Island, which share a common government.) In addition, the IMEA started new initiatives, such as the Clayoquot Economic Development Strategy (CEDS) and the Ma-Mook Development Corporation (MDC). The purpose of the CEDS is to identify opportunities related to the forest industry, such as value-added processing of wood, fisheries, tourism, and small business development, to provide a transition strategy from old forest practices to the new recommendations of the Scientific Panel, securing stable employment in Clayoquot Sound. The MDC is owned by the Central Region First Nations and intends to invest in businesses and projects as means to generate an economic base for the First Nations. One of the first projects is a joint venture with a large forestry company, MacMillan Bloedel, which plans to reflect First Nations' perspectives, needs and values in the forest practices it uses.

1.4.3 Scientific Panel for Sustainable Forest Practices in Clayoquot Sound

The Scientific Panel for Sustainable Forest Practices in Clayoquot Sound (or short: Scientific Panel) was implemented by the government of British Columbia in response to a recommendation from the Commission on Resources and Environment following the provincial government's April 13 1993 decision on land use in Clayoquot Sound. Its 19 members included an array of international scientists and First Nations' elders with expertise in forest related topics. Its objectives were to scientifically review the current forest practice standards in Clayoquot

Sound and to make recommendations for forest practices which are ”scientifically sound, operationally achievable, publicly acceptable, and safe” (Scientific Panel 1995a).

The final results and more than 120 recommendations of the Scientific Panel were published in three volumes: Scientific Panel Reports 3 (Scientific Panel 1995c), 4 (Scientific Panel 1995b), and 5(Scientific Panel 1995a). The Government of British Columbia asserted on July 6, 1995, that it would fully implement the recommendations of the Scientific Panel. It stated that ”[no] logging will take place in undeveloped watersheds until the necessary studies are done and the panel’s recommendations can be fully implemented” (Anon. 1995).

> ”Ecosystems, resources, and resource values are interconnected. The Panel asserts that sustainable forest practices in Clayoquot Sound must be judged by the extent to which all resources are respected and sustained. Sustainability depends on maintaining ecosystem productivity and connections.” (Scientific Panel 1995a)

More precisely the Scientific Panel seeks to:

- maintain watershed integrity
    - maintain the stability and productivity of forest soils;
    - maintain waterflows and critical elements of water quality within the range of natural variability and within natural waterways;
- maintain biological diversity
    - create managed forests that retain near-natural levels of biological diversity, structural diversity and ecological function;
    - maintain viable populations of all indigenous species;
    - sustain species, populations, and the processes associated with late-successional forest stands and structures;
    - maintain the quality and productivity of aquatic environments;
- maintain cultural values
    - protect areas and sites significant to First Nations people;
- maintain scenic, recreational, and tourism values

  - protect areas of significant scenic, recreational, and tourism values; and
- be sustainable
  - provide for a sustainable flow of products from the managed forests of Clayoquot Sound

(Scientific Panel 1995a, p.151)

The variable-retention silvicultural system recommended by the Scientific Panel (1995a) focuses on the trees retained in a certain area, not the trees removed. It seeks to retain forest structures and habitat elements from the original stands by leaving *e.g.*, large decadent trees, groups of trees, snags, and/or downed wood. Marbled Murrelets could profit from retained large trees as nesting sites, once the forest around them has regrown enough to offer some cover and to mitigate edge effects. This period (> 80 years) is probably much shorter than the time necessary for regrowth of suitable nesting trees. Hamer and Nelson (1995b) and Nelson (1997) have described nests found in such remnant old growth trees surrounded by mature second-growth.

Marbled Murrelet research is relevant to several recommendations of the Scientific Panel (1995a):

Recommendations (R) relating to silvicultural systems:

- R3.6 - to assist in identifying areas with significant wildlife resource values that will have high retention rates (at least 70%);
- R3.8 - to assist in selecting specific structures and patches which are important to meet ecological objectives (*e.g.*, provide habitat for threatened species such as the Marbled Murrelet) and in identifying ecological sensitivity as a base for retention rates;
- R3.19 - to assist in assessing the effectiveness of the initial recommendations through monitoring and to alter them as necessary;

Recommendations relating to transportation systems:

- R5.1 - to assist in identifying highly sensitive parts of Marbled Murrelet habitat which are to be considered in planning of roads;

Recommendations relating to planning for sustainable ecosystem management:

- R7.2 - to identify suitable ecological land units to form the basis of planning and identifying watershed-level values of biodiversity;
- R7.3 - to collect appropriate baseline information on biophysical resources and use this information to assess ecological responses to change;
- R7.8 - to contribute to an inventory of forest resources and forest management activities;
- R7.9 - to monitor the effects of plans on Marbled Murrelets.
- R7.14 - to contribute information to planning steps and to monitor for meeting of objectives.
- R7.16 - to map and designate no-harvest reserves at the watershed level to protect a red-listed and nationally threatened species, and identify essential habitats required for this species and contribute to sub-regional planning for its protection.

Recommendations relating to monitoring

- R8.1 and R8.2 to monitor Marbled Murrelet habitat and populations in the long term.

1.4.4 Forest Practices Code (FPC)

The Forest Practices Code of British Columbia Act came into effect on June 15, 1995. It replaces former forestry regulations, which were on a contractual basis with the forest industry rather than on a legal basis with provision for enforcement, administrative penalties, and court ordered fines (Anon.1996). The Forest Practices Code of British Columbia Act is the legislative umbrella authorising the other components of the FPC, which are regulations, standards, and guidebooks.

The regulations lay out the forest practices that apply to all of British Columbia. Standards are expansions on regulations established by the chief forester. The guidebooks have been developed to support regulations, but are not part of the legislation. They include recommendations, which are usually consistent with the legislated requirements of the FPC. The management plan for Ursus Creek SMA will be a higher level plan under the Forest Practices Code. Hence, the planning is done within the legal framework of the Forest Practices Code.

1.4.5 Ursus Valley Terms of Reference

The Clayoquot Implementation Committee approved the Terms of Reference for the Ursus Creek SMA on November 22, 1994. This happened before the coming into effect of the Forest Practices Code and the final report of the Scientific Panel. The Terms of Reference provided for the implementation of an Inter-Agency Planning Team. The planning boundaries were expanded by the Team to include the lower Bedwell, which is the access of industry and anadromous fish to the Ursus and which has important cultural value to the Ahousaht First Nation. In addition to the technical Inter-Agency Planning Team, a Public Advisory Group was established, both co-chaired by the Ministry of Environment, Lands, and Parks and the Ministry of Forests.

1.4.6 Ursus Valley Planning Process

The planning process for the Ursus Valley started with the first meeting of the Public Advisory Group on November 24, 1994 and ended in its initial structure in January of 1996 to be reviewed under the recommendations of the Scientific Panel. The framework for the development of a plan intended to identify:

a) resources (*e.g.*, minerals, soils, flora and fauna, processes) and, by overlaying maps of resources, areas of highest value and sensitivity;
b) resource use and values (*e.g.*, native values, forestry, tourism, fisheries) and, by overlaying maps of resource use and values, areas of conflict of use.

Overlaying of the resultant maps of a) and b) will then help to recognise areas of high conflict, for example the riparian zone where critical, sensitive wildlife habitat meets high value timber.

The planning process continued in 1997 with the establishment of the Clayoquot Planning Committee by the Deputy Ministers' Committee for Clayoquot Sound and the Central Region Board. Furthermore, Watershed Planning Groups were established. The Planning Groups develop plans for all forest-related activities, in accordance with the recommendations of the Scientific Panel report, within the watersheds the groups are assigned to, and submit their plans to the Planning Committee and the CRB for approval. Finally, the plans are submitted to the government which designates them as ”higher level plans” under the Forest Practices Code of British Columbia Act, and thus make them legally binding.

The plans are supposed to identify reserves and areas for logging, under consideration of environmental resources, natural processes, cultural, scenic and recreational values, watershed integrity, unstable terrain, and areas of important forest habitats and habitats of rare and endangered species.

1.5 First Nations

Native Peoples have resided in the Clayoquot Sound area for thousands of years. During this time they have developed an extensive body of traditional knowledge on philosophy and worldview, practices and strategies for resource use, and communication and exchange of information (Table 3, Turner 1997).

Since the first European settlers arrived in North America, indigenous peoples have been oppressed in many ways. Today, First Nations are negotiating and fighting to regain control over their traditional territories, which were never legally acquired by the Crown. I think that any activity on this land is not ethical (resource extraction as well as conservation efforts) without the permission of the native community.

During this oppression the continuity of traditional knowledge was challenged. Its loss is a loss to all humanity because it is needed now, more than ever, to help establish sustainable ways, especially where western science has failed (Turner 1997).

Two important concepts frame the relationship of the Nuu-Chah-Nulth relationship to their territory:

- ***hishuk ish ts’awalk*** (”everything is one”) embodies the Nuu-Chah-Nulth sacredness and respect for all life forms and their approach to resource stewardship.
- ***h̲ah̲uulhi*** is the Nuu-Chah-Nulth system of hereditary ownership and control of traditional territories. It represents a long history of resource use and management in Clayoquot Sound and provides a basis for Nuu-Chah-Nulth co-management of the area and its resources (Scientific Panel 1995c).

The Ursus valley falls within the *h̲ah̲uulhi* of the hereditary chief of the Ahousaht First Nation. Archaeological studies conducted by the Ahousaht First Nation and the Western Canada Wilderness Committee in 1994 and by Millenia Research in 1995 revealed 57 Culturally Modified Trees (CMT) in the lower Ursus Creek.

In the initial planning process, First Nations were involved in the Inter-agency Planning Team and the Public Advisory Group. They are represented in the CRB which stems from the

IMA and the IMEA and which is the most important land and resource agency in Clayoquot Sound.

Table 3: Traditional Ecological Knowledge of the Northwest Coast (adapted from Turner 1997).

Worldview	Strategies for Sustainable Living	Exchange of Knowledge
• belief in the spirituality and innate power of all things • respect for other life forms and entities • ideological systems that enforce sustainable use of resources (social sanctions, sharing) • concepts of interactive relationships with other life forms • close identification with ancestral lands	• knowledge and application of sustainable practices: inventory monitoring, use of ecological indicators; environmental modification; harvesting strategies • understanding of major principles of ecology: relationships among all life forms and the environment; ecological succession • adaptation to change in resource availability and living conditions	• exchange of knowledge and resources within and among groups • language: classification and naming of culturally important features • development of social structures and institutions to promote sustainable living • development of culturally appropriate ways of teaching and learning about the environment and traditional knowledge and attitudes

2. Methods

2.1 Research Program

My research in the Ursus Valley was part of the Marbled Murrelet inventory mandated by the Ministry of Environment, Lands and Parks in Clayoquot Sound, BC. At the outset of the study in 1995, I was leader of the field crew and was responsible for the establishment of nearly all survey stations and for data collection. At this time the inventory was limited to the Ursus Valley. After the field season I entered data and did preliminary analyses. In 1996, when the inventory was expanded all over Clayoquot Sound, I was not involved in the study. In 1997, I establish more survey stations in the Ursus Valley and collected additional vegetation and audio-visual survey data. Furthermore, I conducted a small separate study in which I tried to improve vegetation sampling by identifying centres of activity relative to survey stations and conducting vegetation plots specifically at these locations. My data analysis and write-up was completely independent of the rest of the Marbled Murrelet study conducted by the Ministry of Environment.

In total, I established 29 survey stations in the Ursus Valley, conducted 64 audio-visual surveys, and carried out 38 vegetation plots. The standardised audio-visual morning surveys for Marbled Murrelets and the vegetation sampling in vegetation plots closely followed the survey protocol of the Pacific Seabird Group (PSG) (Ralph *et al.* 1993, 1994) and the Resources Inventory Committee (RIC) standards (1995).

I recorded the data in the field on tape recorders and transcribed it onto paper. Later it was stored and processed in EXCEL 7.0 spreadsheets. I did the statistical analyses with SPSS 7.0, SYSTAT 7.0, and BLOSSOM STATISTICAL PACKAGE (1998). To increase the power of statistical analyses I included survey and vegetation data collected by other researchers in the Ursus Valley over the three years of the inventory. These data were gathered with the same methods that I used and did not have any influence on the way I did my analyses. The variables used in the analyses are listed alphabetically beside short descriptions in Appendix I, Table 1 and the data on which analyses were based are shown in Appendix I, Table 2. Variable names are capitalised.

2.2 Field work

2.2.1 Stations

The survey stations were located in a variety of valley-bottom and slope habitat types (3 biogeoclimatic variants and 16 site series). Every station was sampled at least once but usually several times in the three years of the inventory (1995-97). A goal was to distribute the survey station across the valley. Survey stations had to meet the following criteria:

- accessibility by foot (surveys were done by a team of two people who hiked to camp spots during the day and to the stations in the dark, before surveys);
- acceptable opening in the canopy to allow visual detections of birds passing over the survey station (for effects of opening size see chapter 3.1.4);
- tolerable levels of noise (usually created by running water) to allow auditory detections.

For every survey station the following variables were recorded:

- canopy tree height around the station in meters (TREEHT);
- canopy opening (CANCL) coded as 1 = 75-100%, 2 = 50-75%, 3 = 25-50%, 4 = 0-25%; this canopy opening relates to visibility of birds passing by and is incomparable to the canopy closure assessed during vegetation plots;
- location in the valley as B = valley bottom, L = lower 1/3 of the slope, U = upper 1/3 of the slope, and R = ridge top; this variable was recoded for analysis as B = valley bottom and bottom of higher elevation side-valleys, L = lower slope, and U = upper slope and ridge top (VALLOC).

2.2.2 Audio-Visual Surveys

Marbled Murrelets above land are primarily observed during dawn and dusk. Surveys around dusk did not yield enough detections for analysis; therefore, I focused on dawn surveys. The methods for Marbled Murrelet observations are well established and I followed the RIC (1995) standards, which are derived from the PSG protocol (Ralph *et al.* 1994).

Surveys were started one hour before the official sunrise and ended one hour after sunrise or 20 minutes after the last detection, whichever was later. During this period I recorded every

Marbled Murrelet detection, which is defined as the seeing and/or hearing of one or more Marbled Murrelets acting in the same manner (Ralph *et al.* 1994, RIC 1995, Paton 1995). The surveys were usually conducted lying down with the head raised up. During the surveys I used a tape recorder from which the data was transcribed to data sheets on the same day and later entered in a computer for processing.

The following information was documented for every detection:

- time (to the closest minute);
- the first and last direction that the bird was seen or heard (to the next eighth circle: N, NW, S . . .);
- whether a bird was moving up- or downstream;
- number of calls;
- type of call (one detection can have more than one type of call, in which case numbers for each kind of call are recorded);
- number of birds seen;
- behaviour (direct flight, circling, landing on or departing from trees, exiting or entering the canopy, aerial dive, or calling from a stationary point);
- closest distance to observer, in meters;
- bird height, coded as A = >50 m above canopy, BH = 10-50 m above canopy, BL = <10 m above canopy, and C = below canopy;
- notes, which can include information about complex situations (*e.g.*, the meeting of several birds), more specific data on behaviour (*e.g.*, direction of circling), or other information that does not fit into the established categories.

Furthermore, the following variables were recorded for each survey:

- creek noise coded as N = 0 = none, L = 1 = low, M = 2 = moderate, and H = 3 = high;
- date;
- observer;
- official sunrise;
- start time of survey;

- end time of survey;
- cloud cover (%) and cloud type in the beginning and at the end of the survey with ST = Stratus (low continuous cover), NS = Nimbostratus (low heavy rain clouds), SC = Stratocumulus (low fluffy), AC = Altocumulus (mid fluffy), AS = Altostratus (mid continuous), CU = Cumulus (big tall fluffy), CC = Cirrocumulus (high bands, puffy clouds), and CI = Cirrus (very high, wispy);
- precipitation coded as N = none, F = fog, M = misty drizzle, D = drizzle, and R = rain;
- wind with direction and speed (estimated using the Beaufort scale);
- direction faced by the observer (not recorded for every survey).

2.2.3 Vegetation Plots

Vegetation plots (30 x 30 m) were sampled according to the PSG protocol (Ralph *et al.* 1994) and the RIC (1995) standards to describe the vegetation around survey stations. The location of each plot was as close as possible to the associated survey station. In the event that stations were in habitat that is unsuitable for Marbled Murrelets (*e.g.*, when the survey station was in a river bed), plots were located in the adjacent forest at least 10 m inside the forest edge and usually less than 50 m from the station.

All trees with a diameter at breast height (DBH) equal to or greater than 10 cm were measured and described according to the protocol outlined by RIC (1995). Standing dead trees were included if they were at least 10 m in height. I recorded the following variables for each tree:

- species;
- DBH (cm), measured with a DBH tape;
- stratum reached (emergent, canopy or subcanopy);
- tree height (m), measured with a clinometer for some trees in a plot, estimated for the rest;
- number of potential nest platforms (number of limbs >15 m above ground and >18 cm in diameter, including epiphyte cover) that were visible from the ground;

- number of "realistic" nest platforms, which had to conform to the same criteria as the potential nest platforms plus additional criteria for use by Marbled Murrelets (accessibility, sufficient cover, angle < 45 degree from horizontal);
- epiphyte cover on horizontal surfaces of the tree coded as 0 = none, 1 = trace, 2 = 1-33% cover, 3 = 34-66% cover, and 4 = 67-100% cover;
- epiphyte cover thickness coded as N = none, A = sparse, I = intermediate, and B = thick mats;
- mistletoe infestation in the lower, middle and upper third of the tree coded as 0 = none, 1 = light, and 2 = heavy;
- alive or dead and other notes such as broken tops or moribund trees.

In addition the following variables were recorded for every vegetation plot:

- distance to the ocean (measured along the creek bed in km, DISSEA) using 1:50 000 NTS topographic maps;
- distance (m) to the nearest creek (DISSTRM);
- average canopy closure (CANCLVEG) from estimates of the percentage of sky blocked out by tree foliage, made at four points within the plot and averaged;
- slope in degrees (SLOPE);
- aspect for slopes that did not equal 0 degrees (ASPECT);
- elevation in m above sea height (ALTITUDE) as read off a 1:20 000 TRIM map.

A detailed site description form was completed within each vegetation plot following Luttmerding *et al.* (1990). I estimated the relative abundance (percentage cover) of each identified species and then estimated the percent cover of each of the tree, shrub, herb and moss layers within the vegetation plot. Then I described the plot with respect to slope position, percent slope, moisture and nutrient regime, determined from soil pits. Finally I assigned a site series code by matching my measures to those in the site description handbook for the Vancouver Forest Region (Green and Klinka 1994) employing the appropriate habitat subzone variant. Subzone variants of each plot were identified from the Biogeoclimatic Units of the Vancouver Forest Region Map Sheet (Research Branch, Ministry of Forests, B.C. 1993).

2.3 Data Analysis

2.3.1 General

As with other ecological field data, the activity levels of Marbled Murrelets at individual stations varied greatly among surveys and across all time scales (days, months, years). As stations are the experimental units or subjects, this variation is within-subject variation. Some of the factors that cause this type of unwanted variability are known and can be controlled for, others are known but could not be controlled for in this study (for logistical or statistical reasons), and surely many are not known at all. I analysed and discussed the most important sources of within-subject variation in a separate chapter (3.1) and included adjustments for them in the analyses where possible and appropriate.

Another problem often encountered in ecological field data is the violation of the normal distribution assumption in variables. I tested all variables for normal distribution prior to using them statistically and either employed transformations that remedied the problem or statistics that do not have the assumption of normal distribution. Often logarithmic transformation (new variable = ln(old variable + 1)) corrected non-normal distributions in Marbled Murrelet activity measures because they were often right-skewed due to many zeros or low values and few large values. The prefix “LN” in front of a variable indicates that I used the logarithmic transformation.

Due to variation in the number of surveys conducted at each station in each year, and the fact that the station was my experimental unit, I used the mean detection rates per station in each year for hypothesis tests rather than individual surveys, to avoid pseudoreplication (see Hurlbert 1984). To combine data from the three years I calculated an Index of Relative Activity (IRA) for each station and year (Burger *et al.* 1997). First, for the seventeen stations sampled in all three years, I calculated mean detection rates separately for each station and for each year. Then I calculated the mean detection rate in the whole valley for each year. Last I divided every individual survey result by the mean detection rate of the year the survey was conducted in. The prefix “IRA” indicates that the dependent variable was calculated in this way (*e.g.*, IRADET stands for the Index of Relative Activity of all detections). Again to avoid pseudoreplication I calculated means of IRA’s for each station and year and, because IRA’s are comparable among years, calculated the mean IRA among the three years for each station.

2.3.2 Measures of Activity

The difficulty of locating Marbled Murrelet nests has led scientists to use observations of Marbled Murrelet activity as a measure of habitat preferences. Whereas most detections can only be taken as a general indication that Marbled Murrelets use the area, certain behaviours are interpreted as indicating that a bird performing them is nesting in the proximity of the point of observation. These are called “occupied” behaviours and are defined below with the other variables. The strongest indirect evidence for breeding in a stand, however, is thought to be the subcanopy behaviours, a subset of the occupied behaviours. Unfortunately, subcanopy behaviours are rarely observed and a large number of surveys with zero subcanopy detections limits the usefulness of subcanopy activity measures in analyses.

Another approach is to exclude detections that are far away and not relevant for the evaluation of habitat nesting suitability around a station. I calculated the number of detections closer than 151m and 101m to the observer.

The amount of occupied activity detected depends on the amount of open sky an observer can scan. Therefore, exceptionally large openings, such as gravel bars, bias results. Furthermore, murrelets tend to follow linear structures such as rivers, which causes another increase in detected activity not necessarily related to habitat qualities. As an attempt to compensate for differences in canopy opening sizes and for increased activity due to flight corridors I introduced a ratio between occupied detections and all visual detections. Stations with large openings or stations positioned in flight corridors will have higher visual detection rates and likely also higher occupied detection rates but they will not have a higher proportion of occupied detections out of all visual detections. Thus this proportion can be used as an indicator of a station’s relative importance as breeding habitat.

The following list gives an overview of the variables calculated as measures of activity:

- sum of detections (DET);
- sum of visual detections (VIS)
- sum of detections which were auditory and visual (AUDVIS);
- sum of auditory detections (AUD)
- sum of occupied detections (OCC) which are defined as:

  - birds seen perching, landing or attempting to land on branches;
  - birds calling from a stationary location (at least 3 successive calls);
  - birds flying below, through, into or out of the forest canopy;
  - birds flying in small or large radius circles above the canopy (Ralph *et al.* 1994, Paton 1995).
- sum of subcanopy detections (SUBCAN) which include any observation of birds below canopy level;
- sum of detections closer than 151m (DET150) which is a subset of DET;
- sum of detections closer than 101m (DET100) which is a subset of DET;
- ratio between number of occupied detections and all visual detections (CO = OCC / (VIS + AUDVIS))

2.3.3 Vegetation Characteristics

The structures Marbled Murrelets need for nesting are fairly well known (*e.g.*, Nelson 1997). However, these structures are often not easy to assess and impossible to map on a large scale. Therefore, Marbled Murrelet researchers have attempted to find vegetation measures that are easy to obtain, easy to map, or that are already mapped. Rough forest measurements (*e.g.*, mean DBH, mean tree height, tree density, and canopy closure), species composition, and vegetation units are often used in conjunction with Marbled Murrelet-specific measures (*e.g.*, density of potential nesting platforms and epiphyte cover).

For analyses, I calculated the following variables for each vegetation plot:

- average DBH (DBHMEAN) in cm;
- average tree height (HTMEAN) in m;
- number of trees > 10 cm DBH per hectare (DENSTEM);
- number of trees > 10 cm DBH per hectare for each of the following tree species: amabilis fir (DENAF), western hemlock (DENWH), Sitka spruce (DENSS), mountain hemlock (DENMH), western redcedar (DENRC) and yellow cedar (DENYC);
- number of potential nest platforms per hectare (POPLAHA);
- number of realistic nest platforms per hectare (REPLAHA);

- mean index of epiphyte cover (EPIMEAN) = sum of epiphyte cover ratings / number of trees in the plot;
- mean index of epiphyte cover thickness (EPIMEAN) = sum of epiphyte cover thickness ratings / number of trees in the plot;
- number of trees > 80 cm DBH per hectare (DENLARGE);
- number of trees > 80 cm DBH per hectare for Sitka spruce (DENLSS), amabilis fir (DENLAF) and western redcedar (DENLRC).

If stations had more than one vegetation plot I combined them by treating them as if they had been one 30 x 60 m vegetation plot.

In addition to these variables often used in Marbled Murrelet research, I introduced the following vegetation-related variables for data analysis:

- number of trees per ha with >3 potential nesting platforms (DENTRPL4);
- timbervolume (TIMBVOL) in m^3/ha as average of all timbervolumes occurring in the polygons touched by a 200m diameter circle around the station on the forest cover map by MacMillan Bloedel Limited (1998);
- standard deviation of tree height (SDHT) as a measure of a height-wise well-structured forest with several canopy layers;
- standard deviation of DBH (SDDBH) as a measure of a stage-wise well-structured forest with large trees;
- standard deviation of DBH (SDDBH) and standard deviation of tree height (SDHT) combined by a Principal Component Analysis as a measure of well-structured old-growth forest with large trees (OLDIND);
- standard deviation of DBH (SDDBH), standard deviation of tree height (SDHT), mean tree height (HTMEAN), and mean DBH (DBHMEAN) combined by a Principal Component Analysis as a measure for well structured old-growth forest with an emphasis on the absolute size of trees (OLDIND2);
- three Principal Component Analysis factors (VEG1, VEG2, and VEG3) based on the variables: ALTITUDE, DBHMEAN, HTMEAN, DENMH, DENYC, DENSS, EPIMEAN, POPLAHA, SDHT, SDDBH, OLDIND, OLDIND2, TIMBVOL.

The quantity of possible variables involved in determining suitability of Marbled Murrelet habitat and the intercorrelation among these variables makes a factor reduction a useful descriptive analysis. I included all appropriate vegetation-related and other habitat variables in a Principal Component Analysis (PCA), to find out whether the resulting factors could help to describe the keys to good Marbled Murrelet habitat. Furthermore, these factors are a good starting point for a cluster analysis (Bortz 1993).

An approach encouraged by the Ministry of Environment is to associate habitat requirements of wildlife species with site series. Clement (1995) mapped vegetation units based on site series in the Ursus. Each station was associated with a primary vegetation type according to Clement (1995) (MAPVEG). In addition, I derived site series from my own vegetation plots (SITESER). I tested MAPVEG and SITESER against LNIRAOCC, LNIRACO, EPIMEAN, POPLAHA, DENTRPL4, and SDHT in ANOVA's. However, the number of different site series occurring at our stations was high so that sample sizes were often too low for meaningful statistical analyses of differences among individual site series.

As an attempt to reduce the number of different vegetation groups, I grouped the site series into four productivity groups (Table 4) according to Green and Klinka (1994). I then tested the means of Marbled Murrelet occupied activity rates and of several habitat variables (LNIRAOCC, LNIRACO, EPIMEAN, POPLAHA, DENTRPL4, and SDHT) with groups as a fixed-effort factor in an ANOVA and added a multiple comparison (Tukey).

In addition to grouping stations by their site series I also used a cluster analysis to form groups. I clustered the stations into four groups using Ward's method (Bortz 1993) on the three variables VEG1, VEG2, and VEG3. The measure of similarity was Euclidean distance.

I chose a level of dissimilarity where four groups were formed because it resulted in relatively equal sized groups. Means of two measures of activity and six habitat variables were tested for differences among the groups with an ANOVA and a Tukey multiple comparison. The results were not meant for interpretation as an independent statistical test because the variables included in the PCA were chosen under consideration of earlier correlation tests. Therefore, it is not surprising that the groups resulting from the cluster analysis somewhat reflected Marbled Murrelet activity. However, the tests were helpful for interpretation of the groups.

Table 4: Productivity groups for site series according to Green and Klinka (1994).

Site Series	Productivity Group
CWHvm1-01	I
CWHvm1-03	III
CWHvm1-04	II
CWHvm1-06	II
CWHvm1-07	I
CWHvm1-09	I
CWHvm2-01	II
CWHvm2-03	III
CWHvm2-05	II
CWHvm2-06	II
CWHvm2-08	II
CWHvm2-09	IV
CWHvm2-10	IV
CWHvm2-11	III
CWHmm1-01	IV
CWHmm1-04	IV

2.3.4 Other Station Characteristics

Besides their vegetation cover, stations had other physical characteristics worth considering for Marbled Murrelet suitability: altitude, distance to the next stream, distance to the ocean, slope, aspect, and location in the valley. Their description and codes are in chapters 2.2.1 and 2.2.3 and their analysis is included in chapter 2.3.5.

2.3.5 Correlation Analyses for Habitat Requirements of Marbled Murrelets

As a general approach, I correlated vegetation and physical characteristics of the survey stations with several different measures of Marbled Murrelet activity. To test for correlations among variables I used the following methods:

- Pearson correlation coefficients (with uncorrected probabilities of each correlation coefficient) for normally distributed variables where correlations were hypothesised for biological reasons (POPLAHA, REPLAHA, DENTRPL4, EPIMEAN, SDHT, OLDIND, OLDIND2, LNIRADET, LNIRAOCC, LNIRA100, LNIRA150, LNIRACO);
- Spearman correlation coefficients for variables that significantly deviated from normal distribution but that were hypothesised (ALTITUDE, CANCLSITE, LNIRASUB);

- Pearson correlations with Bonferroni adjustments for the probabilities associated with each correlation coefficient (Bortz 1993) for pairs of variables for that I had no direct biological or other reason for expecting a correlation (random scanning for correlations);
- Least squares deviation (LS) and least absolute deviation (LAD) regressions (Cade and Richards 1996) with the 50th and the 90th quantile regression line (Terrell *et al.* 1996);
- Multiple linear regressions with inclusion of variables based on biological prediction, management considerations, and avoidance of intercorrelation problems.
- ANOVA's to test against H_0: slope of the regression line is zero.

The least absolute deviation (LAD) regression models need further explanation. They are distribution-free statistics, which have higher power than ordinary least squares deviation (LS) regressions when assumptions such as normal distribution and homoscedasticity are violated (Cade and Richards 1996). Furthermore, they are more resistant to the influences of outlying values.

In ecological field data on habitat suitability, the assumption of homoscedasticity in regular regression analyses (LS) is often violated. Typically, low values of an important habitat variable limit the population size of an organism under consideration, but high values do not necessarily correspond with high abundances of the organism because other limiting factors exist. The result is a wedge-shaped pattern with variances of the dependent variable increasing with the independent factor (Terrell *et al.* 1996). An ordinary LS regression models the central tendency of the wedge and not its upper limit. This upper limit and not the central tendency corresponds to the limiting effect of the factor under consideration.

Terrell *et al.* (1996) suggested to use the 90th regression quantile in an LAD model to estimate upper limits of a measure for relative abundance caused by the factor under consideration. The 50th quantile is the median, the 90th quantile is a plane that splits the frequency distribution into unequal parts containing 90% and 10% of the observations. Furthermore, they developed a test to identify limiting factors exhibiting wedge-shaped patterns, but I chose the variables for inclusion by screening correlations, visually inspecting scatter plots, and including biological considerations.

I also created a large correlation matrix, which includes all variables (Appendix II, Tables 1-6). Although I highlighted the correlations with $P < 0.05$ and $P < 0.01$ for orientation, these results are not meant to be interpreted as hypothesis tests. I used this matrix to point out dependencies among variables and other effects but not to randomly find new, unsuspected “significant” correlations. I usually considered correlations with $R > 0.4$ as interesting.

The station UFFN was excluded from any correlation analyses because of its situation on extended rocky outcrops at the entrance of Thunderbird Valley (a side valley of the Ursus). It was an excellent vantage point overlooking both the Ursus and the Thunderbird drainages, at which many occupied detections were observed which were not at all related to the vegetation adjacent to the survey station. I also excluded USC, which was located at the entrance of the Ursus Valley in a clearcut dating back to the 1950’s.

2.3.6 Site Specific Analysis (SSA)

The positioning of vegetation plots is likely a source of bias. The regular vegetation plots were usually close to the survey stations. The stations were chosen according to the criteria outlined in chapter 2.2.1, which were often related to the location’s adequacy as a point of observation, not representation of vegetation. One plot cannot be a sufficient random sample to characterise a highly diverse habitat. However, trying to situate vegetation plots so that they will be representative of the whole area covered by a survey or trying to find the „best“ Marbled Murrelet habitat in that area surely is subjective and a source of bias.

In an attempt to distribute vegetation plots in a way that would be more likely to reflect the best vegetation in the area for Marbled Murrelets, I developed a method of inferring the locations of centres of Marbled Murrelet activity relative to the survey stations, using the data from previously conducted surveys. The stations I chose were stations a) with a high number of recorded detections and b) that I visited in 1997.

I made a score sheet (see Table 5 for an example), which had a cell for every combination of the eight directions (N, NE, . . ., NW) and the six distance categories (<100m, 100-150m, . . . , >300m). Every detection in which the bird or birds were not seen over more than 90^0 or three directions (*e.g.*, NW-NE) received one score in each direction at which the bird(s) were observed, at the distance noted with the detection. All detections with indications of circling behaviour were omitted.

A problem was that a record such as “first detection direction: N; last detection direction: W” could have meant that the bird flew from N to W via NW, or, in a three quarter circle, via S. However, auditory detections covering three-quarters of a circle or more are rare and would probably have been noted as such, and visual detections would have qualified as circling and, therefore, would have been excluded.

Table 5: Site Specific Analysis score sheet for the station UDO. The SSA vegetation plot was done at an angle of 170^0 and a distance of 190m. Each detection that qualified as described in the methods section, has one score in 1-3 of the table fields. The highest score is bolded.

Distance/ Direction	100m	150m	200m	250m	300m	>300m
N	𝍸 III	𝍸 I	II			
NE	II	𝍸 I	III			
E	I	IIII	𝍸	I		
SE	I	𝍸 IIII	𝍸 𝍸 IIII		𝍸 II	
S	𝍸	𝍸 𝍸 𝍸 II	**𝍸 𝍸 𝍸 𝍸**		𝍸 𝍸 II	
SW	II	𝍸 𝍸	𝍸 I	III	𝍸	
W	𝍸 𝍸	𝍸	𝍸 I	I	III	I
NW	IIII	IIII	II	I		

In general, I selected the direction and distance with the highest score to identify centres of activity and with them the best available habitat close to the station. However, I allowed minor deviations from the highest score if the next highest scores were not distributed symmetrically around the highest score.

I did 12 vegetation plots, located at the points identified with the described method, at 11 existing stations (see Table 22 in chapter 3.2.5). The plots were done with the same method as regular plots except that I did not complete a detailed ecosystem data sheet (site series). One of the 12 plots was excluded from analyses because it was in a bog.

I compared regressions of the independent variable LNIRAOCC vs. the major habitat characteristics (HTMEAN, DBHMEAN, POPLAHA, REPLAHA, SDHT, SDDBH, OLDIND, OLDIND2, CANCLVEG, DENSTEM, DENLARGE, EPIMEAN, EPITMEAN) between regular vegetation plots and my site specific plots. Furthermore, I compared the most important habitat characteristics between SSA and regular vegetation plots with paired t-tests.

2.3.7 Sources of Within-Subject Variation

2.3.7.1 Seasonal trends

The inland activity of Marbled Murrelet varies with season (Burger *et al.* 1995, 1997; O'Donnell *et al.* 1995). To illustrate this effect I divided the IRADET of every survey by the highest

IRADET of the station the survey was done at (IRADET/maxIRADET). This ratio makes activity levels comparable among stations as it always ranges between zero and one and is not dependent on the absolute activity levels measured at a station. Then, I plotted the ratios (IRADET/maxIRADET) against every day of the field season (starting with the first day of the core period, May 15th) and fitted a second-degree polynomial trendline through the data points. On days with more than one survey, the relative detection levels were averaged.

In addition, I calculated the same ratio as discussed above for the period between first and last detection (activity period/activity period max) and averaged it for every day of the core period. Then I plotted a graph with day of core period vs. index of relative survey length and fitted a second-degree polynomial trendline.

2.3.7.2 Weather

Preliminary results, field observations and other studies (Burger *et al.* 1995, 1997; Kuletz *et al.* 1995a, 1995b) indicate that Marbled Murrelets are more active during what we perceive as “bad” weather. To avoid losing power in my analyses and because they seem to be enough to describe the effect , I chose only two categories to describe the weather:

- Clear or partly cloudy (CLEAR), defined as less than 95% cloud cover in the beginning and/or the end of the survey, with no precipitation;
- Heavily cloudy and/or precipitation (CLOUDY), defined as more than 95% cloud cover at both the start and the end of the survey and/or any form of precipitation as defined in chapter 2.2.2.

To compare detection rates among different types of weather I had to eliminate as much other variation as possible. Therefore, I chose pairs of surveys, with one survey in each weather type, which were done in a given year at the same station, ignoring seasonal effects. If there was more than one survey per weather type, station and year, I used the average detections among them. In other words I chose a subset of all surveys that included all pairs of surveys done at the same station in one year and both weather types. I then tested the number of detections (DET, OCC) in the surveys done in the different weather types with paired t-tests.

Although other ways of correcting for weather effects would be preferable, given a certain study design, I employed a correction factor to compensate for weather effects. I derived the correction factor from the analysis described above. I then divided all occupied detections of CLOUDY weather surveys by the factor and calculated the ratio occupied to all visual detections in the same way as the variable CO. Finally I calculated the new variable for weather corrected occupied activity (LNIRACWO) for all stations and years in the same manner as LNIRAOCC..

2.3.7.3 Canopy Closure

The amount of visible sky has an influence on the ability of the observer to detect Marbled Murrelets. I tested for the influence of the amount of open sky at a given station on the dependent variables DET, OCC, and SUBCAN. To avoid the influence of other variables paired surveys were conducted on nine mornings: one station was located in an open spot with a large opening size (*e.g.*, on a gravel bar) and the other station was in the adjacent forest with the typical opening size for forest situations (*e.g.*, canopy opening caused by a fallen tree). Pairs of stations were located in nine different areas. I tested the results of the paired surveys with a paired t-test.

I did not attempt to use a correction factor for canopy closure effects because the ratio of occupied to all visual detections, introduced in chapter 2.3.2, is more appropriate.

2.3.7.4 Years

Burger *et al.* (1997b) found significant differences in numbers of Marbled Murrelet entering the Ursus in 1995 and 96 using radar counts. To examine inter-annual differences at stations using audio-visual surveys, I tested the hypothesis that mean detection rates per station (DET, LNOCC, LNSUBCAN) were equal among the three years of research with a repeated measures ANOVA. Differences between individual years were analysed with paired t-tests and a Bonferroni correction. Only the 17 stations that were sampled in all three years were included in this analysis. To test for differences in mean activity levels of the whole watershed among years, I used a regular ANOVA with a multiple comparison (Tukey) for differences between individual years.

2.3.7.5 Direction Faced by the Observer

During surveys, when I moved or raised my head higher, I often suspected that I had missed detections behind my head or had thought that detections were in front of me that were really behind me. Therefore, I tested the mean direction of detections (expressed as an angle) of surveys against the hypotheses that the mean direction equals the direction faced by the observer. This was done with a one-sample test for the mean angle (Zar 1996). The direction faced by the observer was not always recorded; therefore, the initial sample size was only 41 surveys.

To obtain the mean angle I only used detections that had less than 91^0 between the first and last directions at which the bird(s) were seen, to avoid including circling behaviours or other situations where the direction of the detection was not quite clear.

For each survey, I calculated the mean angle of all detections by taking the average of all individual detections' vectors using trigonometry according to Zar (1996). Then I tested it against H_0: the detections are randomly dispersed around the circle using Rayleigh's test. Only the 35 surveys that had a significant mean angle were included in further tests.

Lastly, I tested the distribution of mean angles between the 180^0 the observer had been facing and the other half of the circle, away from the observer. If mean angles were distributed randomly, one would expect their distribution to be 50:50. I used a Chi-square test to test the actual distribution against the hypothesised 50:50 distribution.

3. Results

3.1 Sources of Within-Subject Variation

3.1.1 Inter-annual Variation

The amount of Marbled Murrelet activity varied widely among years, at both the watershed and station level (Figure 4). A one-way ANOVA yielded significant differences in mean detection levels (DET) in the watershed among years ($P = 0.013$, $n = 51$ station means). Specifically, the multiple comparison (Tukey) showed a significant difference between 1995 and 1996 ($P = 0.012$, $n = 17$ pairs of station means). A repeated measures ANOVA showed significant differences in mean detection levels of stations among years for all tested dependent variables ($P = 0.0068$, $P = 0.024$, $P = 0.037$ for DET, LNOCC, LNSUB, respectively; $n = 17$ triplets of station means). Two-tailed Paired t-tests (with Bonferroni corrections) between pairs of years showed significant differences in mean numbers of detections (DET, $P = 0.03$, $n = 17$ pairs of station means) and occupied detections (LNOCC, $P < 0.05$, $n = 17$ pairs of station means) between 1995 and 1996.

The number of repetitions of samples (in this case surveys) is important for the precision of a measurement (Hurlbert 1984). The average number of surveys (± *SD*) done at each station was 2.16 ± 1.49, 1.49 ± 0.70, and 2.57 ± 0.85 in 1995, 96, and 97, respectively. It varied significantly among years (ANOVA: $P = 0.0002$, $n = 101$ station means). Two-tailed T-tests with Bonferroni corrections between pairs of years revealed a significant difference in average number of repetitions between 1996 and 1997 ($P = 5.5\text{E-}07$, $n = 70$ station means). Furthermore, correlations done on variables from each year separately showed that 1996 had fewer significant correlations and generally seemed to be quite different from the other years (see Appendix II, Tables 1-6).

3.1.2 Season

Although Marbled Murrelet activity can be observed over land all year (O'Donnell *et al.* 1995) it shows a strong peak during the bird's breeding season. Figure 5 illustrates how Marbled Murrelet activity slowly increased in the beginning of the core period (May 15th to July 23rd) and slowed down towards the end of the breeding season in the Ursus Valley. The same trend is seen in the average period between first and last detection (activity period) per day of the core period (Figure 5).

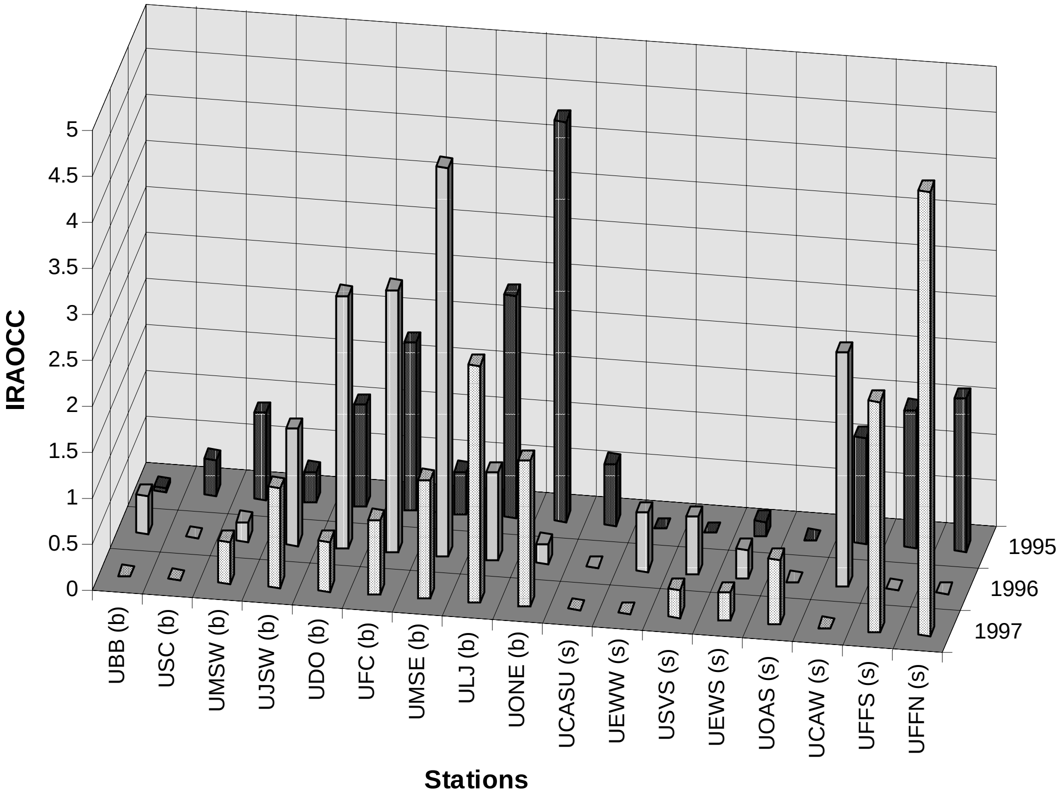

Figure 4: Comparison of mean relative occupied detection rates (IRAOCC) at 17 stations over the three years of the study (1995-97). The stations are separated by valley location ((b) = valley bottom, (s) = slope) and are sorted by increasing average over the three years. Extreme inter-annual differences occur at stations UONE and UFFN. The year 1996 shows the largest differences from other years.

3.1.3 Weather

Marbled Murrelet activity differed significantly between mornings with CLEAR and CLOUDY weather types (two-tailed paired t-test: $P < 0.001$ and $P < 0.01$ for DET and OCC, respectively, $n = 32$ pairs of surveys). On average there were three times as many total detections and four times as many occupied detections on CLOUDY days than on CLEAR days (Figure 6).

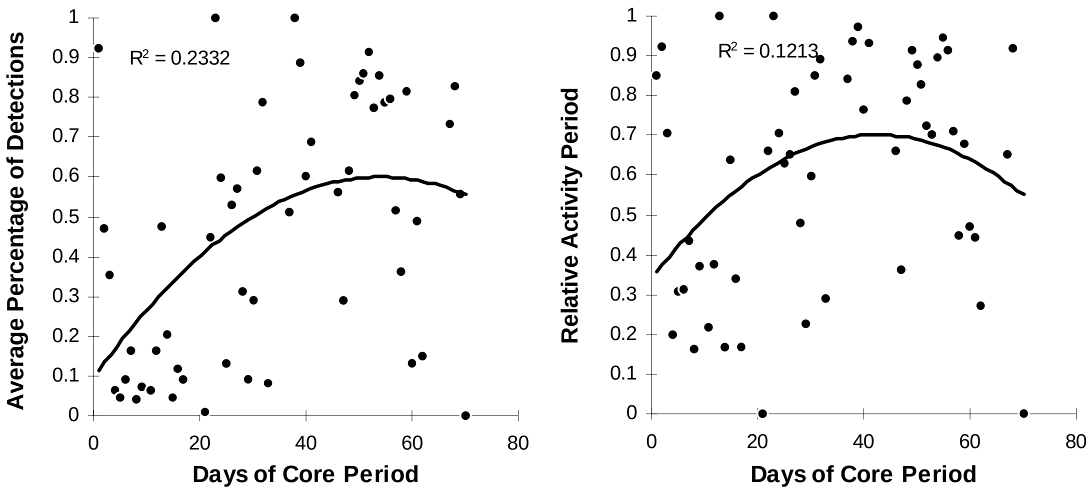

Figure 5: Relationship of Marbled Murrelet activity (IRADETS) and survey length (min) to the progression of the core sampling period (May 15th to July 23rd). Activity measures are expressed relative to the highest activity measured at a given station (IRADET/IRADETmax) and are averaged for every day with more than one survey. The period between first and last detection (activity period) is expressed relative to the longest period at a given station and is averaged for every day with more than one survey. The solid trendlines are second-degree polynomial regressions, *n* = 55 daily means.

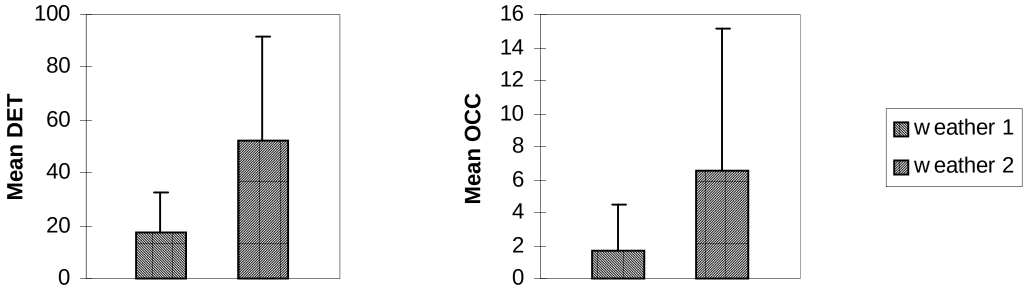

Figure 6: Mean total detections (DET) and mean occupied detections (OCC) with standard deviation bars in two different weather types (weather 1 = CLEAR, weather 2 = CLOUDY). The differences between the two categories are significant in both graphs (two-tailed paired t-tests: *P* < 0.001 and *P* < 0.01 for DET and OCC, respectively, *n* = 32 pairs of surveys).

3.1.4 Canopy Opening

The forest comparison surveys showed that total detections and occupied detections varied significantly with canopy opening (two-tailed paired t-test: $P < 0.05$, $n = 9$ pairs of surveys). While the average number of detections (DET) was "only" double as high in stream channels than in adjacent forest, the average rate of occupied detections (OCC) was almost thirteen times as high in the more open stream channel sites. The ratio correction introduced to occupied activity

(CO) accounted for parts of the effects of canopy opening on detected activity: the ratio was three times higher at open sites than at forest sites (*P* < 0.001, Figure 7).

A comparison of the mean detection rates among the four opening size classes employing all available data was not significant (ANOVA: *P* > 0.05, *n* = 51 station means). However, after the introduction of TIMBVOL as a covariate the ANCOVA was powerful enough to show significant differences among the four opening size classes (*P* < 0.05, *n* = 51 station means). Figure 7 shows that an opening size of 0-25% has a disproportionately high negative effect on detection rates.

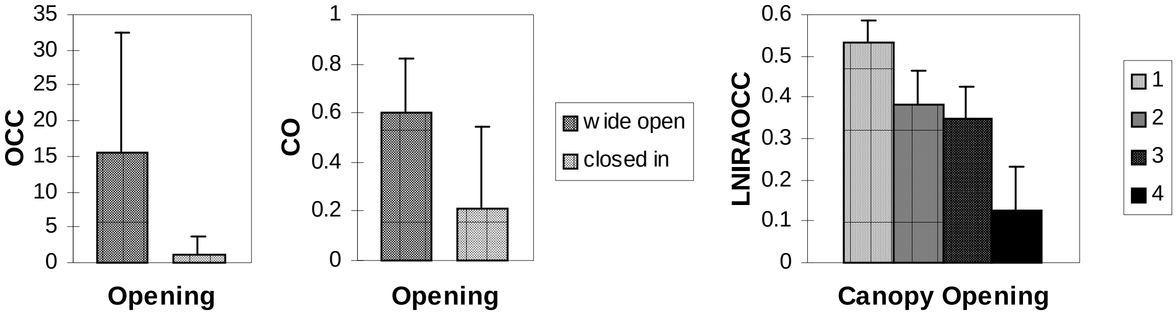

Figure 7: The left two graphs compare occupied (OCC) and corrected occupied (CO) activity at paired survey stations. One station of each pair was in a wide-open spot (*e.g.*, gravel bar), the other at a small opening in the adjacent forest. Error bars show standard deviation, *n* = 9 pairs of surveys. The graph on the right side shows adjusted means of occupied activity (LNIRAOCC), calculated with TIMBVOL as a covariate, at the four categories of canopy opening (1 = 75-100%, 2 = 50-75%, 3 = 25-50%, 4 = 0-25% of the sky was visible, *n* = 22, 12, 11, 6 station means, respectively). Error bars show standard errors.

3.1.5 Direction Faced by Observer

There is strong evidence that the direction faced by the observer influenced the recorded detections. Out of 41 surveys included in the test, 33 had a significant mean angle (*P* < 0.05, *n* = 3 to 134; see chapter 2.3.7.5 for calculation of mean angle and the statistical test used). Of these 33 mean angles 18 were not significantly different from the direction faced (one-sample test for the mean angle: *P* > 0.05, *n* = 3 to 134) and 15 were significantly different (one-sample test for the mean angle: *P* > 0.05, *n* = 4 to 67). However, out of the 15 mean angles that were significantly different from the direction faced by the observer, only 3 deviated more than 90^0 from the direction faced. A chi-square test on this result showed that the probability of 31 mean angles occurring in the half of the circle that the observer was facing and only 2 in the other half, compared to an expected random result of 16.5 mean angles falling in each half, was *P* = 4.46E-07, *n* = 33.

3.2 Habitat Requirements

3.2.1 Site Series and Other Vegetation Units

Marbled Murrelet activity and some of the vegetation structures relevant to Marbled Murrelets varied significantly among vegetation units. However, the numbers of stations per vegetation unit were low (Table 6 and Table 7), so that comparisons between individual units were not feasible.

ANOVA's performed on two measures of occupied activity of Marbled Murrelets (LNIRAOCC and LNIRACO) showed significant differences among site series (SITESER, Table 6) ($P = 0.013$ and $P = 0.017$, respectively; $n = 51$ station means). The categories of MAPVEG (Table 7) showed similar differences in Marbled Murrelet activity ($P = 0.002$ and $P = 0.032$ for LNIRAOCC and LNIRACO, respectively; $n = 51$ station means).

Furthermore, mean epiphyte cover, one of four important habitat characteristics, varied significantly among site series (EPIMEAN, $P = 0.00041$; POPLAHA, $P = 0.49$; SDHT $P = 0.16$; DENTRPL4 $P = 0.43$; $n = 51$ station means) (Table 6) and MAPVEG (EPIMEAN, $P = 0.0014$; POPLAHA, $P = 0.44$; SDHT $P = 0.30$; DENTRPL4 $P = 0.43$; $n = 51$ station means) (Table 7).

Differences in means of Marbled Murrelet occupied activity and in means of selected Marbled Murrelet-relevant habitat structures existed among the site series productivity groups (Table 8). These differences were highly significant for the two measures of occupied activity (ANOVA: $P < 0.0001$ and $P < 0.001$ for LNIRAOCC and LNIRACO, respectively; $n = 51$ station means) and for two out of four tested habitat characteristics: mean standard deviation of tree height and mean epiphyte cover (ANOVA: $P = 0.003$ and $P = 0.0001$ for SDHT and EPIMEAN, respectively; $n = 51$ station means). Multiple comparisons showed that the high significance of the tests was mainly due to the difference between the highest productivity class (class I) and all other classes (class II, III, and IV), which were not significantly different from each other (Table 8). Both measures of platform abundance, platforms per ha and density of trees with more than 3 platforms, were not significantly different among the productivity classes (ANOVA: $P > 0.05$ for POPLAHA and DENTRPL4; $n = 51$ station means).

Table 6: Means ± *SD* of two measures of Marbled Murrelet activity and four habitat characteristics at stations grouped by site series, as recorded in our vegetation plots (SITESER). *P* is the probability derived from ANOVA's on the dependent variables, with the grouping variable SITESER. *N* is the number of stations in each site series.

SITESER	*N*	LNIRAOCC	LNIRACO	POPLAHA	SDHT	EPIMEAN	DENTRPL4
CWHvm1-01	9	0.68 ± 0.45	0.65 ± 0.30	486.4 ± 359.2	15.01 ± 5.28	2.13 ± 0.42	39.51 ± 19.33
CWHvm1-03	4	0.11 ± 0.09	0.25 ± 0.26	283.3 ± 129.1	12.24 ± 2.49	1.59 ± 0.33	27.78 ± 14.34
CWHvm1-04	2	0.85 ± 0.00	0.72 ± 0.04	555.6 ± 518.5	13.43 ± 4.07	2.50 ± 0.47	44.44 ± 31.43
CWHvm1-06	5	0.31 ± 0.30	0.49 ± 0.45	375.6 ± 201.8	15.43 ± 4.84	2.18 ± 0.69	33.33 ± 11.11
CWHvm1-07	5	0.94 ± 0.43	0.85 ± 0.28	271.1 ± 202.1	17.14 ± 3.39	2.94 ± 0.37	20.00 ± 18.26
CWHvm1-09	8	0.83 ± 0.41	0.79 ± 0.24	399.5 ± 375.8	12.85 ± 4.89	3.01 ± 0.82	41.67 ± 31.29
CWHvm2-01	4	0.09 ± 0.14	0.14 ± 0.20	205.6 ± 179.7	11.42 ± 1.18	1.46 ± 0.42	16.67 ± 21.28
CWHvm2-03	2	0.24 ± 0.34	0.34 ± 0.48	294.4 ± 23.6	9.29 ± 1.33	1.79 ± 0.34	27.78 ± 7.86
CWHvm2-05	1	0.00	0.00	188.9	15.02	1.83	22.22
CWHvm2-06	1	0.40	0.89	933.3	12.25	1.87	33.33
CWHvm2-08	1	0.20	0.42	211.1	16.98	1.34	33.33
CWHvm2-09	5	0.26 ± 0.50	0.44 ± 0.44	195.6 ± 214.0	8.16 ± 2.68	1.66 ± 0.48	20.00 ± 18.26
CWHvm2-10	1	0.00	0.00	33.3	11.13	1.01	0.00
CWHvm2-11	1	0.07	0.25	144.4	8.50	0.82	11.11
Mhmm1-01	1	0.00	0.00	55.6	7.59	2.42	0.00
Mhmm1-04	1	0.00	0.00	11.1	10.74	1.91	0.00
P (ANOVA)	51	0.013	0.017	0.44	0.30	0.0014	0.43

Table 7: Means ± *SD* of two measures of Marbled Murrelet activity and four habitat characteristics at stations grouped by vegetation units mapped out by Clement (1995) (MAPVEG). *P* is the probability derived from ANOVA's on the dependent variables, with the grouping variable MAPVEG. *N* is the number of stations in each vegetation unit.

MAPVEG	*N*	LNIRAOCC	LNIRACO	POPLAHA	SDHT	EPIMEAN	DENTRPL4
AB	11	0.67 ± 0.42	0.64 ± 0.32	412.6 ± 343.6	13.53 ± 4.18	2.25 ± 0.58	35.35 ± 20.98
AS	2	0.45 ± 0.35	0.76 ± 0.02	338.9 ± 306.4	16.77 ± 7.63	2.52 ± 0.17	27.78 ± 23.57
CD	3	0.79 ± 0.49	0.74 ± 0.08	455.6 ± 288.9	13.83 ± 2.53	3.36 ± 0.43	40.74 ± 27.96
HD	1	0.19	0.32	511.1	11.56	1.91	44.44
HS	18	0.16 ± 0.28	0.32 ± 0.38	273.5 ± 226.0	11.17 ± 3.07	1.65 ± 0.57	23.46 ± 14.71
LC	1	0.00	0.00	33.3	11.13	1.01	0.00
MB	1	0.00	0.00	55.6	7.59	2.42	0.00
MM	1	0.00	0.00	11.1	10.74	1.91	0.00
RS	8	0.88 ± 0.44	0.76 ± 0.36	507.0 ± 363.4	16.23 ± 5.20	2.51 ± 0.55	37.50 ± 31.95
SF	1	0.20	0.42	211.1	16.98	1.34	33.33
SS	4	0.77 ± 0.44	0.71 ± 0.23	158.7 ± 183.8	12.77 ± 7.27	2.71 ± 1.09	27.78 ± 19.25
P (ANOVA)	51	0.002	0.032	0.44	0.30	0.0014	0.43

One way to show trends among vegetation units is to compare the percentage of stations per vegetation unit that showed occupied behaviour during at least one survey (Table 9 and Table 10). It is very important to note that none of the stations lacking signs of occupied behaviour was sampled adequately (several times a year in at least two consecutive years) to preclude the use of the area as breeding habitat by Marbled Murrelets, according to PSG protocol (Ralph *et al.* 1994) and the RIC standards (1995). Therefore, these results are not to be used for management decisions but only as guidelines for future research.

Table 8: Means ± *SD* of two measures of Marbled Murrelet activity and four habitat characteristics at stations grouped by productivity. *P* is the probability derived from ANOVA's on the dependent variables, with the grouping variable VALLOC. *N* is the number of stations in a group. Different letters behind means indicate significant differences between groups, tested by multiple comparisons (Tukey).

Productivity Group	*N*	LNIRAOCC	LNIRACO	POPLAHA	SDHT	EPIMEAN	DENTRPL4
I	22	0.79 ± 0.43a	0.75 ± 0.27a	405.9 ± 333.3a	14.71 ± 4.85a	2.634 ± 0.708a	35.86 ± 24.71a
II	14	0.30 ± 0.32b	0.41 ± 0.38b	367.5 ± 288.4a	13.85 ± 3.56a	1.913 ± 0.610b	29.37 ± 17.76ab
III	7	0.14 ± 0.17b	0.28 ± 0.27b	266.7 ± 106.6a	10.86 ± 2.53ab	1.540 ± 0.430b	25.40 ± 12.36ab
IV	8	0.16 ± 0.40b	0.27 ± 0.41b	134.7 ± 182.6a	8.78 ± 2.43b	1.702 ± 0.531b	12.50 ± 17.25b
P (ANOVA)	51	2.56E-05	6.41E-04	0.12	3.26E-03	1.15E-04	0.063

Table 9: Number and percent of stations within each biogeoclimatic variant and site series that showed occupied behaviour by Marbled Murrelets (measured by the variable OCC)[1]. *N* refers to the total number of surveys conducted in each vegetation unit.

Variant	Site-series	No. of stations with OCC > 0	Total No. of stations	*N*	Percent of stations with OCC > 0
CWHvm1	CWHvm1-04	3	3	7	100%
	CWHvm1-07	5	5	30	100%
	CWHvm1-09	8	8	52	100%
	CWHvm1-01	9	10	33	90%
	CWHvm1-06	5	7	18	71%
	CWHvm1-03	3	7	11	43%
Subtotal		33	40	151	83%
CWHvm2	CWHvm2-06	1	1	1	100%
	CWHvm2-11	1	1	3	100%
	CWHvm2-09	3	5	15	60%
	CWHvm2-01	2	4	11	50%
	CWHvm2-08	1	2	5	50%
	CWHvm2-03	1	3	5	33%
	CWHvm2-05	0	1	2	0%
	CWHvm2-10	0	2	5	0%
Subtotal		9	19	47	47%
MHmm1	Mhmm1-01	0	1	1	0%
	Mhmm1-04	0	1	2	0%
Subtotal		0	2	3	0%
	No data	3	8	8	37%
Total		45	69	209	65%

[1] Of the stations at which occupied detections have not yet been observed, none has been sampled sufficiently to preclude the use of the area by Marbled Murrelets, according to PSG (Ralph *et al.* 1994) and RIC standards (1995). 17 of the 24 stations without occupied detections were sampled only once.

Out of 69 stations sampled in the Ursus in the core period, 45 (65%) showed signs of occupied behaviour. Out of these 45 stations 33 were in the vm1 zone (83% of 40 vm1 stations), 9 were in vm2 (47% of 19) and 0 were in mm1 (0% of 2). Out of the 24 stations at which no occupied behaviour was observed, 17 had been sampled only once and 22 in one year only. Only two of the stations had been sampled over two years; however, in both cases at least one of those years had been sampled just once.

3.2.2 Location in the Valley

Roughly categorising each stations' locations as either valley bottom (B, which includes the higher elevation floodplains of side valleys), lower slope (L), or upper slopes and ridges (H), has given further support for the relative importance of low and medium elevation habitat for Marbled Murrelets. ANOVA's performed on LNIRAOCC, LNIRACO, SDHT, EPIMEAN, and DENTRPL4, with VALLOC as grouping variable, were all significant (Table 11). Only the density of potential platforms (POPLAHA) did not vary significantly. Multiple comparisons (Tukey) showed that the corrected measure of occupied detections (LNIRACO) placed the lower slopes in an intermediate position whereas the uncorrected measure (LNIRAOCC) grouped them with the upper slopes (Table 11).

Table 10: Number and percent of stations within each vegetation unit as mapped by Clement (1995; MAPVEG), that showed occupied behaviour by Marbled Murrelets (measured by the variable OCC) [1]. *N* refers to the total number of surveys conducted in each vegetation unit.

MAPVEG	No. of stations with OCC > 0	Total No. of stations	*N*	Percent of stations with OCC > 0
AS	3	3	11	100%
CD	3	3	12	100%
RS	9	10	25	90%
SS	5	6	41	83%
AB	12	16	52	75%
HD	2	3	6	67%
SF	1	2	5	50%
HS	11	23	49	48%
LC	0	2	5	0%
MB	0	1	1	0%
MM	0	1	2	0%

[1] Of the stations at which occupied detections have not yet been observed, none has been sampled sufficiently to preclude the use of the area by Marbled Murrelets, according to PSG (Ralph *et al.* 1994) and RIC standards (1995). 17 of the 24 stations without occupied detections were sampled only once.

Table 11: Means ± *SD* of two measures of Marbled Murrelet activity and four habitat characteristics at stations grouped by their position in the valley (VALLOC). *P* is the probability derived from ANOVA's on the dependent variables, with the grouping variable VALLOC. *N* is the number of stations in a group. Different letters behind means indicate significant differences between groups, tested by multiple comparisons (Tukey).

VALLOC	*N*	LNIRAOCC	LNIRACO	POPLAHA	SDHT	EPIMEAN	DENTRPL4
B	21	0.762 ± 0.427a	0.733 ± 0.280a	438.4 ± 355.7a	14.34 ± 4.71a	2.67 ± 0.71a	37.57 ± 25.45a
L	10	0.302 ± 0.295b	0.452 ± 0.358ab	290.0 ± 192.7a	14.08 ± 4.13ab	1.89 ± 0.72b	27.78 ± 15.04ab
H	20	0.246 ± 0.407b	0.319 ± 0.372b	245.6 ± 220.7a	11.10 ± 3.77b	1.71 ± 0.43b	20.56 ± 16.63b
P (ANOVA)	51	0.00028	0.00094	0.088	0.042	2.5E-05	0.037

3.2.3 Principal Component and Cluster Analyses

The three factors extracted in the Principal Component Analysis (VEG1, VEG2, and VEG3) described 74.3 percent of the variation in the 13 habitat variables. Table 12 shows the relationship between the 13 habitat variables and the three factors in correlation matrices. The Varimax rotation minimises the number of variables that have a high loading on a factor and therefore simplifies the interpretation of the factors. VEG1 is dominated by size and variability in size measures of trees; VEG2 mostly negatively describes altitude and the density of species associated with higher altitudes (mountain hemlock and yellow cedar); VEG3 reflects important Marbled Murrelet structures (platforms and epiphyte densities), the density of Sitka spruce which are known to support high quantities of these structures, and timbervolume.

Table 12: Unrotated and Varimax rotated correlation matrices of the three factors VEG1, VEG2, and VEG3 and the 13 habitat variables they were extracted from in a Principal Component Analysis.

Habitat	Unrotated Matrix			Varimax Matrix		
Variable	VEG1	VEG2	VEG3	VEG1	VEG2	VEG3
ALTITUDE	-0.708	0.444	0.256	-0.186	-0.719	-0.462
DBHMEAN	0.792	0.191	0.238	0.766	0.173	0.321
HTMEAN	0.796	0.130	-0.043	0.661	0.415	0.207
DENMH	-0.715	0.175	0.491	-0.299	-0.821	-0.139
DENYC	-0.715	0.047	0.564	-0.361	-0.838	-0.006
DENSS	0.524	-0.409	0.425	0.242	0.075	0.747
EPIMEAN	0.746	-0.262	0.115	0.421	0.389	0.557
POPLAHA	0.373	-0.547	0.391	0.035	0.066	0.766
SDHT	0.758	0.252	0.017	0.724	0.309	0.139
SDDBH	0.772	0.438	0.160	0.886	0.144	0.092
OLDIND	0.866	0.390	0.100	0.911	0.256	0.130
OLDIND2	0.936	0.303	0.115	0.912	0.310	0.231
TIMBVOL	0.711	-0.446	-0.006	0.250	0.525	0.606

The cluster analysis (Figure 8), based on the three PCA factors VEG1, VEG2, and VEG3, produced four distinct groups of stations. An ANOVA on the Marbled Murrelet occupied activity variables LNIRAOCC and LNIRACO showed significant differences among group means (statistics in Table 13). The same is true for the dependent variables ALTITUDE and TIMBVOL (statistics in Table 13). Differences in means among the clustering groups were also significant for the vegetation characteristics variables POPLAHA, EPIMEAN, SDHT and DENTRPL4 (statistics in Table 13 and Table 14).

Table 13 and Table 14 show the means, *SD*'s, and multiple comparisons (Tukey) of each measure of Marbled Murrelet activity and habitat characteristic in each of the four cluster analysis groups. While group 2, which is comprised of the low elevation habitat stations with the highest rates of occupied detections and the highest density of Marbled Murrelet relevant structures, differed significantly from all other groups in all characteristics, the difference among the other groups was often not significant. Group 4 is generally comprised of stations in high elevation habitat with the lowest rates of occupied detections and Marbled Murrelet relevant structures but the differences between it and the two other groups were not significant in most cases. One explanation for this result could be that group 4 included the station UFFN, which has an excellent vantage point on a rocky outcrop overlooking parts of the main valley and of the Thunderbird side valley but has sparse vegetation not suitable for Marbled Murrelet breeding. Group 1 and group 3 were fairly alike, with group 3 having slightly but not significantly higher values in most characteristics. Interestingly, USC and UBB, both valley bottom stations in second growth, cluster with group 1, which has relatively low levels of mean occupied activity and Marbled Murrelet relevant structures.

Table 13: Means ± *SD* of two measures of occupied Marbled Murrelet activity and two habitat characteristics at station groupings outlined by the cluster analysis. *P* is the probability derived from ANOVA's on the dependent variables. *N* is the number of stations in a group. Different letters behind means indicate significant differences between groups, tested by multiple comparisons (Tukey).

Group	*N*	LNIRAOCC	LNIRACO	ALTITUDE	TIMBVOL
1	18	0.356 ± 0.435a	0.460 ± 0.335a	444 ± 266a	598.8 ± 200.1a
2	12	0.859 ± 0.259b	0.862 ± 0.221b	45 ± 156b	957.5 ± 161.7b
3	13	0.433 ± 0.491ab	0.445 ± 0.363a	366 ± 199a	700.8 ± 140.2a
4	8	0.203 ± 0.408a	0.233 ± 0.366a	720 ± 106c	492.7 ± 235.8a
P (ANOVA)	51	3.64E-03	5.75E-04	5.77E-08	2.65E-06

Rescaled Distance Cluster Combine

```
               0         5        10        15        20        25
Station  Group +---------+---------+---------+---------+---------+

  ULPS     1    -+
  UWWE     1    -+-+
  URK      1    -+ +---+
  UTOW     1    ---+   +-----+
  UMCE     1    -+-+   I     I
  UOY2     1    -+ +---+     I
  UHP3     1    ---+         +---+
  UCAW     1    -+           I   I
  UTC      1    -+-+         I   I
  UEWS     1    -+ +---------+   I
  URJS     1    -+-+             I
  USVN     1    -+ I             +-------------------+
  UEWW     1    -+-+             I                   I
  UGR      1    -+               I                   I
  UBB      1    -+-+             I                   I
  UJSE     1    -+ +---+         I                   I
  UOAS     1    ---+   +---------+                   +-----------+
  USC      1    -------+                             I           I
  UBTS     3    -+---------+                         I           I
  URC      3    -+         I                         I           I
  UNA      3    -+         I                         I           I
  UNBS     3    -+         +-------------------------+           I
  UTCW     3    -+-----+   I                                     I
  UWCJ     3    -+     I   I                                     I
  UMCW     3    -+     +---+                                     I
  USL      3    -+---+ I                                         I
  UCASU    3    -+   I I                                         I
  UHPW     3    -+   +-+                                         I
  UMSW     3    -+   I                                           I
  UTHB     3    -+---+                                           I
  USVS     3    -+                                               I
  UFA      2    -+-----+                                         I
  ULJ      2    -+     +-----------+                             I
  UFC      2    -+---+ I           I                             I
  UID      2    -+   +-+           I                             I
  UDO      2    -+---+             +-----------------------------+
  UFFS     2    -+   I             I                             I
  UFH      2    -----+             I                             I
  UBO      2    -+-------+         I                             I
  UMSE     2    -+       +---------+                             I
  UONE     2    -+-+     I                                       I
  UONW     2    -+ +-----+                                       I
  UJSW     2    ---+                                             I
  UTOE     4    -+-+                                             I
  UWWW     4    -+ +-+                                           I
  UFFN     4    ---+ +-+                                         I
  UNV      4    -+---+ I                                         I
  UWOE     4    -+   I +-----------------------------------------+
  UOY      4    -+---+ I
  UWG      4    -+     I
  UWOW     4    -------+
```

Figure 8: Dendrogram using Ward's method (Bortz 1993). Distances between stations were calculated as Euclidean distance based on the three factors VEG1, VEG2, and VEG3. The factors were derived from 13 habitat characteristics in a principle component analysis. Groups were formed at a rescaled distance of 15. Stations are shown with the group number behind them. Groups are alternately bolded and normal.

Table 14: Means ± *SD* of four habitat characteristics at station groupings outlined by the cluster analysis. *P* is the probability derived from ANOVA's on the dependent variables. *N* is the number of stations in a group. Different letters behind means indicate significant differences between groups, tested by multiple comparisons (Tukey).

Group	*N*	POPLAHA	EPIMEAN	SDHT	DENTRPL4
1	18	230.9 ± 169.3a	1.753 ± 0.531ab	11.10 ± 3.56a	23.46 ± 17.83a
2	12	609.8 ± 358.4b	2.987 ± 0.519c	14.56 ± 3.46b	49.07 ± 22.45b
3	13	273.5 ± 184.7a	2.260 ± 0.633a	17.02 ± 3.36b	25.64 ± 17.79a
4	8	248.6 ± 310.5a	1.542 ± 0.489b	8.50 ± 2.35a	16.67 ± 15.71a
P (ANOVA)	51	1.05E-03	3.09E-07	1.21E-06	9.81E-04

3.2.4 Habitat Characteristics

3.2.4.1 Correlation Analyses

Correlations between habitat variables and measures of activity were largely consistent with the results of other studies (*e.g.*, Kuletz *et al.* 1995b; Rodway *et al.* 1993; Burger 1995b). The correlations that were tested as biological hypotheses (Table 15 and Table 16) showed varying results, depending on which measure of activity was used. The strongest correlations occurred between the dependent variables LNIRAOCC and LNIRACO and the independent variables EPIMEAN, DENTRPL4, OLDIND, and ALTITUDE. Interesting were the low correlations between the density of potential nesting platforms and most measures of activity (except for LNIRACO).

Table 15: Pearson correlation matrix of independent variables that had a hypothesised correlation with several measures of Marbled Murrelet activity. Bolded correlation coefficients indicate *P* < 0.01, bolded and italicised ones indicate *P* < 0.001, *n* = 49 station means.

Variable	LNIRADET	LNIRAOCC	LNIRASUB	LNIRA100	LNIRA150	LNIRACO
EPIMEAN	0.149	***0.584***	***0.507***	***0.406***	**0.343**	***0.627***
POPPLAHA	0.130	0.267	0.263	0.263	0.241	***0.402***
REPLAHA	0.184	0.250	**0.337**	0.211	0.209	**0.333**
DENTRPL4	0.111	**0.355**	***0.378***	**0.335**	**0.286**	***0.448***
SDHT	-0.005	***0.395***	**0.313**	**0.282**	0.203	**0.316**
OLDIND	0.238	***0.443***	**0.356**	***0.493***	***0.437***	***0.366***
OLDIND2	0.098	***0.386***	**0.290**	***0.377***	**0.316**	**0.342**

The random scanning for correlations (employing the Bonferroni correction) showed that DENLSS, DENSS, DENLWH, DENYC, DENMH, HTMEAN, TREEHT, and TIMBVOL were significantly or highly significantly correlated with at least one of the two tested measures of activity (LNIRAOCC and LNIRACO) (Table 17 and Table 18).

Table 16: Spearman correlation matrix of non-normally distributed independent variables that had a hypothesised correlation with several measures of Marbled Murrelet activity. Bolded correlation coefficients indicate *P* < 0.01, bolded and italicised ones indicate *P* < 0.001, *n* = 49 station means.

Variable	LNIRADET	LNIRAOCC	LNIRASUB	LNIRA100	LNIRA150	LNIRACO
ALTITUDE	-0.282	***-0.687***	***-0.572***	***-0.588***	***-0.549***	***-0.570***
CANCL	0.129	-0.270	**-0.353**	0.092	0.098	-0.184

Table 17: Pearson correlation coefficients among habitat characteristics that were randomly scanned for correlations. Bolded correlation coefficients indicate *P* < 0.01, bolded and italicised ones indicate *P* < 0.001, *n* = 49 station means. Probabilities are given with Bonferroni corrections (Bortz 1993).

Variable	LNIRAOCC	LNIRACO
CANCLVEG	0.017	0.187
DBHMEAN	0.355	0.286
DENWH	-0.005	0.213
DISSEA	-0.067	-0.226
EPITMEAN	0.267	0.153
HTMEAN	**0.419**	0.313
SLOPE	-0.288	-0.260
TIMBVOL	***0.601***	***0.559***
TREEHT	**0.441**	0.357

The comprehensive correlation matrices (Appendix II, Tables 1-6) gave some interesting results: LNIRADET, LNOCC2, and CO2 had considerably fewer significant correlations than other measures of activity. Furthermore, these variables did not correlate very well with other measures of activity. Judging by the number of significant correlations, the corrected and uncorrected measures of occupied Marbled Murrelet activity (LNIRAOCC, LNIRACO) performed very well, especially in 1997 (CO3). In contrast, the density of platforms was neither very well related to activity measures nor to other habitat variables.

3.2.4.2 Regression Analyses

The ordinary regression analyses (Figure 9 and Table 19) supported the relationships between habitat variables and Marbled Murrelet activity that were identified in correlation analyses. Inspection of the residuals did not suggest non-linear relationships for any of the regressions.

Table 18: Spearman correlation coefficients among non-normally distributed habitat characteristics that were randomly scanned for correlations. Bolded correlation coefficients indicate $P < 0.01$, bolded and italicised ones indicate $P < 0.001$, $n = 49$ station means. Probabilities are given with Bonferroni corrections (Bortz 1993).

Variable	LNIRAOCC	LNIRACO
DENAF	0.260	0.283
DENLAF	0.242	0.112
DENLARGE	0.343	0.261
DENLMH	-0.292	-0.277
DENLRC	-0.046	-0.094
DENLSS	**0.457**	**0.485**
DENLWH	**0.484**	0.348
DENLYC	-0.311	-0.195
DENMH	***-0.538***	***-0.499***
DENRC	-0.226	-0.242
DENSS	**0.461**	***0.492***
DENSTEM	-0.188	-0.061
DENYC	***-0.572***	-0.419
DISSTRM	-0.390	-0.372

Interesting were comparisons between ordinary least squared means regressions (LS) and least absolute deviation regressions (LAD) (Figure 9 and Table 19). Only three out of twelve LAD regressions had lower probabilities of a slope of zero than the equivalent LS regressions. Comparisons between R^2-values were not possible because no equivalent measure exists for the LAD regressions done with Blossom Statistical Packages. The graphs (Figure 9) demonstrate differences in slopes between LS and LAD regressions and show the quality of the 90th regression quantile for modelling the limiting effects of habitat variables in wedge-shaped relationships. While the first two measures show central tendencies, the resulting dotted LAD 90th regression quantile lines represent assumed limits to Marbled Murrelet activity caused by habitat variables.

Among the vegetation-related variables, timbervolume (TIMBVOL) and epiphyte cover consistently showed the best correlations and regressions with occupied activity (LNIRAOCC and LNIRACO) (Table 15, Table 17, and Table 19). The regression of TIMBVOL against LNIRAOCC (Figure 9) shows a threshold of timbervolume (approximately 550 m^3/ha) under which occupied activity is very low. After 600 m^3/ha the stations with medium to high levels of activity appear. Eventually, the highest levels of activity are reached at approximately 800 m^3/ha (Figure 9).

Table 19: R^2 and *P*-values (ANOVA against H_0: slope = 0) of regressions on several habitat variables. Dependent variables are LNIRAOCC and LNIRACO. Regressions are regular least squared means models except for the column LAD50th which stands for the *P*-value of a 50th regression quantile least absolute deviation model (Cade and Richards 1996). *n* = 51 station means.

	LNIRAOCC		LNIRACO		
Variable	R^2	*P*	R^2	*P*	LAD50th
ALTITUDE	0.34	8.03E-06	0.33	1.01E-05	2.00E-04
DENSS	0.13	9.94E-03	0.15	5.83E-03	0.022
DENMH	0.10	0.022	0.18	1.88E-03	2.90E-03
DENYC	0.10	0.021	0.09	0.029	0.017
EPIMEAN	0.37	1.91E-06	0.29	2.82E-05	2.00E-04
HTMEAN	0.09	0.037	0.13	8.26E-03	0.047
OLDIND	0.10	0.024	0.12	0.014	0.021
OLDIND2	0.11	0.015	0.15	4.98E-03	0.016
POPLAHA	0.15	4.76E-03	0.06	0.087	0.014
SDDBH	0.07	0.060	0.06	0.075	0.063
SDHT	0.09	0.035	0.12	0.011	0.026
TIMBVOL	0.31	2.00E-05	0.38	1.73E-06	1.00E-04

With these numbers in mind, I chose 0 m^3/ha as low, 1- 550 m^3/ha as medium, 551 - 800 m^3/ha as high, and > 800 m^3/ha as excellent predicted nesting capability categories, based on timbervolume, to produce a map of predicted nesting capability for the Ursus Valley. Appendix III, Figure 2 shows a GIS map with polygons of different colours corresponding to the three different categories of timbervolumes or predicted nesting capabilities. The map was produced with ARC INFO and was based on a digital forest cover map by MacMillan Bloedel Ltd. (1998). ANOVA’s showed significant differences in means of two measures of activity (LNIRAOCC and LNIRACO) and three habitat variables (EPIMEAN, DENTRPL4, SDHT) among three timbervolume categories (Table 20). (No station was in the lowest category; therefore, I excluded it from the analysis.)

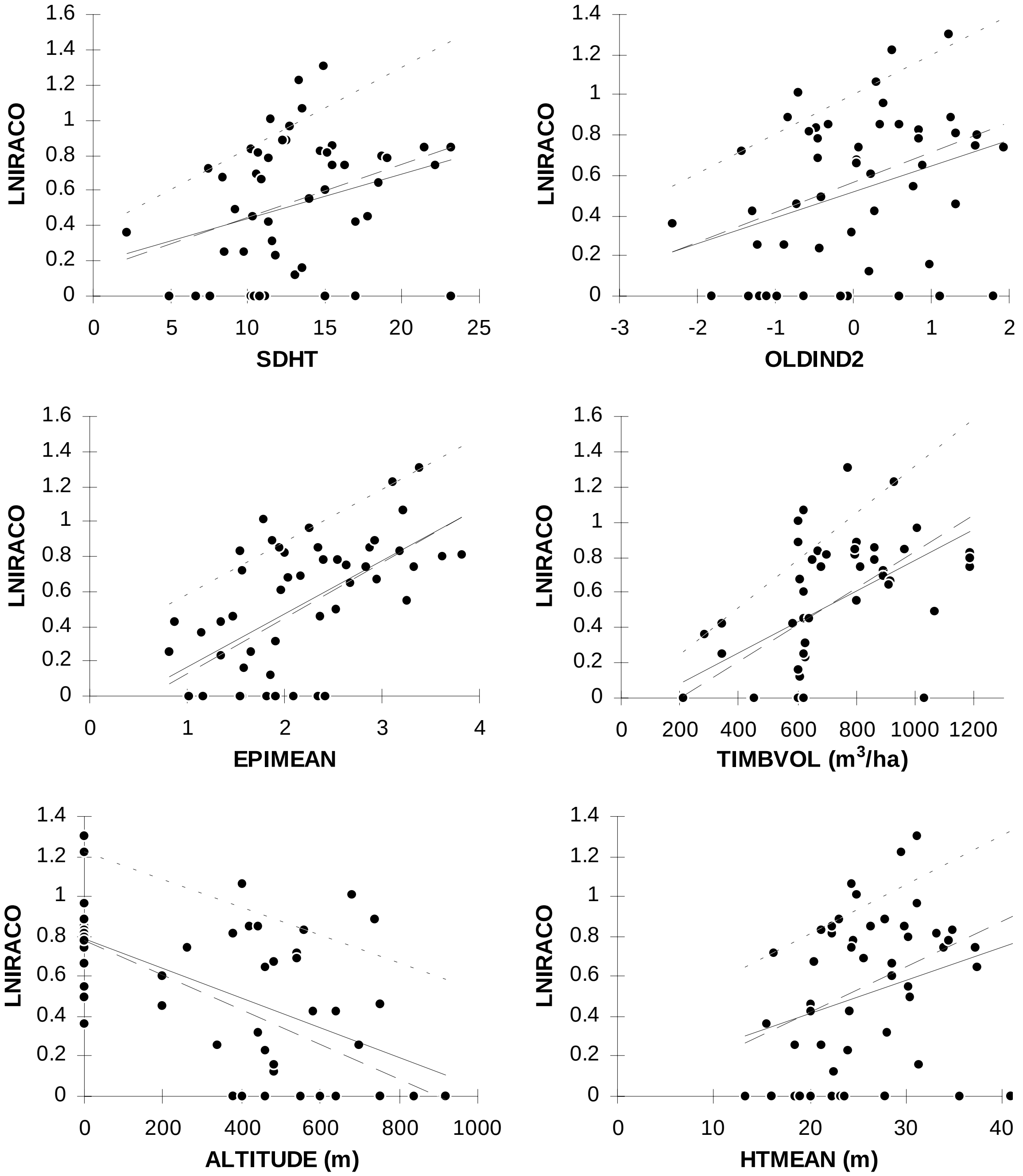

Figure 9: Estimates of least squares regressions (LS, solid line) and least absolute deviations regressions (LAD, 50th regression quantile dashed line, 90th regression quantile dotted line) for corrected occupied Marbled Murrelet activity (LNIRACO) as a function of independent habitat variables. The 90th regression quantiles model the assumed upper limit in Murrelet activity given by a certain habitat variable. *n* = 51 station means.

The best multiple regression in terms of biological meaning, informational value, and statistical soundness employed the dependent variable LNIRAOCC, and the independent variables POPLAHA, CANCLSITE, and TIMBVOL. The inspection of collinearity statistics did not indicate a severe problem with collinearity among the independent variables. The adjusted R^2 values were greatly improved by repeating the analysis on data sets that excluded stations with less than two, three and four surveys (Table 21). The low average in R^2's and significance of ten random samples of 19 stations showed that the increase in R^2 values with increasing minimum number of surveys was not an artefact of the decreasing number of stations included the regression analysis.

Table 20: Means ± *SD* of two measures of Marbled Murrelet activity and four habitat characteristics at stations grouped by their timbervolume classes. *P* is the probability derived from ANOVA's on the dependent variables, with the grouping variable timbervolume class. *N* is the number of stations in a group. Different letters behind means indicate significant differences between groups, tested by multiple comparisons (Tukey).

Timbervolume Class	*N*	LNIRAOCC	LNIRACO	EPIMEAN	DENTRPL4	SDHT
≤ 550 m^3/ha	9	0.12 ± 0.18a	0.05 ± 0.10a	1.37 ± 0.54a	4.94 ± 8.07a	8.21 ± 3.19a
551-800 m^3/ha	25	0.51 ± 0.39b	0.38 ± 0.42a	2.04 ± 0.67b	28.89 ± 15.04b	13.53 ± 3.51b
> 800 m^3/ha	17	0.73 ± 0.25b	0.82 ± 0.39b	2.69 ± 0.54c	41.83 ± 24.07b	14.80 ± 4.62b
P (ANOVA)	51	1.25 E-04	1.89E-05	1.13E-05	3.92E-05	4.88 E-04

Table 21: Multiple regressions with the dependent variable occupied detections (LNIRAOCC) and the independent variables canopy opening (CANCLSITE), potential platforms per ha (POTPLAHA), and timbervolume (TIMBVOL). Included are stations with at least the number of surveys indicated in the first column. The last row contains average results from ten random samples of 19 stations.

Minimum No. of surveys	No. of stations	R^2	Adjusted R^2	*F*	*P*
1	51	0.50	0.42	13.30	2.1E-06
2	41	0.54	0.50	14.31	2.4E-06
3	28	0.60	0.55	12.12	5.0E-05
4	19	0.75	0.69	14.63	1.0E-04
Random Selection	19	0.41[1]	0.27[1]	3.166[1]	0.10[1]

[1] Average of 10 random samples

3.2.5 Site Specific Analysis (SSA)

The SSA revealed one or two relatively unequivocal centres of activity at most stations. Table 22 shows centres of activity relative to the survey stations as defined by the methods of the SSA.

Regressions between LNIRAOCC and habitat variables measured in SSA vegetation plots showed no major differences from the regressions done on the regular vegetation plot data (Table 23). A direct comparison of habitat characteristics revealed that all habitat characteristics relevant to Marbled Murrelets had higher scores in the SSA vegetation plots than in normal ones

(Table 24). However, paired t-tests showed that only two of the differences in means were significant (REPLAHA, and EPIMEAN).

Table 22: Centres of activity, as determined by the SSA, relative to stations.

Station	Direction from station	Distance from station
UDO	170^0	100m
UEWE	345^0	110m
UFC	225^0	200m
UJS	180^0	175m
ULJ	10^0	70m
ULJ	90^0	190m
UMSW	245^0	200m
UONE	335^0	200m
UONW	315^0	200m
UOY2	135^0	200m
USC	170^0	200m
UMSE	180^0	100m

Table 23: Comparison of R^2 values and P-values (F-tests) of linear regressions between habitat variables that were derived from regular vegetation plots and SSA plots. The dependent variable was LNIRAOCC. n = 11 in each regression analysis.

	R^2		P	
Independent variable	SSA	Regular	SSA	Regular
SDDBH	0.001	0.365	0.945	0.049
DENLARGE	0.053	0.471	0.497	0.020
REPLAHA	0.069	0.198	0.436	0.170
DBHMEAN	0.086	0.436	0.380	0.027
OLDIND	0.118	0.451	0.300	0.024
POPLAHA	0.132	0.161	0.272	0.221
OLDIND2	0.245	0.529	0.122	0.011
CANCLVEG	0.288	0.010	0.089	0.767
SDHT	0.333	0.419	0.063	0.031
DENSTEM	0.509	0.270	0.014	0.102
EPITMEAN	0.552	0.048	0.009	0.519
HTMEAN	0.594	0.542	0.006	0.010
EPIMEAN	0.614	0.369	0.004	0.047

Table 24: Results from two-tailed paired t-tests conducted on several different vegetation parameters, comparing SSA vegetation plots with regular ones at the same station. Column three refers to the difference between the means of a given variable in SSA and regular vegetation plots. *n* = 10 pairs of vegetation plots.

Variable	SSA-Regular	*t*-Statistic	*P* (two-tailed)
POPLAHA	69.29	0.98	0.18
REPLAHA	106.6	2.55	0.02
EPIMEAN	0.3586	1.94	0.04
EPITMEAN	0.3103	0.98	0.18
SDHT	0.2538	0.30	0.77
SDDBH	4.409	0.99	0.35

4. Discussion

4.1 Sources of Within-Subject Variation

The detection rates at individual stations varied greatly on a daily, seasonal, and yearly scale. The station was the experimental unit or subject and therefore, this variation was within subjects. Some of the causes of this variation are observable and quantifiable, some are known but hard to measure, and probably many are not known at all. In the following chapters I will discuss the known and suspected sources of variation and suggest ways of accounting for them in the study design, when it is possible and feasible.

Effects not related to physical characteristics of the station (*e.g.*, weather, season, year) should be considered for each individual survey. Statistically, analyses based on individual surveys are only favourable if the number of surveys performed per station does not vary greatly across stations. Otherwise, the analyses will be weighted towards the stations with the most surveys (Hurlbert 1984).

In the Ursus, sample size varied greatly among stations. This was mainly due to the inaccessibility of higher elevation sites, the fact that the valley bottom is most suitable for access and transit, and the fact that surveys were sometimes missed during heavy rain. The first two problems were largely remedied in 1997 by exclusively using helicopters for access and far moves within the valley. However, helicopter transport is costly and was used only once in 1995. Therefore, over the three years of the inventory, the valley bottom stations were sampled many more times than other stations and the high altitude stations were often sampled only one to three times.

The options to avoid pseudoreplication were to a) achieve equal sample sizes by excluding some surveys from analyses or b) average activity levels at stations with the knowledge that some factors such as weather and season could not be accounted for in later analyses. I chose the second option because the first one would have meant excluding approximately 50% of the data collected in the Ursus.

In the future it should be a high priority to try to keep sample sizes equal right from the start. To achieve this goal in the Ursus it would be necessary to use helicopter transportation exclusively (as done in 1997) and to plan for replication of missed surveys. I think that planning for 4 replications per season per station would provide sufficient data even if some planned surveys were missed.

4.1.1 Weather

During this study, Marbled Murrelets were most active in foggy, wet, and very cloudy weather. This result is consistent with other studies, which have shown weather to have a strong influence on Marbled Murrelet activity patterns (Burger *et al.* 1995; Kuletz *et al.* 1995b; Naslund and O'Donnell 1995, Manley *et al.* 1992, Nelson 1989, Paton and Ralph 1988; Rodway *et al.* 1993b). As a random factor, it cannot easily be controlled for. Even with several surveys at each station there is no guarantee that all weather types will be sampled at each station. Nevertheless, study designs that would allow the use of every survey rather than means per station would make the inclusion of weather in analyses feasible (*e.g.*, Kuletz *et al.* 1995b). Even if some empty cells existed in the ANOVA and its statistical power and robustness therefore decreased (Zar 1996), this approach would still be preferable to an analysis using averages of stations and excluding weather effects.

The attempt to correct for influences of different weather types with a general correction factor, derived from an analysis of weather that tried to exclude the effects of most other variables (LNIRACWO), did not show satisfactory results. The correlations done between habitat variables and measures of Marbled Murrelet activity corrected for weather were not an improvement over correlations done with uncorrected measures of activity. I do not think that correction factors can compensate adequately for the complex phenomenon of weather influences on Marbled Murrelet activity and suggest that future study designs attempt to have equal numbers of survey replications at each station to allow inclusion of weather as a factor in the analysis.

4.1.2 Seasonal Variation

The activity levels of Marbled Murrelets vary drastically throughout the year (O'Donnell *et al.* 1995). In British Columbia standard inventories are restricted to the breeding season (May 1st - July 31st). However, even in this time frame, regular patterns of variability occur, with maximum activity occurring mid-season (Manley *et al.* 1992; Burger 1994; Burger *et al.* 1995, 1997a; Rodway *et al.* 1993b). In the Ursus Valley the peak of activity occurred just before mid-July (Figure 5, chapter 3.2.1). Whereas activity levels were fairly comparable between mid-June and the end of July, they were perceivably lower between mid-May and mid-June. In the first two weeks of May in 1995 activity levels in the Ursus were so low that these surveys were omitted from analyses and no surveys were done before May 15th in 1996 and 1997.

The inclusion of seasonal effects on Marbled Murrelet activity in the analysis is possible if individual surveys rather than means are analysed. However, the season would have to be divided into units with distinctly higher and lower activity. This division is difficult as detection levels appear to change fairly continuously. Kuletz *et al.* (1995b) included season as a dummy variable in their multiple regression by dividing the research period into an early and a late one. In the Ursus an appropriate division could be May 15 - June 15 (early) and June 16 - July 31 (late); however, the early period would still encompass high variation in average activity levels. Nevertheless, I think that the best method is to spread the surveys done at a particular station evenly across the season and to cope with the resulting variation by including season as a categorical variable in the analyses (*e.g.*, as early, mid, and late season).

Another possibility would be to restrict sampling to a very narrow period (June to Mid-July). However, this approach has the disadvantage of requiring a large number of field researchers to obtain a sufficient amount of data over a short period of time. Increased effects of different observers (shown by Rodway *et al.* 1993b) and organisational difficulties would likely make this approach unreasonable.

It is likely that the effects of seasonal variation on the analyses in this thesis were not very great; most stations were sampled fairly regularly across the season, and the averaging of detections at individual stations somewhat made up for seasonal variability.

4.1.3 Station Placement

The placement of a survey station can influence the hearing and sighting of Marbled Murrelets (O’Donnell 1995). In the valley bottom, stations were often located close to the stream channel on gravel bars and typically had a large amount of unobstructed view combined with fairly high creek noise. In contrast, the hillside stations were often in dense forest with small canopy openings and relatively low creek noise. Thus visual detections, which were more important for the analyses, were likely underrated in the slopes compared to the valley bottom and auditory detections, in turn, were likely overrated. In addition, the acoustics are better in hillsides and birds can be heard over far distances. However, these auditory effects are of low significance because auditory detections are rarely ever used in analyses. More important are factors influencing visual detections as nearly all occupied detections are visual.

In addition to the larger opening sizes of stations on stream channels, structures such as stream channels are often used as flight paths by Marbled Murrelets (Hamer and Nelson 1995b; Nelson 1997). Therefore, the high detection rates at these stations, usually attributed to the excellent habitat at low elevations, could be artefacts of station placement (Rodway and Regehr unpublished b). In the Ursus Valley, flight corridor effects could be relatively high because the valley has steep sides, and birds may be funnelled along the stream channel. Even though commuting birds passing over would mostly fly in straight lines and well above canopy, and therefore would not contribute to occupied detections, a certain portion could do their commuting below canopy or meet in the valley bottom for “social” circling. Although circling is used as an indicator of nearby nesting (Paton 1995), birds have been observed circling over unsuitable habitat in the proximity of suitable habitat (Hamer and Cummins 1990, 1991; Nelson 1989, 1990a). This indicates that circling is not necessarily done exactly over the nest site but possibly in the same general area. It is not unlikely that birds would nest away from the stream channel in habitat with less edge but meet for circling and socialising in the valley bottom, where most of the commuting takes place as well.

Correcting for station placement by including it as a categorical variable in analyses bears the risk of cancelling out differences in activity levels due to differences in habitat characteristics. Most stations in the valley bottom were placed on the stream channel. Therefore, a placement category “stream channel” would not only correct for the unwanted effects of canopy opening and flight corridors but possibly also eliminate higher detection rates that were, in reality, due to better habitat. Comparisons of habitat characteristics among different parts of the valley showed that the valley bottom generally supports the highest rates of Marbled Murrelet-relevant structures (*e.g.*, platform and epiphyte densities).

A different approach to dealing with opening size and corridor effects is the ratio of occupied detections to all visual detections, which I put forward in this thesis. A restriction of the view of the observer always results in him or her missing some birds. These missed Marbled Murrelets could be passing over the survey stations or exhibiting occupied behaviour. On average, the number of birds missed in each behaviour category is directly proportional to the number of birds exhibiting each behaviour in the vicinity of the survey station. Accordingly, absolute numbers of occupied detections and all visual detections decrease with a decline in unobstructed view, but the ratio between these two categories does not change. However, the ratio only works as long as canopy openings are large enough to identify occupied behaviour. With very small openings the time a bird is seen could be too short to determine whether it is circling or flying in a straight line.

The case is not quite as clear for the effect of flight corridors on visual detections. Assuming that most birds using corridors are commuting, they could even decrease the aforementioned ratio to lower values than would be adequate for the quality of the station. However, considering that some birds might use the valley bottom for social circling and some birds might commute below canopy, the ratio might work well as an expression of Marbled Murrelet habitat preferences, as indicated by the results of this thesis.

The ratio was not able to eliminate all differences in measured occupied Marbled Murrelet activity between paired stations in the forest comparison, where one station was at a wide-open location and the other at a smaller opening in the adjacent forest. Possible reasons could be that a) the ratio did not properly account for corridor effects, or b) the low canopy opening at the forest stations too often eliminated all occupied detections during a survey in which case the ratio is zero and will not be able to adequately control for opening effects. Rigorous testing will be necessary to establish the ratio of occupied to all visual detections as a useful measure of habitat preferences of Marbled Murrelets.

A problem for the aforementioned method of correction is extremely good vantage points, overlooking large expanses of habitat, such as UFFN in the Ursus Valley. This station is on a local height overlooking both the main valley of the Ursus and the side valley Thunderbird Creek. It is in a terrain of exposed rocky outcrops and is completely unsuitable as Marbled Murrelet breeding habitat. Nevertheless, it has very high occupied detection rates owing to activity in the Thunderbird and Ursus valleys as well as birds circling between those two as they enter or leave the Thunderbird. This problem is so obvious in this case that I felt justified in excluding this station from habitat suitability analyses. Data from stations such as this one are still interesting, as the good vantage point provides many detections and can contribute to the examination of inter-annual differences in Marbled Murrelet activity, behavioural questions or other questions not directly related to habitat characteristics.

A problem remains when no birds exhibiting occupied behaviours are seen at all. This scenario occurs relatively often and renders stations indistinguishable in terms of activity, no matter how many effects contributing to it are included in the analyses. The largest and only significant drop in mean activity occurred between the second lowest (26-50%) and the lowest (0-25%) category of canopy opening. Therefore, it would be desirable to completely avoid placing survey stations in this category. During the field season, the workload of conducting surveys and vegetation plots, and moving between stations is often so high that not enough time is spent searching for optimal stations. My suggestion would be to choose adequate survey stations on an independent trip before the survey period begins.

4.1.4 Direction Faced by the Observer

As shown in chapter 3.1.5, the direction faced by the observer has a strong influence on the detection of Marbled Murrelets. There are two possible explanations for the pronounced directional hearing (and to a lesser degree vision) of the observers: a) observers missed more Marbled Murrelets behind their backs than towards the direction they were facing, or b) observers perceived and recorded Marbled Murrelets calling behind their back as calling in front of them. Sometimes when I lifted and turned my head I saw birds that I had not seen before or I realised that birds that I had perceived as calling in front of me that were actually calling from behind.

Most of the detections included in the analysis of this directional effect were acoustic. Therefore, the effect is not relevant to most analyses, as auditory detections are rarely included and the problem is fairly constant among all observers. It gains some importance on hillsides where observers usually face down slope and, therefore, are biased towards recording the many detections from the valley bottom and miss the lower number of detections occurring up slope from them. Another problem arises for my Site-Specific Analysis (chapter 3.2.5): the identified centres of activity, which are based on the direction in which audio and visual detections were observed, could be biased depending on the direction faced by the observer.

4.1.5 Inter-Annual Variation

Although Ralph (1995) did not find significant inter-annual differences in Marbled Murrelet activity in some inland California stands, the strong yearly variation detected in this study deserves some attention. I would like to discuss three possible levels at which inter-annual variation can be examined: a) the whole watershed, b) stations and parts of the watershed, and c) data collection.

The mean detection rates measured by audio-visual surveys varied significantly among the three years of the study. While the amount of mean activity observed in the Ursus was significantly higher in 1995 than in 1996, mean detection rates of 1997 were intermediate, neither significantly higher than in 1996 nor significantly lower than in 1995. In addition, Burger *et al.* (1997b) found by radar counts that the number of Marbled Murrelets entering the Bedwell-Ursus watershed had declined by 44% from 1995 to 1996. These results indicate strongly that Marbled Murrelets shift their breeding activity among watersheds from season to season. This shift in focus could a) reflect prey distributions, b) be a strategy to avoid predators, or c) be related to other factors in Marbled Murrelet biology, such as social behaviour. It is unlikely that the variations are related to changes in absolute population size, because the Marbled Murrelet is a rather long-lived species with low reproductive rates.

None of the above explanations could be tested easily without many years of research. And even if it could be shown that, for example, Marbled Murrelets react to prey distribution, the relationship would still be vague and impractical to include as a factor in research related to breeding habitat. Without the opportunity to explain inter-annual variation with measurable variables, audio-visual surveys will always have to be conducted over several years to control for inter-annual variation and to come to valid conclusions. It is preferable that they be conducted in equal numbers per station per year and at the same stations each year so that individual surveys and years can be treated as repeated measurements in statistical analyses.

Besides changes in absolute activity in the watershed, the relative activity at individual stations shifted among years (Figure, 3 chapter 3.1.1). Changes in quality of breeding habitat around a station can be excluded as an explanation because large-scale disturbances are very rare in coastal temperate rain forests (Kellogg 1992). A more likely explanation may be predator avoidance. Predation rates on Marbled Murrelet nests are very high (Nelson and Hamer 1995b) and the Marbled Murrelet has evolved several strategies to elude predators (*e.g.*, camouflage plumage, trips to and from the nest during low light periods). Perhaps another strategy is to change breeding areas on a regular basis. If this explanation for inter-annual variation among stations is true, it could not be controlled for in data analyses and would require multi-year sampling to reach valid conclusions.

The last important factor I would like to mention in the discussion of inter-annual variation is data collection. The analyses of data from individual years have shown that the results from 1996 were quite different from those of the other two years. The correlations between measures of activity and habitat variables were weaker in most cases in the 1996 data (see Appendix I, Table 2 and Table 4) and the relative importance of stations shifted greatly in comparison to 1995 and 97. The surveys and vegetation plots were done with the same methods in all three years but the average number of surveys done at each station varied significantly (P = 0.0002, n = 101); it was lower in 1996 than in 1995 and 97. However, many other factors unrelated to data collection may have played a role in the difference between 1996 data and the data from other years.

4.1.6 Observer Variability

Among other sources of within-subject variability that are known or suspected but neither examined nor accounted for in this thesis are differences among observers. Rodway *et al.* (1993b) found significant inter-observer variation in the number of visual detections. An indication of inter-observer variation in audio-visual survey data as well as in vegetation plots is provided by the 1996 data from the Ursus Creek. In that year 10 observers collected the data, compared to 6 and 4 in 1995 and 1997, respectively. Thus, the lower number of significant correlations among measures of Marbled Murrelet activity and habitat variables in 1996 compared to the other two years could be interpreted as being due to unwanted variation in the data stemming from high numbers of observers, as well as lack of power due to the previously discussed low number of repetitions. In addition, only 10% of the observers in 1996 had previous experience with Marbled Murrelets compared to 50% in 1995 and 100% in 1997.

It is redundant to suggest keeping the number of observers low because this number is usually determined by demands on data collection and is rarely increased above the absolute minimum necessary. However, it may be a good idea to survey areas that will be compared directly (*e.g.*, for management decisions) with the same researchers.

4.1.7 Creek Noise

For auditory detections, noise, usually caused by creeks, is an important disturbance. When survey stations are selected, one criterion is the amount of open sky available for Marbled Murrelet observation. In an old growth forest most suitable openings are caused by and are close to streams. Unfortunately this means that observers often must deal with considerable amounts of creek noise, which tends to drown out remote auditory detections (although these are the least useful detections anyway). It is difficult to draw conclusions about the effects of creek noise because it is a property of a particular station and comparing detection rates among different amounts of creek noise implies comparing detection rates at different stations. That in turn makes it hard to differentiate the effect of creek noise from other effects. Furthermore, low creek noise tends to be associated with small canopy openings and will therefore be partly accounted for by including canopy closure in the analyses.

As mentioned before, auditory detections are not very useful in analyses; therefore, I do not think that creek noise needs special consideration in Marbled Murrelet research. However, it is not much effort to record it and to include it in appropriate analyses as a factor or covariate.

4.2 Critique of Methods and Suggestions for Alternatives

The development of field methods in ecology is dominated by the pursuit of efficiency. The impossibility of controlling most factors in field experiments causes much unwanted variation in ecological field data and necessitates high numbers of sampling and treatment replicates. Combined with difficulties in access to study areas and in collecting data under rough conditions, the effort and costs involved in ecological field studies are exceptionally high. Therefore, study designs attempt to minimise the effort necessary for data collection and to maximise the contribution of data towards statistical significance of results.

In research on Marbled Murrelet breeding habitat requirements this search for efficiency has led to the use of audio-visual detections of Marbled Murrelets as an indicator of Marbled Murrelet nesting activity. In comparison to finding Marbled Murrelet nests, the collection of activity data is easy. However, so far a direct relationship between occupied activity and nesting activity, or even the number of birds present, has not been established. Although many correlation results between occupied activity and habitat features were biologically meaningful and consistent among different studies (*e.g.*, Kuletz *et al.* 1995b; Burger 1995b; Hamer 1995; Grenier and Nelson 1995; Miller and Ralph 1995), this kind of study will always remain somewhat speculative and its power will always remain severely limited due to high unexplained variation in Marbled Murrelet activity patterns.

Further insight into and more accurate quantification of Marbled Murrelet breeding habitat requirements will depend on vegetation surveys around known nest sites. Although the locating of Marbled Murrelet nests is time consuming and costly, it is the only way to improve on and increase existing knowledge.

So far, vegetation surveys of a stand around a survey station in this study were done by placing a 30 x 30 m vegetation plot in the proximity of the station. Considering the extremely variable vegetation in old-growth forests, this one plot can hardly be a sufficient sample to describe an at least 12 ha large area (assuming that surveys sample a radius of 200m). Especially measures such as the number of potential nesting platforms per ha can vary drastically with the in- or exclusion of a pocket of large trees in the area. I think that vegetation surveys around a survey station should at least include three randomly placed 30 x 30 m plots and one stratified 30 x 200 m transect for adequate representation of vegetation structures relevant to Marbled Murrelets.

To reduce the workload in vegetation sampling it is be possible to reduce the data collection to dominant trees (larger than 60 - 80cm in dbh) or to trees with potential nesting platforms (Manley pers. comm.). This would still sample most Marbled Murrelet-relevant structures although the measures of standard deviation in tree height and dbh I put forward in this thesis would no longer be possible.

An attempt to increase the quality of vegetation data collection, the Site Specific Analysis, did not improve sampling results to a statistically significant level. Although the SSA often showed relatively unambiguous centres of activity the question remains whether these centres adequately reflected outstanding habitat. The method with which directions of detections were written down during surveys is not ideal for finding a mean angle and the estimates of the distances of detections were likely very variable among observers. In addition, observers' hearing is highly dependent on the direction faced by him or her (chapter 3.1.5). Therefore, the sites for the SSA vegetation plots probably did not accurately reflect patches of outstanding habitat even if they provided a clue about areas important to Marbled Murrelets.

4.3 Habitat Requirements of Marbled Murrelets

I would like to discuss specific habitat requirements of Marbled Murrelets in the Ursus Creek as determined by this study. To clarify the nature of Marbled Murrelet requirements, I will categorise them as primary or secondary requirements.

Primary requirements encompass direct needs of the Marbled Murrelet for breeding, such as a sufficiently large platform, some form of cushioning on the platform and access to the platform. Secondary requirements include all habitat variables which are thought to be indirectly related to primary ones, such as mean tree height and DBH, densities of large trees, timbervolume, and the density of certain tree species. These factors are often used for correlation with Marbled Murrelet activity because they are either easier and more accurately recorded than primary factors, or are available from already existing sources that cover large areas, such as vegetation and forest cover maps.

Potentially, there could be some overlap between the two types of requirements, because it is still unclear how Marbled Murrelets really select their breeding habitat. Even if it is evident that they need platforms to nest on, it is unlikely that they will count platforms and nest in the area with highest platform densities. However, if they choose the first suitable platform they can find, the density of platforms would to a certain degree reflect the number of Marbled Murrelets breeding in an area. I think that the Marbled Murrelet's search for suitable habitat includes similar factors as our search for suitable Marbled Murrelet habitat: coastal rainforest with multi-layered canopies, large trees, many platforms, and abundant epiphytes.

The most indisputable method to determine which habitats Marbled Murrelets select is to record habitat characteristics at known nest sites. However, nests are hard to find. Despite extensive efforts, only about 136 tree nests have been found in North America (Quinlan and Hughes 1990; Singer *et al.* 1991, 1995; Hamer and Nelson 1995b; Naslund *et al.* 1995, Nelson and Sealy 1995; Nelson 1997). Therefore, it is common to infer habitat requirements of Marbled Murrelets by correlating presence or activity measures of Marbled Murrelets, indicating breeding in the area, with habitat characteristics.

However, a definite link between Marbled Murrelet activity, as measured in audio-visual surveys, and actual breeding activity has never been established. It is not possible to translate the measured activity into actual numbers of birds or nests. Therefore, habitat requirements of Marbled Murrelets, as inferred from audio-visual survey data, will always remain somewhat speculative. More effort should be focused on direct methods such as random searches for nests by tree climbers.

A problem in the determination of habitat requirements of Marbled Murrelets is the high intercorrelation among different variables used in the description of primary and secondary requirements. Many multivariate analyses assume independence among all variables. Although certain levels of correlation among these variables are acceptable, high intercorrelation leads to spurious results (Zar 1996). Furthermore, the large number of ways to express habitat attributes has led to many different habitat variables. Deciding which of these variables to include in multivariate analyses is often arbitrary or based on previous tests, defying the principles of hypothesis testing by not stating the hypothesis previous to statistical tests. The Principal

Component Analysis (PCA) resolves both problems by including all variables and reducing them to a few uncorrelated factors. The more intercorrelated the included variables are, the fewer factors will be necessary to adequately describe them.

The PCA included in this thesis produced three factors (VEG1, VEG2, and VEG3) which could be roughly interpreted as a) structural variability among trees (important for access to trees) (VEG1), b) effects of altitude on vegetation, and c) structural characteristics of trees. Unfortunately, these results will be incomparable with other studies even if the same methods would be used because with different values of included variables the PCA factors will likely be structured differently and, for example, a value of 0.5 for the factor VEG1 will never be comparable to values of factors in other studies.

In studies based on audio-visual survey data, indicators of Marbled Murrelet habitat suitability have often been determined through stepwise multiple regressions. It in- and excludes independent variables from the model on the basis of predefined criteria on how much variation in the dependent variable they explain. I do not agree that a statistical method can “decide” on biological matters such as Marbled Murrelet suitability. The stepwise multiple regression merely chooses variables which suit the model best in a purely mathematical sense and, since Marbled Murrelet data are very variable, this choice is to a certain degree random. Furthermore, it defies the statistical concept of hypothesis, which requires that a hypothesis be formulated before tests are conducted, to avoid biases.

Another potential source of error in the search for secondary factors that are important features of Marbled Murrelet habitat is the random scanning of correlation matrices for significant relationships between habitat variables and measures of activity. As factors become more abundant and matrices become larger, the probability of finding randomly occurring correlations that appear to be significant becomes larger. Again, randomly scanning matrices for significant correlations violates the principles of hypothesis testing and a correction (*e.g.*, Bonferroni correction, Bortz 1993) must be applied to compensate for the probability of randomly finding correlations.

4.3.1 Primary Habitat Requirements

The most obvious requirement of a Marbled Murrelet for breeding is a large branch, forming a platform, which supports the egg and later the chick (Figure 10). An exception is the approximately 3 % of the Alaskan population which nests on the ground on sea-facing talus slopes or cliffs, mostly in areas where adequate nesting trees are not available (Piatt and Ford 1993; Simons 1980; Hirsch *et al.* 1981; Day *et al.* 1983, Johnston and Carter 1985; Ford and Brown 1995; Nelson 1997).

Figure 10: Marbled Murrelet nest 20m off the ground on a yellow-cedar branch(*Chamaecyparis nootkatensis*) in the Caren Range, Sunshine Coast, British Columbia.

Platforms are created by normal growth, disease, mistletoe (*Arceuthobium campylopodum)*, mechanical damage, and other deformities, and occur mostly in forests with old-growth characteristics or at least remnant old-growth trees (except for two nests in young conifer forests with extreme mistletoe deformation; Nelson 1997).

In vegetation plots, potential nesting platforms, defined as being greater than 18 cm in diameter, inclusive of the moss (RIC 1995), are normally counted from the ground. The density of platforms per hectare (POPLAHA) is often used in analyses. In this study, POPLAHA did not correlate significantly with occupied detections (LNIRAOCC) but correlated significantly with the ratio of occupied detections to all visual detections (LNIRACO). Furthermore, although the density of platforms correlated with timbervolume, it did not correlate with the density of trees > 80cm DBH (DENLARGE) or DBH. There are several possible reasons that, in the Ursus, this apparent requirement of Marbled Murrelets is so weakly correlated with Marbled Murrelet occupied activity and with other structural characteristics important to Marbled Murrelets:

a) Marbled Murrelets do not necessarily prefer habitat with a high density of platforms. A feasible explanation could be that stands with a very high density of nesting platforms do not allow easy access and orientation as they likely consist of a relatively dense array of large trees;

b) the vegetation plots are not representative of the area sampled by the surveys because the area covered by a survey can be relatively large compared to the scale of significant vegetation changes (Rodway 1993b). The abundance of platforms in particular varies greatly on a small scale with the presence of pockets of large trees;

c) estimations of nesting platform numbers from the ground are not accurate; a project involving tree climbing, conducted after the Marbled Murrelet breeding period in the Ursus, revealed that ground observers regularly underestimated the number of platforms on trees (mean difference = 10 ± 17 (*SD*); $P < 0.001$), especially in big Sitka spruces (Rodway and Regehr, unpublished a). Estimates by ground observers rarely exceeded 15 platforms per tree whereas the tree climber counted at times more than 80 in a single tree. Beauchamp *et al.* (1998) found that ground observers overestimated the numbers of platforms in smaller diameter trees.

I think that the problem with platform densities as measures of habitat suitability lies in sampling difficulties. Adequate sampling should consist of either several randomly placed plots or some form of transects around the survey station to account for small-scale variability in the vegetation. Because it is likely that observers overestimate numbers of platforms in small trees and underestimate them in large trees, observers should be calibrated with counts done by tree climbers. Furthermore, it is questionable whether the density of platforms per ha is an adequate measure of habitat suitability because one huge Sitka spruce in a plot could have enough platforms to make the area appear to be exceptionally good habitat. However, I doubt that more than one pair of Marbled Murrelets would ever nest in such a tree at the same time. The same number of platforms spread across several trees in the sampled area, however, could potentially support more than one pair of breeding birds.

Therefore, a better measure of the availability of Marbled Murrelet nesting spots in a habitat is the density of trees with platforms. I chose to include only trees with more than three potential nesting platforms. Nelson *et al.* (1995) found that 15 Marbled Murrelet nests in Oregon and Washington were all in trees with more than 3 platforms. Drever *et al.* (1998) found an average of 2.7 ± 0.17 (*SE*) platforms on 32 nesting trees. Therefore, it seems justified to consider trees with less than four platforms as not being very important to Marbled Murrelets and eliminating them from the analysis. The rationale behind this step is to decrease the probability that habitats with high densities of medium sized trees with few potential nesting platforms, which are hardly suitable for Marbled Murrelets, score higher than habitats with a spaced array of prime Marbled Murrelet nesting trees (usually with more than 3 platforms).

Another key component of Marbled Murrelet nesting habitat is the cover on the nesting platforms, which supports the egg and keeps it from rolling off (Hamer and Nelson 1995b). Since the nest is only a small depression, sufficient material covering the nesting branch is quite crucial for successful nesting. In British Columbia the cover usually consists of epiphytes growing on the limbs (Jordan and Hughes 1995, Manley and Kelson 1995). The measure of the abundance of those epiphytes (EPICOVER) correlated highly significantly with Marbled Murrelet occupied activity in this study.

One apparent reason for the superior performance of this independent variable over platform density is the ease of recording epiphyte abundance and its greater homogeneity throughout the area sampled by a survey. Platform densities, on the other hand, change over small distances.

The methods of surveying epiphyte densities in vegetation plots seem to be adequate. More research could be conducted on the factors influencing epiphyte abundance, with special focus on the influence of timber extraction on epiphytes. An attempt could be made to predict epiphyte abundances on the basis of large-scale climatic information and make them available on maps.

The accessibility of Marbled Murrelet nesting platforms is more difficult to measure. Being adapted for diving and flying, the Marbled Murrelet has a high wing load, flies with rapid wing beats and reaches speeds of up to 158 km/h (Burger 1997). It usually approaches the nesting tree below canopy and below the height of the platform, sharply pulling up to reduce its flight speed just before landing (Nelson and Hamer 1995a; pers. observations). The impact of the landing is still high enough to eventually clear a patch in the epiphyte cover at the landing spot. To use this approach, Marbled Murrelets require large gaps in the forest for flight paths and platforms with an opening towards the side of access (Nelson and Hamer 1995a; Nelson and Peck 1995). Old growth forests often exhibit adequate gaps at creeks and where large old trees have fallen. However, it is very difficult to assess habitat for adequate gaps using an easily obtained parameter, such as canopy closure. Although the quantification of this aspect of breeding habitat has been attempted (Manley, pers. comm.), I think that collecting this type of data across large areas could be very difficult and costly. Potentially, the interpretation of aerial photographs could provide some information on the spatial distribution of gaps in the canopy.

An indirect measure of the adequate forest structure discussed above may be the standard deviation of tree height (SDHT), which I present in this thesis. It is a quantitative measure of the layeredness of a canopy, a characteristic of the forest thought to be important for Marbled Murrelet nesting (Hamer and Nelson 1995b). High standard deviations indicate a mixture of large trees and small trees which usually grow in forest gaps. Low standard deviations in tree height either indicate uniform second growth stands, often with dense canopies and therefore inaccessible to Marbled Murrelets even if platforms should occur, or stands with small trees.

The same idea can be expressed as the standard deviation of tree diameter at breast height (SDDBH). However, this is an even more indirect measure, as large dbh's do not necessarily coincide with tall trees and vice versa. Nevertheless, it has the advantage of easy and precise data collection, whereas the heights of tall trees are difficult to measure or estimate within the forest. Combined in a factor analysis (OLDIND), high values of the two measures indicate a highly structured old-growth forest, which is a basic requirement for Marbled Murrelet access to nesting platforms. The strong relationships between the aforementioned variables and Marbled Murrelet occupied activity in correlation and regression analyses is encouraging and should be applied further.

Cover over the nest branch and temperature at the platform are other parameters that have been suggested or observed to be directly important for Marbled Murrelet breeding but are hard to quantify. Cover over the nest branch is important for camouflage from predators and for protection against inclement weather (Nelson and Hamer 1995b). To account for cover over the nesting platform and accessibility of the nesting branch I attempted to use a measure called realistic platforms (REPLAHA) which should take the above factors into account when platforms in vegetation plots are counted, but which is largely subjective and includes much observer bias. It did not perform very well in the correlation analyses and will likely need much calibration among observers before it will be useful. Another approach is to estimate the cover above each counted platform (I. Manley, pers. comm.).

Lower temperatures in old-growth forests might be important for a well-insulated bird like the Marbled Murrelet, which is adapted to diving in cold ocean waters (Ralph *et al.* 1995). Therefore, temperature measurements could be useful, especially in the context of evaluating the effects of clearcuts. However, the effort necessary to collect adequate data would be very high.

Another important habitat requirement of Marbled Murrelets is low predation levels. Nesting success of Marbled Murrelets is strongly decreased by predation (Nelson and Hamer 1995b). The levels of Marbled Murrelet predators increase with higher amounts of forest edge and numbers of disturbances (Burger 1995b; Nelson and Hamer 1995b). Marbled Murrelets were not found to breed close to the ocean, where predators such as gulls and corvids are more abundant than in contiguous forests (Hamer and Nelson 1995b; Hamer 1995). Thus, predator abundances deserve special attention in habitat evaluations and logging impact assessments.

The last parameters of direct importance to Marbled Murrelet nesting habitat to be discussed are distance to the ocean and altitude. Both parameters measure the distance between the food source and breeding site of Marbled Murrelets and therefore, at high values, set the ultimate limits on Marbled Murrelet nesting due to physiological constraints. With increasing vertical and horizontal distance to the ocean, feeding trips become energetically more costly and breeding success likely decreases. As the Ursus creek is close to the ocean (less than 20km), in comparison to some stands in which Marbled Murrelets have been observed (> 100 km, Nelson 1997), I did not expect distance to the ocean to be an important parameter in my analysis. The results of random checks for correlations are consistent with this assumption. On the landscape level, distance to the ocean could be a valuable parameter and should be considered in habitat conservation efforts.

Altitude, in contrast, was strongly correlated with Marbled Murrelet activity in the Ursus Valley. However, this effect is more likely to be related to changes in vegetation than to physical constraints on Marbled Murrelets: with increasing altitude productivity tends to decline, trees tend to be smaller and habitat tends to be less suitable for Marbled Murrelets. Nonetheless, I found a Marbled Murrelet nest at higher than 1000 m above sea level in the Caren Range, Sunshine Coast, BC, and considerable Marbled Murrelet activity occurred over the whole area. Hamer (1995) found that levels of Marbled Murrelet occupied activity decreased rapidly above 1067 m elevation in Washington. Therefore, altitudes of up to 1000 m are probably not a physical problem for Marbled Murrelets; rather, it is the altitude-associated changes in vegetation characteristics that matter. Whereas the Caren Range is a plateau on the sheltered mainland to the east of Vancouver Island, the higher parts of the Ursus are either steep slopes or exposed ridges with rocky outcrops, supporting vegetation types of low productivity with small trees. As changes in vegetation are better described by more direct habitat variables such as number of trees with platforms, epiphyte cover, and timbervolume, I suggest that altitude as an independent variable predicting Marbled Murrelet habitat suitability should only be used at elevations above 800 m.

4.3.2 Secondary Habitat Requirements

Vegetation units such as site series are often used to indirectly predict suitable habitat for organisms under consideration. This approach to Marbled Murrelet habitat evaluation was encouraged by the Ministry of Environment because a mapping of vegetation units had already been done in the Ursus by Clement (1995). Although differences in mean detection rates were significant among site series, this difference was mostly due to the high mean activity in one or two valley bottom vegetation units, which never occur in areas of low productivity or at higher altitudes. Furthermore, site series were too numerous in the Ursus to be sampled adequately. Therefore, differences among the less-productive vegetation units could not be shown in this study and, if they exist at all, would need unfeasible amounts of research to be proven. An application of site series for Marbled Murrelet management purposes would likely result in an unjustified focus on a few site series, mostly confined to the valley bottom, and a negligence of most site series which might well be capable of producing suitable Marbled Murrelet habitat.

Broader categories of vegetation units, such as biogeoclimatic variants, increased sample sizes and resulted in significant differences between vm1 and mm1 variants in the Ursus Valley. The analysis of location in the valley showed similar results with significant differences between valley bottom and upper slope stations in all occupied activity measures and most habitat variables. Lower slope stations took an intermediate position differing significantly from valley bottom stations in a few variables. However, as mentioned, the Ursus Valley does not have significant numbers of productive high elevation stands and the difference found between vm1 and mm1, as well as valley bottom and upper slopes, might be an artefact of the specific situation. I would caution against the use of variants or location in the valley for management purposes for the same reasons that I would caution against the use of altitude.

An alternative is the grouping of site series by productivity. The low number of productivity groups (4) provided for statistical power and meaningful results. However, these results had the same problem as the comparisons among site series: the significant difference shown in tests originated mostly from the difference between the highest productivity group and the other groups, which were not significantly different from each other. Nevertheless, I am convinced that good Marbled Murrelet habitat is not restricted to the highest productivity class, although further research will be needed to establish differences among the other classes. In general I think that productivity could be a useful indirect parameter for prediction of suitable Marbled Murrelet nesting habitat.

Another option is the creation of a grouping of vegetation plots with cluster analysis. The combination of primary and secondary habitat requirements in the analysis results in a grouping variable, which can be used for indirect evaluation of Marbled Murrelet habitat. A cluster analysis based on PCA factors has the advantage that it can include highly intercorrelated habitat variables and provide groupings at a level of complexity that cannot be achieved by simple judgement. The disadvantage is that results cannot be transferred to other locations but must be redone for every concrete set of considered plots. Furthermore, results are highly dependent on the methods used for clustering and on the variables included in the analysis.

The results of the clustering introduced here (chapter 3.2.3) provided groups that differed highly significantly in all tested measures of occupied activity and habitat characteristics. This is not very surprising because I only included habitat variables which had correlated with Marbled Murrelet activity and the habitat variables tested for differences among groups had all been included in the cluster analysis. As in other groupings the differences among groups was mostly due to an outstanding group (here group 2), which again exclusively contained valley bottom stations. Next outstanding but in many measures not significantly different was group 4, which contained very high elevation and very exposed stations. The groups 1 and 3 were statistically indistinguishable.

The random scanning of the correlation matrix after the Bonferroni correction had been applied showed that Marbled Murrelet occupied activity (LNIRAOCC and LNIRACO) was significantly correlated with DENLSS, DENSS, DENLWH, DENYC, DENMH, HTMEAN, TREEHT, and TIMBVOL. All correlations coefficients were positive except those of DENYC and DENMH. From a biological point of view it is hard to interpret the correlation of Marbled

Murrelet occupied activity with the first five variables above, which are related to the density of individual tree species. Do Marbled Murrelets really prefer to nest in a certain tree species or do they nest in any tree species that provides adequate structures? Species associated with lower elevation habitats, such as western hemlock, Sitka spruce, and Douglas-fir, tend to have higher numbers of potential platforms than higher elevation conifers such as yellow cedar and mountain hemlock (Hamer and Nelson 1995b). Nevertheless, Beauchamp *et al.* (1998) found 8 nests in yellow cedar and one nest in mountain hemlock, indicating that Marbled Murrelets do use these species for nesting provided that they have adequate structures. Therefore, I do not think that Marbled Murrelets discriminate on the basis of species. Consequently, differences in the abundance of Marbled Murrelet relevant structures might be better determined directly with vegetation surveys than indirectly with species abundances.

The next two variables identified by the random scanning, HTMEAN and TREEHT, are both measures of average tree height and to a degree express habitat quality indirectly. Marbled Murrelets do nest in large trees (an average of 58m ± 15m (*SD*), $n = 9$, in British Columbia, Hamer and Nelson 1995b). However, large trees in old-growth forests are often adjacent to small trees regenerating in gaps; therefore, the average tree height in old growth stands could work out to be the same as that of a mature second growth forest with even tree heights. To avoid this, an option could be to use the average height of the tallest 10% of trees in a plot, but I think a combination of tree height and standard deviation of tree height would be better. The standard deviation of tree height is dependent on the average height, but a combination of the two variables could give the average height more weight. I combined the four variables mean DBH, mean tree height, standard deviation of DBH, and standard deviation of tree height in a PCA (OLDIND2) and correlated this index with occupied Marbled Murrelet behaviour with satisfactory results. I think that this index expresses the structural heterogeneity required by the Marbled Murrelet quite well.

The last result of the random scanning is very important because timbervolume is available on forest industry maps. Although high timbervolume can mean either large trees interspersed with very small trees or narrowly-spaced medium-sized trees, the former is more likely than the latter in an old-growth forest. Therefore, timbervolume quite adequately indirectly describes the habitat needs of Marbled Murrelets in an old-growth forest without large-scale disturbances. Unlike vegetation units, such as site series, which are also available on maps for the Ursus, timbervolume correlated strongly and unambiguously with occupied activity of Marbled Murrelets. Therefore, I used it as a tool to create a preliminary map of potential Marbled Murrelet nesting capability in the Ursus (Appendix III, Figure 2). Despite the limitations of a secondary factor in describing Marbled Murrelet breeding suitability and the danger that it become a cheap and inadequate surrogate for field research, I think it can be a valuable tool for planning more detailed studies and making predictions to be verified by ground truthing. Furthermore, the potential exists to use timbervolume in conjunction with variables available on some types of forest cover maps; for example, including height class would reduce the chance that a stand of narrowly-spaced, small trees is misidentified as good Marbled Murrelet habitat.

Some habitat parameters that showed correlations with Marbled Murrelet activity in other studies did not prove to be important in the Ursus. Slope, for example, was not significantly (Bonferroni corrected) correlated with occupied activity although an apparent threshold for Marbled Murrelet suitability exists when slopes get too steep to support adequate vegetation. However, we did not conduct vegetation plots in dangerously steep terrain, even if stations took advantage of rocky outcrops as vantage points. In general, Marbled Murrelet nests have been found in slopes with moderate gradients (23% ± 23 (*SD*) for Pacific Northwest, 69% ± 16 in Alaska, Hamer and Nelson 1995b) with a maximum of 100% (Naslund *et al.* 1995). When considering accessibility, a nesting tree positioned on the slope could be advantageous to Marbled Murrelets because trees in slopes are likely to be more exposed. However, observations of Marbled Murrelet nests indicate that Marbled Murrelets fly a certain distance below the canopy prior to landing at the nest site. This behaviour is thought to be for predator avoidance (Singer *et al.* 1995; Nelson and Peck 1995; Nelson and Hamer 1995a). Therefore, an exposed nesting tree in a steep slope might not be the first choice of Marbled Murrelets. Nevertheless, the indications that Marbled Murrelets prefer one type of slope situation over another are too weak to include this aspect in any habitat evaluation or management decision. The extreme slope situations are better considered in terms of their influence on vegetation characteristics.

Another factor discussed in other studies is the distance between the survey station and the next closest stream. Marbled Murrelets have been observed using streams as a flight path to a nest site (Nelson and Hamer 1995a). Therefore, it was hypothesised that nests are more likely to be located in the proximity of streams. Random scanning did not yield a significant correlation between DISSTR and occupied activity in the Ursus. A problem with the data collection was that the size of streams considered for distance estimates by different observers varied greatly. Sometimes the Ursus exclusively was used as a reference, other times the nearest small stream. Because of its complex relationship with nest sites and the ubiquity of streams of all sizes in the Ursus, I do not think that distance to the next stream is an important or operable factor for Marbled Murrelet breeding habitat assessment in the Ursus.

Some of the indirect measures found in other studies are apparently only locally valid, such as redwood densities in California, mistletoe densities in Oregon (we rarely found significant amounts of mistletoe), and site location relative to the heads of bays in Alaska, where suitable habitat is mostly restricted to the lower valleys.

4.4 Conclusion

Considering the many sources of unwanted variability and the current level of knowledge on Marbled Murrelet habitat requirements it seems that the capability of audio-visual surveys to give new insight into Marbled Murrelet habitat preferences has reached its limits. From now on, the use of these surveys should be focused on management goals, such as monitoring activity levels or establishing occupancies of stands, and not on determining small-scale habitat preferences. Where audio-visual surveys are still used it should be attempted to keep sample sizes equal among years, so that individual survey results can be analysed and known sources of unwanted variability in Marbled Murrelet activity data can be corrected for. Furthermore, the number of stations should be kept low enough to allow sufficient numbers of surveys at each station (at least 3 per station and year).

Future research should focus on more direct methods of determining Marbled Murrelet habitat requirements, such as radio tagging and nest searches by tree climbing.

Another problem that urgently needs to be addressed is the adequate description of vegetation in relation to Marbled Murrelet habitat suitability. I think that, on a landscape level, timbervolume (possibly in conjunction with other mapped variables) is a good planning tool. On finer planning scales vegetation surveys will remain essential. However, my results indicate that the vegetation sampling method used in this study was not sufficient to adequately characterise the vegetation of the area sampled by a given audio-visual survey. The vegetation in old-growth forests often changes rapidly over small distances. Therefore, sampling methods using transects or several stratified random vegetation plots are more suitable for the description of vegetation than a single vegetation plot per station.

The most useful and important variables for predicting the suitability of Marbled Murrelet habitat identified in this thesis were density of trees with more than 3 platforms (DENTRPL4), epiphyte cover (EPIMEAN), standard deviation of tree height (SDHT), a PCA combination of mean DBH, mean tree height, standard deviation of DBH and standard deviation of tree height (OLDIND2), and timbervolume (TIMBVOL). The number of potential nesting platforms per ha (POPLAHA) is an important variable and could be useful given that the vegetation sampling is improved. Variables that were valid in the Ursus but might not be transferable to other situations (*e.g.*, where high elevation productive habitat exists) were the density of large (DBH > 80 cm) Sitka spruce and western hemlock, the density of all mountain hemlock, yellow-cedar, and Sitka spruce, and altitude. Distance to the ocean was not important in the Ursus because the valley lies within 20 km of the ocean. However, this variable, as well as altitude, certainly expresses Marbled Murrelet habitat suitability in terms of the proximity of feeding and breeding habitats on a larger scale.

For future research I would suggest testing the ability of the aforementioned variables to predict good Marbled Murrelet habitat. Additions to and deletions from the list of predictive variables should be made based on new results obtained from the analysis of vegetation around known nest sites.

5. A Habitat Suitability Index Model for the Marbled Murrelet

To use the Marbled Murrelet in management decisions, methods must be developed to evaluate potential Marbled Murrelet habitat in a standardised way. The Habitat Evaluation Procedure (HEP), developed by the US Fish and Wildlife Service (1980), is a standardised model for habitat evaluation, which has been widely applied in North America (Gray *et al.* 1996). It is based on a Habitat Suitability Index (US Fish and Wildlife Service 1981), which is calculated using variables known or perceived to be important to a species.

I have constructed an HSI for the Marbled Murrelet, based on the habitat requirements identified in this thesis. It is not meant to be the final solution to the problems encountered in Marbled Murrelet breeding habitat evaluation, but rather a starting point for discussion among Marbled Murrelet experts in British Columbia and elsewhere. Much more data on habitat requirements of Marbled Murrelets is available in British Columbia than has been considered in this study. Therefore, changes in the variables included and their evaluation must be anticipated. Most importantly, the final model should be based on data gathered from known nest sites, not on data from audio-visual surveys, as this first draft is. The relationship between activity measured in audio-visual surveys and real nesting density is not known; therefore, inferences built on survey data are of a speculative nature.

The construction of the HSI closely followed the steps outlined in the original manual (US Fish and Wildlife Service 1981):

a) Set objectives;
b) identify model variables;
c) structure the model;
d) document the model (during all other steps);
e) verify the model.

The main objective for building this model was to provide a management tool for the evaluation of coastal temperate rain forest as breeding habitat for Marbled Murrelets. It does not consider any other habitat requirements of the Marbled Murrelet (*e.g.*, foraging habitat). The ideal evaluation output from the model would be linearly related to nesting density and success of

Marbled Murrelets. My suggestion for the geographic area this model could be applicable to would be the Coast and Mountains Ecoprovince. This range may be too wide and therefore must come into special consideration when the model undergoes verification.

The basis for the identification of important variables and their modelling are the results of this thesis (see chapter 3), biological meaningfulness, and additional information from the literature. Further considerations are the assumption of independence of the habitat variables in the model and the intended application of it. Unfortunately, many of the important variables identified in this thesis are highly intercorrelated. For example, timbervolume and epiphyte cover have a Pearson correlation coefficient of $R = 0.662$, which makes the inclusion of both variables unacceptable.

The intended application of this model is fine scale planning through the evaluation of discrete stands. Large scale habitat evaluation, as employed in GAP analyses (Gray *et al.* 1996), which requires information mapped for large areas, could be attempted with a very simplified model, which would include timbervolume, height class, altitude and distance to the ocean as variables. However, my intention was to build a model for finer scale planning, which would incorporate more variables.

I chose the following variables for inclusion in the model:

- Mean epiphyte cover on trees (EPIMEAN);
- Number of trees per ha with more than three platforms (DENTRPL4);
- Standard deviation of tree height (m) (SDHT);
- Canopy closure (CANCLVEG);
- Distance to the Ocean (km) (DISSEA);
- Altitude (m) (ALTITUDE);
- Distance to the nearest forest edge (m) (DISEDGE).

The next step in building the model was the construction of adequate graphs, which describe the relationship between a measure of the variable and habitat suitability. To do this I fit 90^{th} quantile regression lines (see chapter 2.3.5) through graphs with the dependent variable LNIRACO and the habitat parameters EPIMEAN, DENTRPL4, SDHT, and CANCLVEG as independent variables. Then I fit a curve through the graphs with the idea that the regression line represents an upper ceiling, equivalent to the limit placed on Marbled Murrelet activity by the habitat variable under consideration. The curves are visually fitted constructs based on mathematical equations and biological meaningfulness (Figure 11 - Figure 14). The intention of these curves was not a mathematical modelling of Marbled Murrelet activity but a biologically meaningful evaluation of their habitat. Lastly, I translated the y-axes of the graphs into habitat suitability scores of 0 to 1 by assigning the value 1 to the 95th quantile of LNIRACO.

The spatial variables that I had identified as being important (DISSEA, ALTITUDE, distance to forest edge) could not be sampled adequately in the Ursus or were strongly related to other variables. Therefore, I based the suitability graphs for these variables on information from the literature (Figure 16 - Figure 17).

Epiphyte cover (EPIMEAN), estimated as the percentage of tree branch area covered by epiphytes, has been shown to be a good predictor of Marbled Murrelet activity (see chapter 3.2.4). Biologically, this variable makes sense, as most Marbled Murrelet nests occur on moss. Furthermore, the data collection for this variable is relatively unproblematic as epiphyte densities do not seem to vary greatly on a small scale. Therefore, the potential exists to predict or map epiphyte density on a larger scale.

Large platforms are usually quite old and therefore provide time and space for epiphyte colonisation. In places where epiphyte cover is low to medium overall, platforms tend to be sufficiently covered. Therefore, the value of a habitat increases quickly with relatively small increases in epiphyte cover and changes slowly in the highest classes of epiphyte cover. Consequently, I chose a logarithmic function to rate epiphyte density (suitability index = 0.541 * LN(0.2 * EPIMEAN + 0.15) + 1.027, Figure 11).

The construction of a suitability index for a measure of available nesting platforms based on data from the Ursus was very problematic. I used the same technique as for epiphyte cover, but the result is not as clear (suitability index = 0.265*LN(0.02 * DENTRPL4 + 0.05) + 0.795, Figure 12). As discussed (chapter 4.3.1), I think that the representative measurement of potential platforms in a given area is problematic as the distribution of trees with suitable platforms varies greatly on a small scale. A new vegetation sampling technique should be explored in conjunction with data from known nest tree sites to improve the suitability index for potential nesting platforms. The number of trees per ha with >3 platforms was the measure I chose to include, as Marbled Murrelets seem to avoid trees with fewer platforms (Hamer and Nelson 1995b). The mapping of densities of potential nesting platforms on a large scale will probably never be feasible. Therefore, models aiming at preliminary, large-scale habitat evaluation from maps should use timbervolume as a surrogate predictor variable.

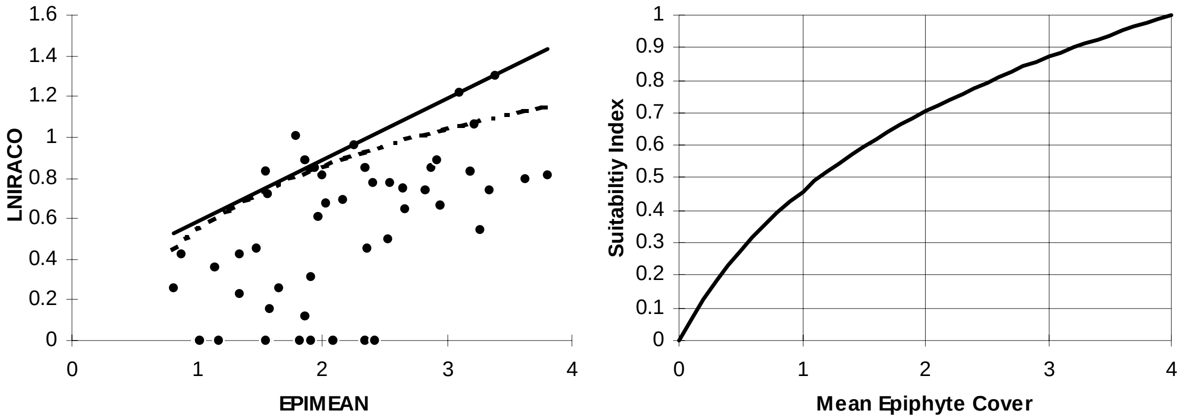

Figure 11: Construction of the suitability index for epiphyte cover (EPIMEAN) in Marbled Murrelet breeding habitat. Left, the scatterplot with mean epiphyte ratings of 51 stations in the Ursus Valley against the mean occupied detection rate (LNIRACO). The solid line is the least absolute deviation 90th quantile regression line and the dotted line is the suggested logarithmic description of habitat suitability. Right, the translation of the fitted logarithmic function (suitability index = 0.541 * LN(0.2 * EPIMEAN + 0.15) + 1.027) in a suitability index from 0 to 1.

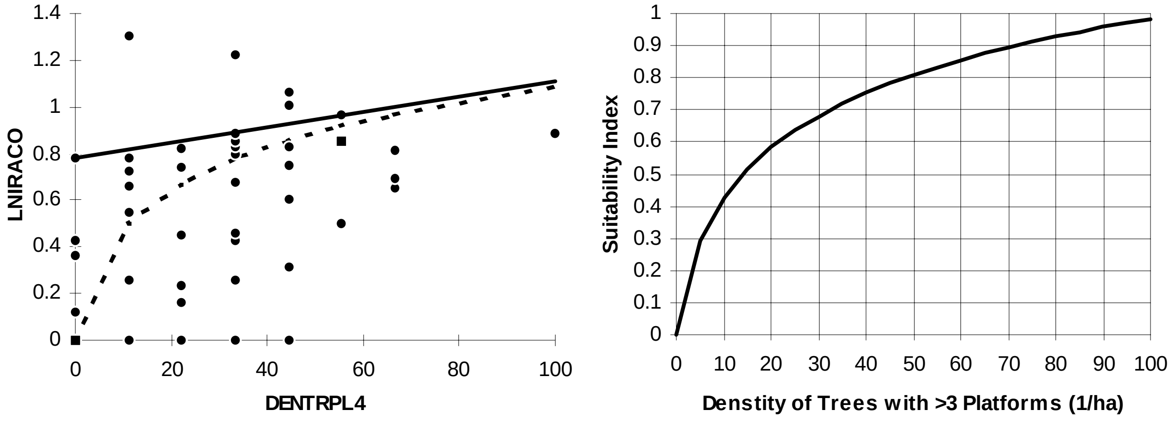

Figure 12: Construction of the suitability index for the number of trees per ha with >3 platforms (DENTRPL4) in Marbled Murrelet breeding habitat. Left, the scatterplot with DENTRPL4 ratings of 51 stations in the Ursus Valley against the mean occupied detection rate (LNIRACO). The solid line is the least absolute deviation 90th quantile regression line and the dotted line is the suggested logarithmic description of habitat suitability. Right, the translation of the fitted logarithmic function (suitability index = 0.265 * LN(0.02 * DENTRPL4 + 0.05) + 0.795) in a suitability index from 0 to 1.

The last vegetation characteristic variable modelled in the same way as the previous two variables is standard deviation of tree height (SDHT). Representing the vertically well structured (multi-layered canopy) old-growth forest necessary for Marbled Murrelet nesting (Hamer and Nelson 1995b), it showed satisfactory results in the regression analyses (chapter 3.2.4.2). Logarithmic modelling (suitability index = 0.3 * LN(0.2 * SDHT - 0.5) + 0.57) fit the data from the Ursus Valley well (Figure 13). The potential to roughly map this variable on the large scale from aerial photographs may exist.

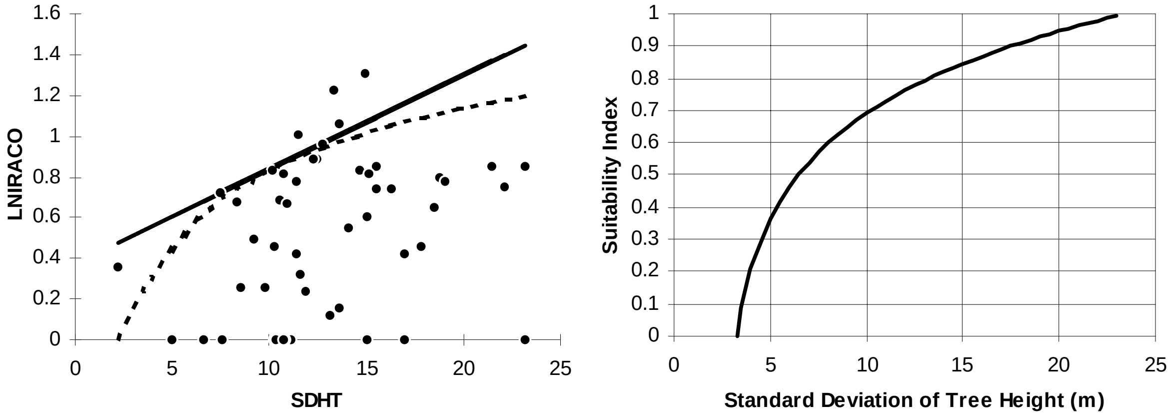

Figure 13: Construction of the suitability index for the standard deviation of tree height (SDHT) in Marbled Murrelet breeding habitat. Left, the scatterplot with SDHT ratings of 51 stations in the Ursus Valley against the mean occupied detection rate (LNIRACO). The solid line is the least absolute deviation 90th quantile regression line and the dotted line is the suggested logarithmic description of habitat suitability. Right, the translation of the fitted logarithmic function (suitability index = 0.3 * LN(0.2 * SDHT - 0.5) + 0.57) in a suitability index from 0 to 1.

The last vegetation characteristic in the model, canopy closure (CANCLVEG), has a non-linear, non-monotonous relationship to habitat quality. Furthermore, the estimation of canopy closure is difficult and varies widely with observer. Therefore, the suggested suitability graph (Figure 14) is a rough estimate, related to both the Ursus data and data from the literature (Hamer and Nelson 1995b). The potential exists for estimation of canopy closure on a large scale from aerial photographs.

The graphs developed for the spatial variables were derived completely from the literature because the data from the Ursus Valley were not sufficient. The Ursus Valley does not contain a large enough range of distances from the ocean nor enough forest edges to provide comprehensive data on these two variables. For altitude, the changes in vegetation and therefore suitability of the habitat were not typical in the Ursus as it has steep sides and exposed ridges and consequently its high elevation habitat has low densities of Marbled Murrelet-relevant structures. Elsewhere, high elevation habitat has been shown to support considerable numbers of nesting Marbled Murrelets (Drever *et al.* 1998).

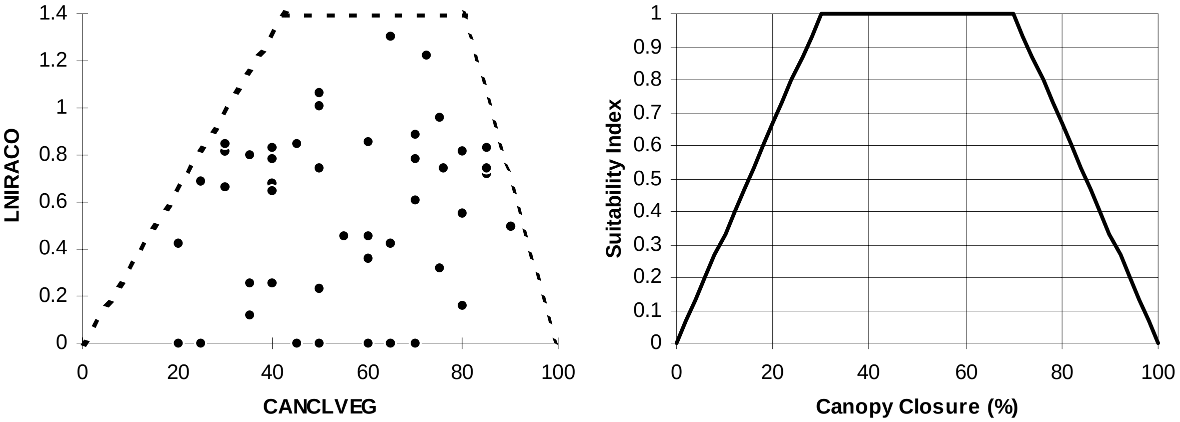

Figure 14: Construction of the suitability index for canopy closure (CANCLVEG, %) in Marbled Murrelet breeding habitat. Left, the scatterplot with CANCLVEG ratings of 51 stations in the Ursus Valley against the mean occupied detection rate (LNIRACO). The dotted line is the suggested description of habitat suitability. Right, the translation of the suggested function (suitability index = CANCLVEG / 30 for CANCLVEG < 30; 1 for 30 ≤ CANCLVEG ≤ 70; and -CANCLVEG/30+10/3 for CANCLVEG >70) in a suitability index from 0 to 1 based on information from the literature (Hamer and Nelson 1995b).

Distance from the ocean as a habitat characteristic has two separate considerations. One is that Marbled Murrelets tend to nest in trees that are not directly on the coast, possibly to avoid predators (Hamer and Nelson 1995b). In a study in Washington, Hamer (1995) found several stands of suitable Marbled Murrelet habitat < 800m from the shore unoccupied. The other consideration is the physiological constraint on how far Marbled Murrelets can fly inland to feed their young with single prey items. Nelson (1997) stated that all nests found in North America so far have been < 50 km away from the shore, most of them within 30 km of the coast. However, a grounded fledgling has been found as far as 101 km inland (Rodway *et al.* 1992). An exact quantification of both effects requires information on nest densities from random samples and information on nesting success at different distances from the ocean. I chose a linear increase in suitability from 0 - 2 km inland and a linear decrease from 30 - 100 km inland (Figure 15). To accommodate both effects in one graph, I chose a logarithmic scale for distance from the ocean.

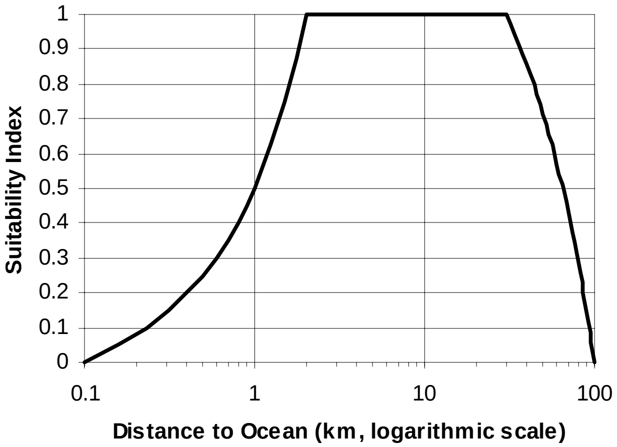

Figure 15: Suitability index for distance from the ocean (km, logarithmic scale) of Marbled Murrelet breeding habitat. The suitability score linearly increases from 0 to 1 from 0 - 2 km inland, remains at 1 from 2 - 30 km inland, and linearly decreases from 1 to 0 from 30 - 100 km off the coast.

Edge effects on Marbled Murrelet nesting have been discussed by several authors (Beauchamp *et al.* 1998, Hamer and Nelson 1995b; Burger 1995b). Nesting close to an edge means not only reduced cover, but also higher densities of known Marbled Murrelet nest predators (*e.g.*, corvids) than in the interior forests. Wilcove (1985) has shown edge-related increases in predation on artificial songbird nests 300 - 600 m into the forest. Manley (pers. comm.) found that successful nests (*n* = 7) were on average 254 m away from the nearest unnatural edge, while nests that were unsuccessful due to predation (*n* = 9) were 79 m away. The edge effect may not influence nesting density as much as nesting success. Therefore, studies that quantify nesting success will be required to fully understand and model habitat quality as it relates to the distance to the nearest forest edge. Another important question is whether the effects of artificial and natural edges on Marbled Murrelet nesting must be evaluated separately.

As a preliminary model for edge effects, I chose a sigmoid function (suitability index = 1.05 / (1 + (1.05 / 0.05 - 1)*(EXP(-0.02 * distance to the edge))) - 0.05; Figure 16) because the habitat quality likely improves slowly over the first few meters away from the edge and probably levels out as conditions change to typical interior forest. The effects of edges on Marbled Murrelet breeding habitat quality will be of high significance in the creation of protected areas. Major edges could be read off aerial photographs and be mapped out on a large scale.

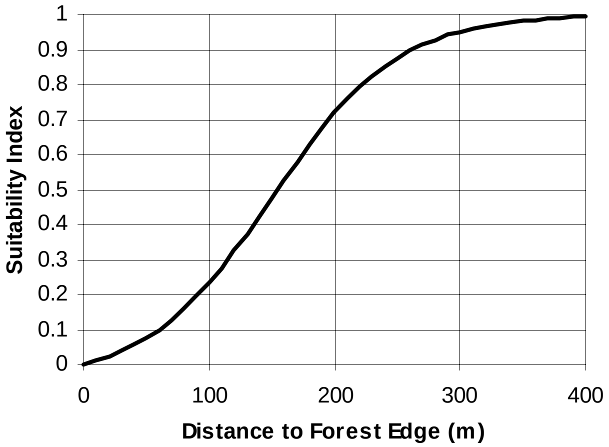

Figure 16: Suitability index for the distance to the nearest forest edge in Marbled Murrelet breeding habitat. The graph is a sigmoid function (1.05 / (1 + (1.05 / 0.05 - 1)*(EXP(-0.02 * distance to the edge))) - 0.05), translating the distance to the forest edge into a suitability score from 0 to 1.

As with distance to the ocean, I have considered altitude mainly as a physiological constraint and not so much as an influence on vegetation. The relationship between altitude and structural characteristics important to Marbled Murrelets is considered more directly through other variables. Little data is available on how high Marbled Murrelets will fly in search of suitable nesting habitat and how altitude influences nesting success. Hamer (1995) found that occupied activity dropped quickly above 1000 m elevation in Washington. Hamer and Nelson (1995b) stated that the best Marbled Murrelet habitat is probably below 945 m. In the Caren Range (Sunshine Coast, BC), considerable occupied activity and a successful nest were detected above 1000m elevation (pers. observations). Thorough studies on the influence of altitude on Marbled Murrelet nesting habitat quality will be extremely difficult, as the effect will be difficult to separate from the effects of altitude on vegetation. As a rough estimation, I chose a sigmoid decrease in habitat quality starting 900m and ending at 1400m elevation (suitability index = 1 for 0 m < altitude < 900 m and = 1 - (1.01 / (1 + (1.01 / 0.01 - 1) * (EXP(-0.02 * (altitude-900)))) - 0.01) for altitude > 900 m; Figure 17) above which I do not expect Marbled Murrelet activity in British Columbia.

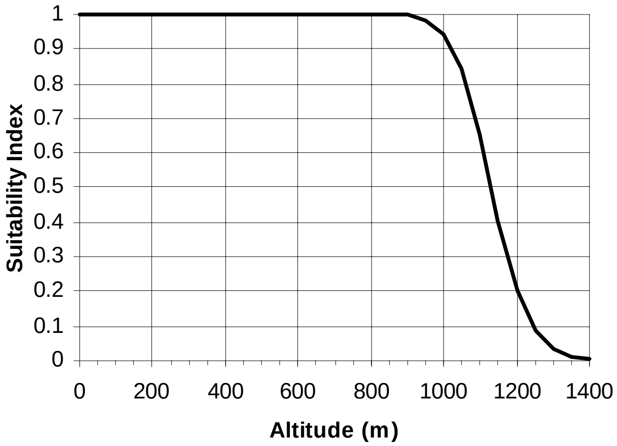

Figure 17: Suitability index for altitude (m above sea level) of Marbled Murrelet nesting habitat. The suitability score = 1 up to 900m of elevation and follows a sigmoid decrease further up (1 - (1.01 / (1 + (1.01 / 0.01 - 1) * (EXP(-0.02 * (altitude-900)))) - 0.01)) to become 0 at 1400m.

The combination of the individual suitability indices to form a single habitat suitability index is attempted in form of a mathematical expression. While some of the variables have a mainly compensatory relationship (canopy closure, epiphyte cover, standard deviation of tree height, and distance from edge) others have a dominantly limiting character (density of trees with >3 platforms, distance to the ocean, and altitude). I included compensatory variables in an additive way (arithmetic mean) and limiting factors in a multiplicative way (geometric mean). Furthermore, I gave epiphyte cover and density of trees with >3 platforms double weight as I consider them to be more important than the other variables. The resultant equation is **(the variable names stand for the Suitability Index of the variable, not the absolute value)**:

$$\mathbf{HSI} = \left[\left(\frac{CANCLVEG + SDHT + 2{*}EPIMEAN + DISEDGE}{5} \right)^{\frac{1}{4}} {*}(DENTRPLA4)^{2}{*}DISSEA{*}ALTITUDE \right]^{\frac{1}{8}}$$

I am aware that the construction of the preliminary individual SI's is based on audio-visual survey data from one valley, which are likely not representative of other areas and cannot be directly translated into nesting densities or nesting success of Marbled Murrelets. More direct studies of Marbled Murrelet nesting preferences are critical for the construction of a habitat suitability index, which can satisfactorily evaluate breeding habitat of Marbled Murrelets.

Another important issue is the measurement of habitat variables. The method of vegetation sampling used in this project, one 30 x 30m plot per station, may not be adequate. The sampling of a delineated stand should be done by stratified random sampling with several plots or by transects to accommodate small-scale changes in vegetation and Marbled Murrelet suitability. A random sample consisting of one vegetation plot is not sufficient. More work on vegetation sampling will be necessary to establish adequate methods.

The last step will be the verification of the HSI model. Before reaching this step, much more discussion and input from experts is required to refine the model suggested here. The testing of Marbled Murrelet nesting suitability predicted by the preliminary model could at the same time provide new information on Marbled Murrelet habitat preferences. The method of testing should be comparisons of nesting densities and success as determined by random design tree climbing studies and not comparisons of relative activities determined by surveys.

6. Conservation Implications

Although the BC government has announced that the new Forest Practices Code (see chapter 1.4.4) will drastically change forest practices in British Columbia towards world-class standards and protection of environment and wildlife (Premier Mike Harcourt in Anon. 1993, 1994), 97% of the current logging in coastal temperate rain forests is done by clear-cutting (Sierra Legal Defence Fund 1997). This technique removes Marbled Murrelet habitat for a period of > 250 years, which is beyond current planning time frames.

Conservation of the Marbled Murrelet and management of ecosystems with the Marbled Murrelet as a tool is impossible if British Columbia does not implement different forest practices. With only 6% of the low elevation old-growth rainforest in BC protected (Land Use Coordination Office 1996; Sierra Club of BC 1997), and considering that not all of these protected forests are suitable for Marbled Murrelet breeding, the Marbled Murrelet will likely go extinct under current silvicultural systems and cutting rates, or survive only in vulnerable remnant populations in the few bigger protected areas.

95% of all logging in British Columbia in 1997 was in old-growth forests (MacKinnon quoted in Greenpeace 1997). The BC Ministry of Forests (1996) estimates that it will be another 50 years before significant amounts of second growth forest can be harvested. Therefore, the logging of primary forests will continue for many more years. Considering that 284 of 353 (82%) coastal rainforest watersheds larger than 5000 ha have been fragmented already (Sierra Club of BC 1997), further fragmentation of pristine watersheds has to be excluded from any serious conservation plans. Pristine watersheds are functional units disturbed to a largely unknown degree by any forest practices. They have to be representatively protected as an entity or blueprint on which future generations can draw for baseline information on natural ecosystems. This information is essential for any scientific nature conservation or restoration endeavours (Lertzman *et al.* 1997). The development of ecologically sustainable forest practices (*sensu* Callicott and Mumford 1997) must be exclusively focused on already-fragmented watersheds.

The duty of conservation biologists is not only to justify and to design protected areas but also to help create ways of sound land use (Plachter 1996b, 1997). Without sustainable ecosystem management, resources become depleted and the pressure on unused land steadily increases, until even reserves are threatened. In contrast to Europe, where cultural landscapes dominate, we are mostly dealing with primary forests in Clayoquot Sound. The pressure on old-growth forests in the region forces conservation biologists to find out how to creatively fragment a landscape (Laurance and Gascon 1997).

This approach has positive and negative sides. It enables proactive instead of reactive conservation planning. However, this planning should be based on a deep understanding of pristine ecosystems that largely does not exist yet (Ehrlich 1996). The only long-term sustainable management of these ecosystems has been practised by First Nations, who have resided in the area for thousands of years without depleting the resources.

The need for more information before making decisions on land use in Clayoquot Sound has been expressed several times. When the government of British Columbia adopted the recommendations of the Scientific Panel (1995a) and assured that they would be fully implemented, Forests Minister Andrew Petter (cited in: Anon. 1995) stated that "[u]ndisturbed watersheds will not be open to logging until comprehensive ecological assessments are completed and the recommendations can be fully implemented, . . ." Chief Louie Frank wrote in a position paper of the Ahousaht Band Council:

> "The Ahousaht First Nations have used and benefited from the resources in the Ursus valley for many centuries. Spiritual practices were performed for many families in this valley not unlike a cathedral to many of the Christian faiths. . . . So unless it can be guaranteed that no damage to the Ursus Creek and valley would occur by the removal of our resources in Ursus Valley, our Chiefs, Elders, and membership of the Ahousaht First Nation would not give our permission to log or mine or build a road in the Ursus Valley." (cited in Anon. 1996)

The work of the Scientific Panel (1995a, 1995b, 1995c) was a large effort in the direction of sustainable ecosystem management. Their three final reports set the standards for forest practices and planning in Clayoquot Sound. The experts on the panel, some of which were First Nations members, produced a comprehensive report on the First Nations' point of view and inclusion in the planning process instead of just "considering" them as done so often in the past. In addition, they examined values of non-First Nations and values other than timber resources of the area. They critically reviewed the forest practices in Clayoquot Sound, and gave new detailed recommendations for timber extraction, yarding, transport, and temporal storage of logs. Furthermore, they compiled available information on ecosystems, organisms, processes, and made recommendations on monitoring, which is indispensable for the validation of management efforts and for adaptive management (Plachter 1991a, 1991b, 1992b; Grumbine 1997; Brown and Rowell 1997).

The recommendations put forward by the scientific panel give a very well-researched and arranged framework for concrete research and planning. The expanded study on Marbled Murrelets in Clayoquot Sound, 1996-97, can be seen as a research effort initiated by the recommendations of the Scientific Panel on inventories and monitoring of threatened species. With the help of the data collected during this study and analysed in this thesis, I hope to add information and conceptual depth to the goals outlined by the Scientific Panel.

The Scientific Panel realised that comprehensive ecological information on individual species is sparse in Clayoquot Sound. Therefore, they have focused on monitoring habitat by its structure rather than by its organisms. Although I agree that there is hardly sufficient information available for detailed management of any species occurring in Clayoquot Sound, I disagree that habitat monitoring is the best solution to the problem. The Scientific Panel (1995a) has named dynamic change as one of the most important characteristics of an ecosystem (see also Plachter 1996a). Habitat structures often change during succession, landshaping processes, and other disturbances. Therefore, the making of concrete goals for habitat structure is difficult and is not the best answer to the question of how to manage ecosystems, although it certainly plays an important role in planning on a landscape level (Franklin 1993).

In contrast, observing the species that live in the ecosystem is a good indicator for its integrity and functionality because species do not change in the planning time scales (Walter *et al.* 1998; Hansen *et al.* 1993). High fluctuations in abundances and distributions will make this approach difficult but at least the function, ecology and identity of the observed species will remain constant. The lack of information on individual species cannot justify passiveness towards application of an important strategy in nature conservation. “The risk of non-action may be greater than the risk of inappropriate action” (Soulé 1986). Thus I suggest shifting the focus of the ecosystem management strategy in Clayoquot Sound to a species-based approach.

6.1 The Target Species Concept

There are several related strategies dealing with the idea of managing ecosystems by an array of selected species:

- management indicator species, often employed by the US Forest Service (*e.g.*, Woodruff 1989, Wilgrove 1989);
- target species (Reck *et al.* 1994; Walter et al 1998, Hansen *et al.* 1993);
- umbrella species (*e.g.*, Launer and Murphy 1994);
- array of indicator species (Plachter 1991b; 1992a);
- keystone species (Paine 1966; Lawton and Brown 1993);
- focal species (Lambeck 1997);
- the flagship species strategy (*e.g.*, Yen 1993);
- indicator species strategy (*e.g.*, Soulé and Kohm 1990, Kremen *et al.* 1993).

Even the Endangered Species Act (ESA) is related to this approach. Although the ESA aims at the recovery of endangered and threatened species, other species often profit largely from the same conservation measures (Woodruff 1989; Noon and McKelvey 1996).

Essentially, all of the previously mentioned strategies aim at the prevention of habitat degradation and further loss of biodiversity by monitoring selected species and maintaining, at the very least, a certain minimal population level. The strategies differ in how these species are selected, what they stand for, and at what levels they are protected or monitored. I will use the term target species (Woodruff 1989; Walter *et al.* 1998) and will use the following definition:

A target species is a species used in defining and monitoring conservation goals.

Management strategies, such as ecosystem sustainability, will remain weak and hard to implement without quantification of goals and quality standards (Plachter 1991b; Hansen *et al.* 1993). By setting certain lower limits of tolerance for abundance of the target species, environmental quality goals become clearly defined (Walter *et al.* 1998; Heidt *et al.* 1997; Heidt and Plachter 1996; Plachter 1996b).

In statistical terms, these limits of tolerance would be the limits we set for what we perceive as a significant ecological change. The null hypothesis would be that there is no change in abundance of a certain species and the power of the test would be the probability of correctly retaining the null hypothesis (typically chosen at 80%). The probability of not detecting a significant change would be 20 % in this case. Given these parameters and the natural variability in population size, we could calculate exactly how big the sampling effort would have to be for successful monitoring (Reed and Blaustein 1997; Zar 1993).

In the same manner as the limits of tolerance are chosen, the selection of an array of target species is a normative convention of experts (Walter *et al.* 1998; Reich 1994). The selection process should follow certain rules, which would have to be adapted for every specific situation and region. For Clayoquot Sound I would suggest the criteria outlined in Table 1. The list of target species should be as comprehensive as possible and should be amended as new information becomes available. It should comprise species of all sizes and trophic levels, not only the large vertebrates. The biggest gap in the species considered and researched in Clayoquot Sound so far is comprised of organisms of lower trophic levels and smaller body sizes. Very little is known about invertebrates of Clayoquot Sound, which are very important for small-scale conservation management (Kremen *et al.* 1993, Økland 1996).

Summarised, the strategy of target species has the following advantages for ecosystem management (Walter *et al.* 1998; Reck *et al.* 1994; Mühlenberg 1993; Vogel *et al.* 1996; Altmoos 1997; Hovestadt *et al.* 1991; Hansen *et al.* 1993; Reich 1994; Plachter 1991b):

- abstract goals and rationales of conservation such as ecosystem health or sustainability receive a concrete meaning.
- goals of ecosystem management become quantifiable;
- quantified goals can be monitored;
- saves time and money compared to all-inclusive approaches;
- indirectly contributes to the conservation of other species, habitats, and processes (umbrella effect);
- a hierarchical (in both a trophic and body size sense) array of target species allows the management and conservation of species and protected areas which considers all spatial scales;
- species remain the same in the planning time frames whereas ecosystems often change or fluctuate within planning time frames;

- some species rely on larger-scale connections and landscape functions that might be overlooked with other approaches;
- different executors of management plans will come to similar conclusions by using a quantitative, well-defined approach;
- more pressure exists for forest industry or other resource users to prove that the extraction is not harmful to the environment, because the damage becomes quantifiable;

To manage a target species some basic information is required. It is essential to know the distribution and abundance (at least semi-quantitatively), the ecology (feeding and breeding, habitat requirements, dispersal), and the basic life history attributes (survival, longevity, fecundity) of the species. Also important is information on the home range (where applicable), and threats.

Table 1: Selection criteria for target species (changed from Altmoos 1997)

Required Characteristics:	Preferred Characteristics:
• indigenous to the region • has a chance to survive through the next planning periods without artificial support • representative for other species (umbrella species) • sensitive to habitat alterations	• important to First Nations • threatened (mostly by habitat depletion not directly by human-induced mortality) • complex and high habitat requirements (specialist, not ubiquist) • geographically restricted distribution • indicator species • keystone species • not migratory • low dispersal • ecological and demographic information available • feasibility of research • economically significant • popular/attractive

Very good planning tools are population models such as the Minimum Viable Population (MVP) analysis (Shaffer 1981; Soulé 1986; Gilpin and Soulé 1986; Vogel *et al.* 1996), which provides information on the minimum population required to survive a certain time (often 100 years or more) with a certain probability, and the Population Viability Analysis (PVA) (Boyce 1992; Gilpin and Soulé 1986), for estimates of the ability of a population to survive different scenarios. The MVP can be translated into a minimum amount of habitat required for the survival of a certain species if the habitat requirements of a propagation unit are known. The PVA can analyse the relative significance of individual parameters to the survival of a species and thus can help identify the most important threats. Unfortunately, MVP and PVA both require a large amount of specific information on a species, which is not feasible to attain for a high number of target species. However, Hansen *et al.* (1993) pointed out that the demography of a species must not necessarily be known to estimate the minimum population and habitat size required for survival.

Most of the criticism of the target species strategy relates to a lack of knowledge about the target species and the inability of scientists to determine complex interactions and relationships. For example, the representation of other species' needs by target species has rarely been proven, and has especially been questioned for rare species (Walter *et al.* 1998). Furthermore, temporary movements of species make small-scale evaluations difficult. If the predicted indicative function of the target species fails, for example, due to unexpected ecological flexibility, public acceptance can quickly turn into even stronger negative publicity for the strategy (Reich 1994).

Reck *et al.* (1994) and Walter *et al.* (1998) put forward a strategy that includes three categories of conservation using target species in Baden-Württemberg, Germany:

- conservation of species and habitats;
- definition of environmental minimum quality standards required for the different forms of land-use;
- conservation of processes.

Adapted to Clayoquot Sound this strategy could be specified as:

- conservation of species and habitats with focus on the late-seral old-growth forests and associated species;
- definition of environmental minimum quality standards for forest practices (*e.g.*, percentage and kind of retention of old-growth in cut blocks);
- conservation of processes with focus on hydroriparian zones (*e.g.*, creek and floodplain dynamics).

6.2 The Marbled Murrelet as Target Species

When evaluated according to the criteria for target species, the Marbled Murrelet is a promising candidate. It is highly threatened under current forest practices but is not likely to go extinct if the promised changes in forestry come into effect. It is indigenous to British Columbia and is highly dependent on old-growth forests as breeding habitat. Any alteration of breeding habitat is likely to cause decreases in fecundity and long-term decreases in abundance of the Marbled Murrelet (see chapter 1.1.5). With its high requirements in terms of breeding habitat, the Marbled Murrelet would very likely provide for the protection of many other old-growth dependent species. The Marbled Murrelet is not known for large-scale migrations although certain seasonal movements are known. In addition, the causes of its “endangered” status are mainly attributable to breeding habitat loss and not threats in other seasonal habitats. Furthermore, the Marbled Murrelet is thought to exhibit a certain breeding area fidelity, what means that it probably does not disperse quickly, although it is known to fly quite long distances in search of breeding habitat (see chapter 1.1).

A drawback is that, despite the relatively large amounts of effort and money that have been put into Marbled Murrelet research, very little is known about its basic life history parameters. Furthermore, all demographic research is overshadowed by high variability in Marbled Murrelet activity and much spatial movement on all time scales. Therefore, much more research is needed in the areas of life history and demography.

Unfortunately, I was not able to find any indications that the Marbled Murrelet had or has cultural significance to the First Nations in Clayoquot Sound. However, the Tlingit cultural group of Southeast Alaska considers the Marbled Murrelet to be “the mother of Raven”, a position of great power and mystique (de Laguna 1972). Tlingit and Haida have murrelets as depictions on ceremonial headgear.

Last but not least, in contrast to four years ago when I first researched Marbled Murrelets, today I rarely have to explain to someone what a Marbled Murrelet is. Back then I remember my mother telling my brother that I had found the nest of some sort of flying penguin. Nowadays, the Marbled Murrelet is one of the high profile species in North America.

Different species can serve to define and monitor different goals (Lambeck 1997). With its dependence on old-growth forests, the Marbled Murrelet can serve as not only an indicator of the sufficiency of the overall retained old-growth forest, but can also indicate the success of silvicultural systems that leave significant numbers of remnant trees, such as the variable-retention system (Scientific Panel 1995a) or, even better, selective logging. In other words, it can be used in the protection of habitat and other old-growth dependent species, as well as in the definition of minimum standards for forest practices. It is not useful in a strategy for the conservation of processes or connectivity in the landscape.

The approach to using the Marbled Murrelet as a target species and to deciding what specific levels of parameters to employ must be adjusted to each situation and watershed.

Figure 18 shows a decision-making model, which could help at an early stage of planning. As a general approach I would suggest using radar counts at the estuaries as a semi-quantitative measure of overall breeding activity in a watershed (Burger 1997), using timber volume as a rough- and the HSI put forward in this thesis as a fine-scale tool for the evaluation and monitoring of breeding habitat, performing ground surveys at relatively few, strategic points in the watersheds for semi-quantitative monitoring of activity on a finer scale, and climbing trees in search of nests for fine-scale habitat evaluations and management decisions.

Radar counts are the ideal means for the rough long-term monitoring of Marbled Murrelet population sizes in watersheds. An exact determination of the breeding population is not possible, because a) birds could enter the watersheds several times in a single morning (leads to overestimation); b) probably not all of the birds entering a watershed are breeding (leads to overestimation); c) groups of birds entering the watershed are not counted as more than two individuals (leads to underestimation); d) not all birds enter the watershed by the estuary (leads to underestimation); and e) some birds entering through the estuary may be nesting in a different watershed (leads to overestimation). However, trends in population sizes can still be measured validly and that is enough for management purposes. A problem exists if large numbers of birds go to other watersheds via the watershed under consideration. These situations (*e.g.*, Watta Creek, Burger *et al.* 1997b) need special consideration as abundances might change for reasons not related to the watershed under consideration.

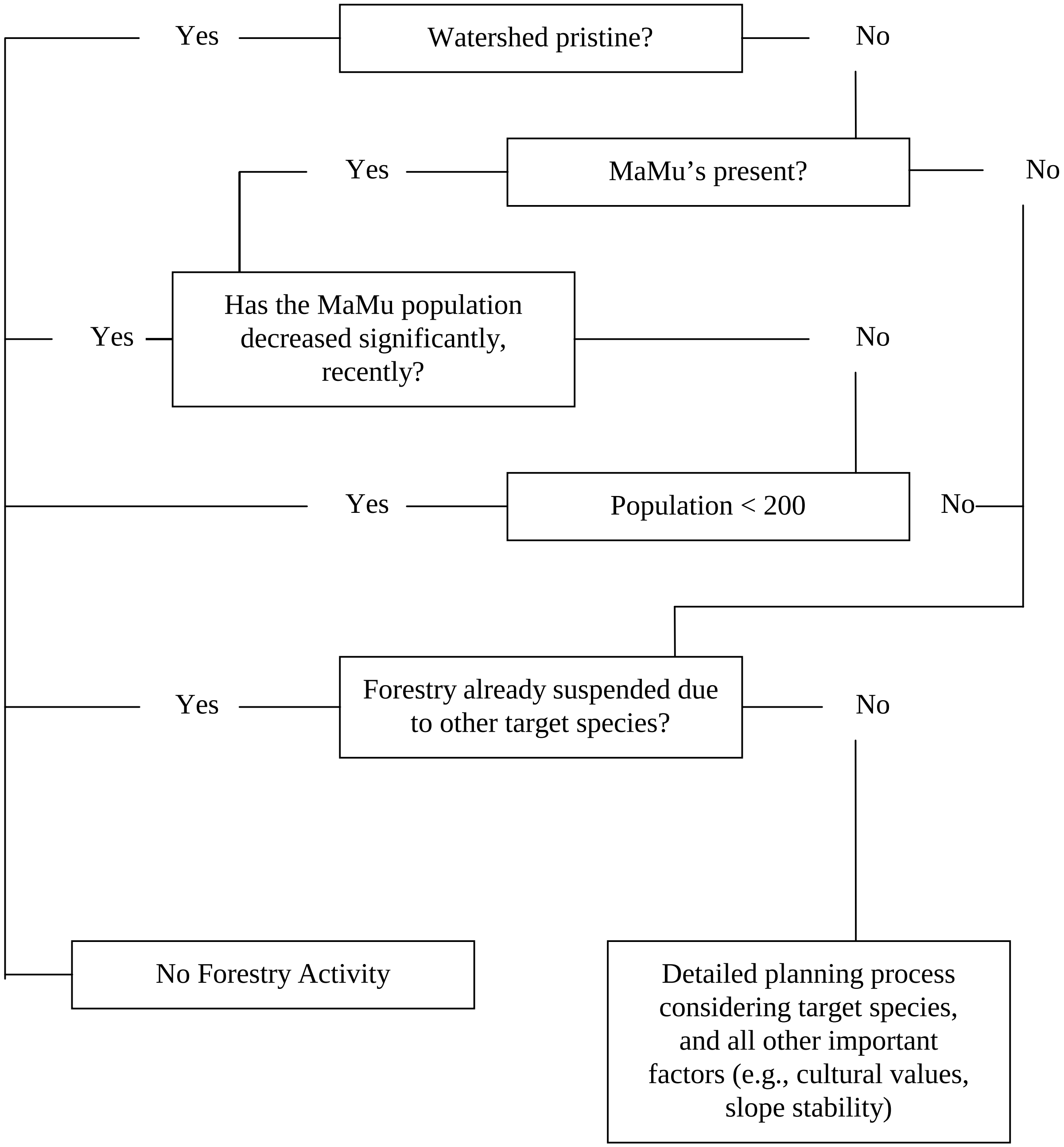

Figure 18: Decision-making model using the Marbled Murrelet as target species in an early planning stage.

The limits of tolerance for the evaluation of ecosystem management using radar counts could be defined in absolute numbers of Marbled Murrelets or in a change in numbers defined to be ecologically significant (as discussed in chapter 6.1). Whereas the latter option would provide for a calculation of the necessary monitoring effort, the first option is more problematic because of the difficulties in estimating absolute numbers. Nevertheless, considering that murrelets might exhibit a certain breeding site fidelity (Divoky and Horton 1995), the birds breeding in a watershed could be defined as a population, and certain numbers suggested as a minimum requirement for healthy populations could be applied. Hansen *et al.* (1993) have suggested that 200 individuals is a good rule of thumb for a viable population of vertebrates, especially when other populations exist in the proximity. Therefore, I would suggest using this number as a goal for medium sized, developed watersheds in the proximity of protected pristine watersheds. On the other hand, the normative definition of tolerable change in population size would have to be made individually for every managed watershed. A heavily logged watershed would receive low limits of tolerance, while a marginally logged watershed would receive slightly higher ones.

When forest activity is planned in an already-developed watershed, timber volume could be used as a first rough indicator of habitat relevant to Marbled Murrelets. My results suggest that a timber volume of 550 m^3/ha could be a threshold under which there is a slim chance that the habitat would be suitable for Marbled Murrelet nesting. This figure is open to input and correction from current and future studies in British Columbia, in particular those where nests were found. Polygons with timber volumes higher than 800 m^3/ha contained the best Marbled Murrelet habitat and should be excluded from timber extraction. Alternatively, high volume areas could be logged selectively with a minimal retention of 800 m^3/ha of large old trees.

If sites suitable for timber extraction are identified, detailed plans must be initiated. Small scale planning at extraction sites should involve vegetation surveys, which include the recording of parameters significant to Marbled Murrelets, to set priorities for forest retention. For this planning step I developed a habitat suitability index for Marbled Murrelets (chapter 5), which translates the actual state of the vegetation into an evaluation of Marbled Murrelet suitability in a standardised way. It is the core of the Habitat Evaluation Procedure, which should be a vital part of the detailed spatial planning process. This tool enables every trained individual to evaluate vegetation with regard to Marbled Murrelet suitability and should lead to similar results among observers and comparable results among different sites.

Parallel to differentiated habitat evaluation, audio-visual surveys should be established at some sites around the planning area to a) confirm the presence of Marbled Murrelets and b) initiate monitoring with the recording of activity levels prior to timber extraction. Where needed, tree climbing in search of nests would be the ultimate method to determine habitat preferences of Marbled Murrelets and to establish the occupancy of a certain stand.

For the evaluation and adaptation of ecosystem management continuous monitoring is indispensable (Grumbine 1997; Brown and Rowell 1997; Plachter 1991a). For Marbled Murrelets I would suggest routine counts by radar and at sea during the breeding season, to monitor relative abundances in watersheds and absolute ones in the whole Clayoquot Sound area. Fragmented watersheds that are considered for more timber extraction should be closely monitored using radar counts and audio-visual surveys at a certain number of permanent survey stations, to provide baseline data for the evaluation of future management measures. Pristine watersheds could be monitored as null models and should be the subject of further research on the habitat preferences of Marbled Murrelets in undisturbed circumstances, especially using tree climbing.

The last step of planning is synoptic. It must integrate the results of Marbled Murrelet related planning with the results of all other management considerations (*e.g.*, other target species, slope stability, connectivity among retained forest, protection of a representative array of vegetation units, etc.) in a standardised way (Plachter 1994), to give an evaluation of the planning area condition and processes. Finally, based on these results, management decision can be made.

6.3 Conclusion

The previous chapters make clear that much research must be done to fill conceptual frameworks with quantitative goals and detailed strategies. But how much more research is necessary so that ecosystem management is not a large experiment anymore and the target species concept is fully operable?

Right now, only a handful of vertebrate species have been studied in Clayoquot Sound. To make the target species strategy work, many more species coming from many more taxa must be included. However, in comparison to the high diversity of land-uses in Germany, which are partly responsible for the huge array of target species (700) used in Baden-Württemberg (Walter *et al.* 1998), the situation in Clayoquot Sound is less complex. The only large-scale land-use with a high impact on the ecosystems under consideration in Clayoquot Sound at this moment is the forest industry. Therefore, there is hope that a smaller number of target species than in Baden-Württemberg will be sufficient for detailed ecosystem management.

A priority should be the identification of non-vertebrates suited as target species. For example, plant species have the highest diversity in open areas such as riparian zones and bogs (Alaback and Pojar. 1997). They would most likely be suited to monitor those areas. In addition, forest plant species with short-lived diaspore banks and low dispersal rates deserve special conservation attention (Poschlod and Binder 1991; Poschlod *et al.* 1996). Canopy insects could be very interesting for the small-scale evaluation of timber extraction through the monitoring of retained trees. With their high diversity, terrestrial arthropods can be an excellent data source for planning and management (Kremen *et al.* 1993).

Undoubtedly, adequate research will take a long time. Mühlenberg (1993) estimates that the research necessary to acquire enough information on the demography of a target species takes 5-10 years. The monitoring done by observing population levels of target species will take more than 5 years as well. Together with the implementation and evaluation of several different methods of logging and other kinds of land use, the whole process will surely take several decades.

However, that does not mean that it must be business-as-usual until new strategies are validated. On the contrary, invoking the precautionary principle, as the Scientific Panel (1995a) suggests, means that the forest industry should adopt the most progressive (or for nature the most conservative) forest practices right away, to prevent making irreparable or very expensive mistakes due to lack of knowledge on ecosystems.

A progressive approach to ecologically sustainable forestry is the mimicking of natural disturbance patterns (Lertzman *et al.* 1997). However, except for very exposed places where larger-scale windthrow occurs, large disturbances are uncommon in temperate rainforest (Kellogg 1992). Natural openings resulting from disturbances in these forests are generally less than two tree lengths in diameter (Meidinger and Pojar 1991). This makes clearcutting a rather inadequate method of logging in temperate rainforest. Furthermore, vegetation cover has an important function in intercepting the large amounts of precipitation, thus mitigating peak discharges and limiting erosion. In the past, clearcutting has led to increased soil erosion and stream degradation by sediment input and direct destruction (Scientific Panel 1995a; Simenstad *et al.* 1997).

However, clearcutting is the most cost-effective method of timber extraction. Who will pay for the higher costs of alternative methods? An economic report by Schwindt and Heaps (1996) indicates that, although amount of timber extracted has increased by 40% over the last 25 years, employment by the forest industry has remained about the same and the relative direct contribution of the industry to the gross domestic product of British Columbia has dropped from

11% to 8%. At the same time other values of the forest are increasingly expressed in monetary return, mostly through tourism and fisheries (commercial and recreational).

Furthermore, Schwindt and Heaps (1996) found some evidence that the Crown undercharges for timber extraction. The Coalition for Fair Lumber Imports in the USA allege that the undercharges of the Crown lead to unfair subsidisation of Canadian timber exporters and are pressuring for export controls on Canadian timber (Schwindt and Heaps 1996). In addition, increasing worldwide awareness of decreasing forest resources and inadequate forest practices has already led to boycotts against those BC forest products that originate from old-growth forests.

It would make sense to charge the forest industry adequately and to use this money to research and implement better forest practices. Jobs would be created in research and implementation, improvements in forest practices would please people at home and abroad concerned about the future of the forests, export controls would be prevented, timber harvest rates would decrease to a sustainable level, and tourists would spend money to see magnificent areas of continuous old growth temperate rainforest unique to this area.

As an example from the Pacific Northwest that the downsizing of forest industry, as one specific economic activity, does not necessarily have devastating or even negative impacts on the economy, Schwindt and Heaps (1996) reported from the US states Idaho, Montana, Oregon, and Washington: although reductions in the regions’ core industries (aerospace, timber, agriculture, fishing, and mining) had eliminated tens of thousands of jobs, the economies of the four states were doing well, outperforming the national average.

Clayoquot Sound is on its way to becoming a model of regional development that integrates conservation and resource use. Here new forest practices are being implemented, monitored and evaluated. Many results will be applicable to other regions with certain adjustments. The process, based on the aboriginal and non-aboriginal communities, is meant to create long-term sources of employment. The development in Clayoquot Sound will take time and money. Nevertheless, I believe that these resources are well-invested in a moral, social, and ecological sense, and, in the long run, in an economical sense as well.

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Appendix I - Variable Names and Analysis Data Set

Appendix I, Table 1: Names and definitions of variables used in this thesis. The two prefixes "IRA-" and "LN-" can occur in combination with all measures of activity and can occur individually or together in a variable.

Variable	Description
ALTITUDE	elevation in m above sea height, read off a 1:20 000 TRIM map
ASPECT	aspect for slopes ≠ 0 degrees
AUD	sum of auditory detections
AUDVIS	sum of detections which were auditory and visual
CANCL	canopy opening coded as 1=0-25%, 2=26-50%, 3=51-75% or 4=76-100%; this canopy opening relates to visibility of birds passing by and is incomparable to the canopy closure assessed during vegetation plots
CANCLVEG	average canopy closure from estimates of the percentage of sky blocked out by tree foliage, made at four points within the plot and averaged
CO	ratio between number of occupied detections and all visual detections (CO = OCC / (VIS + AUDVIS))
CO1, CO2, CO3	average of CO at a particular station in a certain year (1 = 1995, 2 = 1996, 3 = 1997)
CWO	CO corrected for weather by division by a correction factor
DBHMEAN	average DBH in cm
DENAF	number of amabilis fir > 10 cm DBH per hectare
DENLAF	number of amabilis fir > 80 cm DBH per hectare
DENLARGE	number of trees > 80 cm DBH per hectare
DENLMH	number of mountain hemlock > 80 cm DBH per hectare
DENLRC	number of western redcedar > 80 cm DBH per hectare
DENLSS	number of Sitka spruce > 80 cm DBH per hectare
DENLWH	number of western hemlock > 80 cm DBH per hectare
DENLYC	number of yellow cedar > 80 cm DBH per hectare
DENMH	number of mountain hemlock > 10 cm DBH per hectare
DENRC	number of western redcedar > 10 cm DBH per hectare
DENSS	number of Sitka spruce > 10 cm DBH per hectare
DENSTEM	number of trees > 10 cm DBH per hectare
DENTRPL4	number of trees per ha with >3 potential nesting platforms
DENWH	number of western hemlock > 10 cm DBH per hectare
DENYC	number of yellow cedar > 10 cm DBH per hectare
DET	sum of detections
DET100	sum of detections closer than 101m which is a subset of DET
DET150	sum of detections closer than 151m which is a subset of DET
DISEDGE	distance to the nearest forest edge in meters
DISSEA	distance to the ocean (measured along the creek bed in km) using 1:50,000 NTS topographic maps
DISSTRM	distance (m) to the nearest creek
EPIMEAN	mean index of epiphyte cover = sum of epiphyte cover ratings / number of trees in the plot
EPITMEAN	mean index of epiphyte cover thickness = sum of epiphyte thickness rating / number of trees in plot
HTMEAN	average tree height in m

Appendix I, Table 1 (continued)

Variable	Description
IRA . . .	Prefix to indicate an Index of Relative Activity calculated on Marbled Murrelet activity measures for each station and year to combine data from the three years (see chapter 2.3.2)
LN . . .	Prefix indicating logarithmic transformation (new variable = ln(old variable + 1)), often used on Marbled Murrelet activity measures to acquire normal distribution
MAPVEG	vegetation unit by Clement (1995)
OCC	sum of occupied detections of a survey which are defined as: birds seen perching, landing or attempting to land on branches; birds calling from a stationary location (at least 3 successive calls); birds flying below, through, into or out of the forest canopy; birds flying in small or large radius circles above the canopy (Ralph *et al.* 1994, Paton 1995).
OCC1, OCC2, OCC3	average of occupied detections (OCC) at a particular station in a certain year (1 = 1995, 2 = 1996, 3 = 1997)
OLDIND	standard deviation of DBH (SDDBH) and standard deviation of tree height (SDHT) combined by a Principal Component Analysis as a measure of well-structured old-growth forest with big trees
OLDIND2	standard deviation of DBH (SDDBH), standard deviation of tree height (SDHT), mean tree height (HTMEAN), and mean DBH (DBHMEAN) combined by a Principal Component Analysis as a measure for well structured old-growth forest with an emphasis on the absolute size of trees
POPLAHA	number of potential nest platforms per hectare
REPLAHA	number of realistic nest platforms per hectare
SDDBH	standard deviation of DBH as a measure of a stage-wise well-structured forest with big trees
SDHT	standard deviation of tree height, a measure of a height-wise well-structured forest with several canopy layers
SITESER	Biogeoclimatic site series determined in vegetation plots
SLOPE	slope in degrees
SUBCAN	sum of subcanopy detections which include any observation of birds below canopy level
SURVNO	number of surveys
TIMBVOL	timbervolume in m^3/ha as average of all timbervolumes occurring in the polygons touched by a 200m diameter circle around the station on the forest cover map by MacMillan Bloedel Limited (1998)
TREEHT	canopy tree height around the station in meters
VALLOC	location in the valley as B = valley bottom and bottom of higher elevation side-valleys, L = lower slope, and U = upper slope and ridge top
VEG1, VEG2, VEG3	three Principal Component Analysis vectors based on the variables: ALTITUDE, DBHMEAN, HTMEAN, DENMH, DENYC, DENSS, EPIMEAN, POPLAHA, SDHT, SDDBH, OLDIND, OLDIND2, TIMBVOL
VIS	sum of visual detections

Appendix I, Table 2: Data set used in most analyses.

Station	DISSEA (km)	CANCL	CANCLVEG (%)	ASPECT (degree)	SLOPE (degree)	ALTITUDE (M)	DISSTRM (m)	DENSTEM (per ha)	DENSS (per ha)	DENAF (per ha)	DENWH (per ha)	DENMH (per ha)
UBB	10.0	2.5	70	N	0.0	0	30	444.4	0.0	333.3	111.1	0.0
UBO	5.0	1	76	N	0.0	0	15	344.4	100.0	0.0	133.3	0.0
UBTS	16.0	2	65	130	5.7	380	200	488.9	0.0	33.3	322.2	0.0
UCASU	15.0	1	65	70	10.0	580	20	388.9	22.2	255.6	111.1	0.0
UCAW	14.5	1	85	270	14.0	560	30	488.9	0.0	377.8	100.0	0.0
UDO	10.0	1	60	N	0.0	0	30	611.1	33.3	288.9	288.9	0.0
UEWS	8.0	3	50	160	10.0	460	1200	522.2	0.0	277.8	77.8	0.0
UEWW	8.0	4	75	0	26.6	440	1000	511.1	0.0	111.1	166.7	0.0
UFA	9	1	50	180	20.0	0	10	266.7	44.4	77.8	144.4	0.0
UFC	4	1	72.5	N	0.0	0		377.8	22.2	127.8	188.9	0.0
UFFN	14.0	1	85	52	10.0	540	20	455.6	0.0	0.0	22.2	166.7
UFFS	14.0	3	25	N	0.0	540	30	788.9	0.0	388.9	155.6	0.0
UFH	4.5	4	90	N	0.0	0	150	933.3	0.0	800.0	133.3	0.0
UGR	13.0	2.5	80	315	26.6	380	2000	588.9	0.0	211.1	122.2	0.0
UHP3	13	3	40	0	10.0	480	0	311.1	0.0	88.9	77.8	0.0
UHPW	13.3	1	35	240	14.0	480	600	400.0	0.0	244.4	100.0	0.0
UID	9.5	1	40	N	0.0	0	10	233.3	22.2	55.6	155.6	0.0
UJSE	6.5	1	30	N	0.0	0	30	200.0	0.0	33.3	88.9	0.0
UJSW	7.0	1	30	N	0.0	0	100	233.3	22.2	0.0	155.6	0.0
ULJ	7.5	1	75	180	15.0	0	10	422.2	55.6	166.7	200.0	0.0
ULPS	5	1.5	20	275	15.0	550	300	433.3	0.0	5.6	55.6	94.4
UMCE	5	2	50	350	10.2	680	30	633.3	0.0	188.9	277.8	0.0
UMCW	5	2	65	120	12.4	640	15	255.6	0.0	22.2	155.6	0.0
UMSE	6.0	1	70	N	0.0	0	10	411.1	66.7	100.0	122.2	0.0
UMSW	6.0	1	80	N	0.0	0	30	255.6	0.0	0.0	255.6	0.0
UNA	18.0	2	70	65	19.3	460	10	388.9	0.0	300.0	88.9	0.0
UNBS	17.0	2	45	32	16.7	420	10	388.9	0.0	300.0	88.9	0.0
UNV	5.5	1	35	230	11.3	700	ND	488.9	0.0	44.4	22.2	244.4
UOAS	12.0	2	40	225	11.3	340	500	511.1	0.0	22.2	311.1	0.0
UONE	8.5	1	35	N	0.0	0	200	177.8	44.4	0.0	122.2	0.0
UONW	7.75	2	65	N	0.0	0		200.0	16.7	38.9	105.6	0.0
UOY	9.5	4	70	180	5.7	600	1500	522.2	0.0	33.3	133.3	100.0
UOY2	10	4	60	170	30.0	750	50	466.7	0.0	88.9	222.2	0.0
URC	12.5	3	85	45	16.7	260	500	266.7	0.0	88.9	88.9	0.0
URJS	17.0	2	30	284	35.0	440	60	633.3	0.0	455.6	155.6	0.0
URK	5.5	1	20	310	11.3	640	600	422.2	0.0	0.0	66.7	111.1
USC	3.5	1	60	N	0.0	0	30	933.3	0.0	44.4	0.0	0.0
USL	13.0	4	80	270	11.3	480	500	422.2	0.0	55.6	233.3	0.0
USVN	11.5	3	70	225	5.7	200	500	400.0	0.0	55.6	255.6	0.0
USVS	11.5	3	55	225	34.0	200	500	377.8	0.0	11.1	233.3	0.0
UTC	10.0	3	60	157.5	1.0	400	1000	266.7	0.0	22.2	133.3	0.0
UTCW	10.5	3	50	20	20.0	400	100	511.1	0.0	0.0	455.6	0.0
UTHB	12.5	1	40	330	0.0	0	15	344.4	0.0	233.3	100.0	0.0
UTOE	16	2	25	45	45.0	750	800	611.1	0.0	44.4	111.1	133.3
UTOW	15.5	1	45	300	25.0	750	400	511.1	0.0	88.9	122.2	66.7
UWCJ	17.5	2	40	260	14.0	460	10	633.3	0.0	388.9	222.2	0.0
UWG	9.5	4	70	212	30.0	750	50	588.9	0.0	77.8	211.1	77.8
UWOE	13.5	2	50	270	5.7	840	2000	422.2	0.0	100.0	0.0	211.1
UWOW	13.5	3	70	225	16.7	740	2000	1022.2	0.0	444.4	0.0	88.9
UWWE	14	1	20	360	ND	920	20	355.6	0.0	22.2	44.4	88.9
UWWW	14	1	25	50	7.4	840	1000	466.7	0.0	22.2	0.0	188.9

Appendix I, Table 2 (continued): Data set used in most analyses .

Station	DENRC (per ha)	DENYC (per ha)	DENLARGE (per ha)	DENLSS (per ha)	DENLAF (per ha)	DENLWH (per ha)	DENLMH (per ha)	DENLRC (per ha)	DENLYC (per ha)	DBHMEAN (cm)
UBB	0.0	0.0	33.3	0.0	0.0	33.3	0.0	0.00	0.00	39.75
UBO	22.2	0.0	111.1	66.7	0.0	0.0	0.0	11.11	0.00	61.87
UBTS	133.3	0.0	133.3	0.0	0.0	11.1	0.0	122.22	0.00	61.07
UCASU	0.0	0.0	66.7	22.2	33.3	11.1	0.0	0.00	0.00	43.63
UCAW	11.1	0.0	55.6	0.0	0.0	55.6	0.0	0.00	0.00	39.86
UDO	0.0	0.0	55.6	22.2	0.0	33.3	0.0	0.00	0.00	31.67
UEWS	166.7	0.0	33.3	0.0	0.0	0.0	0.0	33.33	0.00	36.96
UEWW	222.2	0.0	33.3	0.0	0.0	0.0	0.0	33.33	0.00	45.39
UFA	0.0	0.0	44.4	44.4	0.0	0.0	0.0	0.00	0.00	42.83
UFC	0.0	0.0	66.7	16.7	11.1	22.2	0.0	0.00	0.00	56.70
UFFN	0.0	266.7	11.1	0.0	0.0	0.0	0.0	0.00	11.11	31.90
UFFS	44.4	0.0	44.4	0.0	11.1	22.2	0.0	11.11	0.00	40.32
UFH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.00	0.00	42.36
UGR	211.1	44.4	33.3	0.0	0.0	0.0	0.0	22.22	11.11	38.42
UHP3	55.6	77.8	77.8	0.0	0.0	22.2	0.0	22.22	33.33	57.04
UHPW	44.4	11.1	77.8	0.0	11.1	33.3	0.0	33.33	0.00	46.14
UID	0.0	0.0	55.6	22.2	0.0	33.3	0.0	0.00	0.00	54.67
UJSE	11.1	0.0	33.3	0.0	0.0	22.2	0.0	0.00	0.00	55.44
UJSW	0.0	0.0	88.9	22.2	0.0	66.7	0.0	0.00	0.00	71.48
ULJ	0.0	0.0	55.6	44.4	0.0	11.1	0.0	0.00	0.00	51.92
ULPS	122.2	127.8	16.7	0.0	0.0	0.0	0.0	11.11	0.00	26.87
UMCE	22.2	133.3	11.1	0.0	0.0	0.0	0.0	0.00	11.11	32.46
UMCW	44.4	0.0	33.3	0.0	0.0	22.2	0.0	0.00	0.00	59.87
UMSE	11.1	0.0	77.8	66.7	0.0	11.1	0.0	0.00	0.00	66.95
UMSW	0.0	0.0	44.4	0.0	0.0	44.4	0.0	0.00	0.00	48.87
UNA	0.0	0.0	66.7	0.0	22.2	44.4	0.0	0.00	0.00	39.82
UNBS	0.0	0.0	66.7	0.0	22.2	44.4	0.0	0.00	0.00	39.83
UNV	0.0	166.7	22.2	0.0	0.0	0.0	11.1	0.00	11.11	36.64
UOAS	166.7	0.0	11.1	0.0	0.0	0.0	0.0	0.00	0.00	29.80
UONE	0.0	0.0	55.6	44.4	0.0	122.2	0.0	0.00	0.00	65.38
UONW	38.9	0.0	55.6	16.7	0.0	16.7	0.0	22.22	0.00	63.25
UOY	44.4	200.0	22.2	0.0	0.0	0.0	11.1	0.00	11.11	39.94
UOY2	11.1	133.3	33.3	0.0	0.0	11.1	0.0	0.00	11.11	39.17
URC	88.9	0.0	100.0	0.0	0.0	11.1	0.0	88.89	0.00	73.00
URJS	22.2	0.0	44.4	0.0	11.1	22.2	0.0	11.11	0.00	33.67
URK	188.9	44.4	0.0	0.0	0.0	0.0	0.0	0.00	0.00	27.08
USC	44.4	0.0	0.0	0.0	0.0	0.0	0.0	0.00	0.00	23.81
USL	133.3	0.0	88.9	0.0	0.0	0.0	0.0	88.89	0.00	59.84
USVN	88.9	0.0	44.4	0.0	0.0	0.0	0.0	44.44	0.00	42.83
USVS	100.0	0.0	66.7	0.0	0.0	11.1	0.0	55.56	0.00	53.76
UTC	88.9	22.2	44.4	0.0	0.0	0.0	0.0	33.33	11.11	52.04
UTCW	55.6	0.0	55.6	0.0	0.0	0.0	0.0	55.56	0.00	39.09
UTHB	0.0	0.0	77.8	0.0	33.3	33.3	0.0	0.00	0.00	42.90
UTOE	0.0	322.2	0.0	0.0	0.0	0.0	0.0	0.00	0.00	27.76
UTOW	55.6	166.7	11.1	0.0	0.0	0.0	0.0	0.00	0.00	29.48
UWCJ	22.2	0.0	66.7	0.0	11.1	44.4	0.0	11.11	0.00	43.53
UWG	22.2	200.0	77.8	0.0	0.0	11.1	22.2	11.11	33.33	47.58
UWOE	0.0	111.1	0.0	0.0	0.0	0.0	0.0	0.00	0.00	37.87
UWOW	133.3	355.6	0.0	0.0	0.0	0.0	0.0	0.00	0.00	34.61
UWWE	122.2	77.8	0.0	0.0	0.0	0.0	0.0	0.00	0.00	31.22
UWWW	0.0	244.4	22.2	0.0	0.0	0.0	0.0	0.00	22.22	35.74

Appendix I, Table 2 (continued): Data set used in most analyses .

Station	HTMEAN (m)	POPLAHA (per ha)	REPLAHA (per ha)	EPIMEAN	EPITMEAN	MAPVEG	SITESER	TREEHT (m)	VALLOC	TIMBVOL (m^3/ha)
UBB	24.60	122.22	0.00	2.40	1.10	AS	CWHvm1-01	40.00	B	861.50
UBO	37.29	555.56	77.78	2.65	1.32	AS	CWHvm1-07	45.00	B	813.00
UBTS	35.61	177.78	100.00	2.09	1.61	HS	CWHvm1-06	50.00	U	605.33
UCASU	24.23	211.11	0.00	1.34	1.00	SF	CWHvm2-x / -08	30.00	B	581.50
UCAW	21.14	244.44	77.78	1.55	1.05	RS	CWHvm1-01	30.00	B	670.33
UDO	26.36	288.89	77.78	2.87	1.02	SS	CWHvm1-07	35.00	B	861.50
UEWS	23.94	144.44	0.00	1.34	1.26	HS	CWHvm1-06	25.00	L	627.00
UEWW	28.04	511.11	155.56	1.91	1.26	HD	CWHvm1-06	25.00	L	627.00
UFA	24.38	611.11	244.44	3.33	1.79	CD	CWHvm1-09	45.00	B	1184.50
UFC	29.57	383.33	88.89	3.10	1.43	AB	CWHvm1-09	40.00	B	929.00
UFFN	16.24	55.56	22.22	1.56	1.10	HS	CWHvm2-09	10.00	U	893.50
UFFS	25.61	922.22	166.67	2.17	1.41	RS	CWHvm1-04	35.00	B	893.50
UFH	30.45	1111.11	0.00	2.52	1.76	AB	CWHvm1-01	40.00	B	1064.50
UGR	22.25	277.78	22.22	2.00	1.45	AB	CWHvm1-01	40.00	U	700.00
UHP3	20.54	311.11	66.67	2.04	1.57	AB	CWHvm2-03	25.00	U	607.00
UHPW	22.56	111.11	33.33	1.86	1.11	AB	CWHvm2-01	20.00	U	607.00
UID	34.76	344.44	66.67	3.19	1.81	SS	CWHvm1-09	40.00	B	1184.50
UJSE	28.56	122.22	0.00	2.94	2.33	CD	CWHvm1-09	40.00	B	912.00
UJSW	33.10	633.33	133.33	3.81	0.67	CD	CWHvm1-09	40.00	B	795.50
ULJ	31.11	1011.11	166.67	2.26	0.95	AB	CWHvm1-01	40.00	B	1004.00
ULPS	18.36	33.33	0.00	1.01	0.86	LC	CWHvm2-10	20.00	L	447.33
UMCE	24.91	322.22	111.11	1.79	1.28	HS	CWHvm2-09	40.00	U	599.25
UMCW	41.00	188.89	66.67	1.83	2.17	HS	CWHvm2-05	45.00	U	599.25
UMSE	27.89	1100.00	277.78	2.92	1.59	RS	CWHvm1-09	40.00	B	802.00
UMSW	30.22	88.89	0.00	3.26	2.65	AB	CWHvm1-07	40.00	B	802.00
UNA	22.26	589.00	ND	2.34	1.74	RS	CWHvm1-01	60.00	B	1027.75
UNBS	22.29	588.89	0.00	2.34	1.06	RS	CWHvm1-06	35.00	L	792.25
UNV	18.52	144.44	44.44	0.82	0.82	HS	CWHvm2-11	30.00	U	343.00
UOAS	21.17	222.22	22.22	1.65	1.63	AB	CWHvm1-03	40.00	L	618.00
UONE	30.25	1.50	0.69	3.63	2.63	SS	CWHvm1-09	45.00	B	1184.50
UONW	31.08	355.56	88.89	3.39	1.89	RS	CWHvm1-07	45.00	B	773.00
UOY	23.21	277.78	77.78	1.55	1.49	HS	CWHvm2-03	35.00	U	618.00
UOY2	20.02	511.11	111.11	2.36	1.64	HS	CWHvm2-09	30.00	U	618.00
URC	33.96	188.89	44.44	2.83	1.13	RS	CWHvm1-04 / -06	47.50	L	679.00
URJS	29.81	433.33	333.33	1.95	1.51	AB	CWHvm1-01	50.00	U	965.50
URK	20.08	22.22	0.00	0.87	0.63	HS	CWHvm2-01	40.00	U	343.00
USC	15.48	0.00	0.00	1.14	2.81	SS	CWHvm1-09	30.00	B	285.00
USL	31.32	300.00	44.44	1.58	1.24	HS	CWHvm1-03	37.50	U	599.00
USVN	28.64	455.56	88.89	1.97	1.31	HS	CWHvm1-03	35.00	L	618.00
USVS	41.94	144.44	100.00	1.47	1.06	AB	CWHvm1-01	45.00	L	637.00
UTC	23.67	155.56	44.44	1.17	0.88	HS	CWHvm1-03	35.00	L	618.00
UTCW	24.33	455.56	11.11	3.22	1.35	HS	CWHvm1-06	30.00	L	618.00
UTHB	34.45	66.67	55.56	2.55	1.39	RS	CWHvm1-07	50.00	B	651.67
UTOE	13.20	11.11	0.00	1.55	1.11	HS	CWHvm2-09	20.00	U	208.00
UTOW	15.96	255.56	88.89	1.57	1.41	HS	CWHvm2-01	20.00	U	208.00
UWCJ	37.46	444.44	22.22	2.67	1.54	AB	CWHvm1-01 / -05	40.00	B	910.00
UWG	27.81	433.33	77.78	1.55	1.51	HS	CWHvm2-01	30.00	U	618.00
UWOE	19.16	55.56	0.00	2.42	1.08	MB	CWHmm1-01	25.00	U	208.00
UWOW	22.96	933.33	266.67	1.87	1.65	HS	CWHvm2-06	35.00	U	599.00
UWWE	20.06	11.11	0.00	1.91	1.28	MM	CWHmm1-04	30.00	U	454.00
UWWW	19.05	77.78	33.33	1.02	0.81	HS	CWHvm2-09	30.00	U	454.00

Appendix I, Table 2 (continued): Data set used in most analyses .

Station	SURVNO	IRADET	IRAOCC	IRASUB	IRADET100	IRADET150	OCC1	OCC2	OCC3	LNIRADET	LNIRAOCC
UBB	8	0.62	0.22	0.00	0.38	0.55	0.25	1.00	0.00	0.48	0.20
UBO	2	0.77	0.99	0.62	0.78	0.71	6.00			0.57	0.69
UBTS	1	0.69	0.00	0.00	0.44	0.56		0.00		0.53	0.00
UCASU	5	0.30	0.22	0.41	0.24	0.31	4.00	0.00	0.00	0.26	0.20
UCAW	3	0.47	1.22	0.86	0.69	0.64	7.00	4.00	0.00	0.38	0.80
UDO	12	0.62	1.45	0.82	0.70	0.73	6.67	4.33	2.67	0.48	0.90
UEWS	5	2.09	0.26	0.22	1.66	1.90	1.00	0.50	1.50	1.13	0.23
UEWW	4	1.42	0.21	0.00	2.02	1.64	0.00	1.00	0.00	0.89	0.19
UFA	3	1.08	0.47	0.14	0.67	0.86			2.33	0.73	0.39
UFC	6	0.82	1.82	3.16	1.04	0.97	11.00	4.50	4.00	0.60	1.04
UFFN	7	1.33	2.16	0.67	1.50	1.39	10.00	0.00	23.75	0.85	1.15
UFFS	5	1.33	1.33	2.04	1.42	1.43	9.00	0.00	12.33	0.85	0.85
UFH	2	1.47	0.58	0.31	0.99	1.35	3.50			0.91	0.46
UGR	2	1.86	1.66	0.93	2.47	2.27	10.00			1.05	0.98
UHP3	3	1.96	0.61	0.00	1.94	2.10			3.00	1.08	0.48
UHPW	4	0.90	0.07	0.00	0.18	0.55		0.00	0.67	0.64	0.07
UID	3	1.14	1.56	1.58	1.29	1.10			7.67	0.76	0.94
UJSE	2	0.95	2.82	2.58	1.03	1.00		4.50		0.67	1.34
UJSW	7	0.80	0.89	0.81	0.66	0.76	2.00	2.00	5.33	0.59	0.64
ULJ	10	1.06	1.98	1.81	1.44	1.26	14.60	1.50	12.67	0.72	1.09
ULPS	5	0.74	0.00	0.00	0.16	0.17	0.00		0.00	0.55	0.00
UMCE	2	0.87	0.10	0.22	0.23	0.41			0.50	0.63	0.10
UMCW	2	0.92	0.00	0.00	0.29	0.31			0.00	0.65	0.00
UMSE	10	1.07	1.97	3.18	1.19	1.17	2.75	6.67	6.33	0.73	1.09
UMSW	10	0.78	0.54	0.39	0.71	0.69	5.67	0.33	2.25	0.57	0.43
UNA	1	0.17	0.00	0.00	0.33	0.24		0.00		0.16	0.00
UNBS	1	0.22	1.25	0.00	0.54	0.40		2.00		0.20	0.81
UNV	3	0.74	0.07	0.00	0.13	0.34			0.33	0.55	0.07
UOAS	4	0.95	0.24	0.22	0.63	0.68	0.00	0.00	3.50	0.67	0.21
UONE	11	1.40	2.05	2.06	1.51	1.48	26.25	0.33	7.75	0.88	1.11
UONW	5	1.37	2.06	2.42	1.79	1.66		3.00	11.00	0.86	1.12
UOY	2	0.00	0.00	0.00	0.00	0.00	0.00			0.00	0.00
UOY2	3	0.92	0.07	0.00	0.56	0.53			0.33	0.65	0.07
URC	2	2.69	1.33	0.00	2.36	2.70	8.00			1.31	0.84
URJS	1	1.08	2.50	3.87	1.31	1.28		4.00		0.73	1.25
URK	3	1.77	0.34	0.00	0.60	1.09			1.67	1.02	0.29
USC	10	0.45	0.13	0.21	0.14	0.21	2.33	0.00	0.00	0.37	0.12
USL	2	1.86	0.08	0.00	1.56	1.61	0.50			1.05	0.08
USVN	2	0.37	0.17	0.00	0.56	0.53	1.00			0.32	0.15
USVS	5	1.50	0.31	0.14	1.08	1.20	0.00	1.00	1.50	0.92	0.27
UTC	2	0.11	0.00	0.00	0.02	0.02	0.00			0.10	0.00
UTCW	3	0.70	0.36	0.65	0.41	0.53		1.00	0.50	0.53	0.31
UTHB	1	1.00	3.75	6.46	1.96	1.68		6.00		0.69	1.56
UTOE	1	0.13	0.00	0.00	0.06	0.05			0.00	0.13	0.00
UTOW	1	1.04	0.00	0.00	0.06	0.26			0.00	0.71	0.00
UWCJ	1	0.48	1.88	2.58	1.20	0.88		3.00		0.39	1.06
UWG	3	0.36	0.00	0.00	0.30	0.34			0.00	0.31	0.00
UWOE	1	0.30	0.00	0.00	0.00	0.00	0.00			0.26	0.00
UWOW	1	1.38	0.50	0.62	0.53	0.77	3.00			0.87	0.40
UWWE	2	0.50	0.00	0.00	0.06	0.13			0.00	0.41	0.00
UWWW	2	0.44	0.00	0.00	0.03	0.18			0.00	0.36	0.00

Appendix I, Table 2 (continued): Data set used in most analyses .

Station	LNIRASUB	LNIRA100	LNIRA150	DET	OCC	SUB	DET100	DET150	IRACO	LNIRACO	IRACWO
UBB	0.00	0.32	0.44	21.08	0.42	0.00	7.00	11.58	1.18	0.78	1.75
UBO	0.48	0.58	0.54	36.50	6.00	1.00	19.00	22.00	1.11	0.75	0.59
UBTS	0.00	0.36	0.45	16.00	0.00	0.00	4.00	7.00	0.00	0.00	0.00
UCASU	0.34	0.22	0.27	11.83	1.33	0.67	5.33	8.67	0.53	0.42	0.28
UCAW	0.62	0.53	0.50	17.33	3.67	0.67	11.33	14.00	1.30	0.83	0.56
UDO	0.60	0.53	0.55	20.44	4.56	1.44	10.17	14.44	1.35	0.85	2.48
UEWS	0.20	0.98	1.07	63.50	1.00	0.50	23.33	34.33	0.26	0.23	0.19
UEWW	0.00	1.11	0.97	43.00	0.33	0.00	25.50	27.83	0.37	0.32	0.54
UFA	0.13	0.51	0.62	32.33	2.33	0.33	10.33	16.67	1.10	0.74	1.40
UFC	1.43	0.71	0.68	24.83	6.50	4.00	14.17	17.33	2.40	1.22	1.57
UFFN	0.52	0.92	0.87	45.83	11.25	1.42	26.17	29.92	1.06	0.72	0.56
UFFS	1.11	0.88	0.89	47.11	7.11	4.44	25.89	33.11	0.99	0.69	0.62
UFH	0.27	0.69	0.85	69.50	3.50	0.50	24.00	42.00	0.64	0.50	0.34
UGR	0.65	1.24	1.18	87.50	10.00	1.50	60.00	70.50	1.27	0.82	0.67
UHP3	0.00	1.08	1.13	58.33	3.00	0.00	30.00	40.67	0.97	0.68	1.42
UHPW	0.00	0.17	0.44	26.33	0.33	0.00	2.83	10.00	0.13	0.12	0.07
UID	0.95	0.83	0.74	34.00	7.67	3.67	20.00	21.33	1.29	0.83	2.71
UJSE	1.28	0.71	0.69	22.00	4.50	2.00	9.50	12.50	0.94	0.66	1.35
UJSW	0.59	0.50	0.56	22.72	3.11	1.33	9.22	13.17	1.26	0.81	1.28
ULJ	1.03	0.89	0.82	39.26	9.59	3.52	26.30	29.81	1.62	0.96	1.65
ULPS	0.00	0.14	0.15	31.88	0.00	0.00	3.50	4.38	0.00	0.00	0.00
UMCE	0.20	0.20	0.35	26.00	0.50	0.50	3.50	8.00	1.74	1.01	0.91
UMCW	0.00	0.25	0.27	27.50	0.00	0.00	4.50	6.00	0.00	0.00	0.00
UMSE	1.43	0.78	0.77	34.06	5.25	3.17	17.75	23.17	1.43	0.89	1.04
UMSW	0.33	0.54	0.52	26.75	2.75	0.53	12.08	15.11	0.73	0.55	0.37
UNA	0.00	0.28	0.22	4.00	0.00	0.00	3.00	3.00	0.00	0.00	0.00
UNBS	0.00	0.43	0.34	5.00	2.00	0.00	5.00	5.00	1.34	0.85	0.48
UNV	0.00	0.12	0.30	22.00	0.33	0.00	2.00	6.67	0.29	0.25	0.15
UOAS	0.20	0.49	0.52	28.50	1.17	0.50	10.33	14.17	0.29	0.25	0.61
UONE	1.12	0.92	0.91	55.89	11.44	3.83	32.06	38.86	1.22	0.80	1.48
UONW	1.23	1.02	0.98	37.00	7.00	2.63	21.50	26.13	2.69	1.30	3.51
UOY	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
UOY2	0.00	0.44	0.43	27.33	0.33	0.00	8.67	10.33	0.58	0.46	1.22
URC	0.00	1.21	1.31	127.00	8.00	0.00	57.50	84.00	1.10	0.74	0.58
URJS	1.58	0.84	0.83	25.00	4.00	3.00	12.00	16.00	1.34	0.85	0.48
URK	0.00	0.47	0.74	52.67	1.67	0.00	9.33	21.00	0.53	0.42	0.27
USC	0.19	0.13	0.19	11.94	0.78	0.33	2.39	3.89	0.43	0.36	0.93
USL	0.00	0.94	0.96	87.50	0.50	0.00	38.00	50.00	0.17	0.16	0.36
USVN	0.00	0.44	0.43	17.50	1.00	0.00	13.50	16.50	0.83	0.61	1.39
USVS	0.13	0.73	0.79	53.00	0.83	0.33	18.67	27.00	0.57	0.45	1.11
UTC	0.00	0.02	0.02	5.00	0.00	0.00	0.50	0.50	0.00	0.00	0.00
UTCW	0.50	0.35	0.43	17.00	0.75	0.50	4.00	7.00	1.89	1.06	2.52
UTHB	2.01	1.09	0.99	23.00	6.00	5.00	18.00	21.00	1.18	0.78	0.42
UTOE	0.00	0.06	0.05	4.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00
UTOW	0.00	0.06	0.23	31.00	0.00	0.00	1.00	5.00	0.00	0.00	0.00
UWCJ	1.28	0.79	0.63	11.00	3.00	2.00	11.00	11.00	0.91	0.65	1.31
UWG	0.00	0.26	0.30	10.67	0.00	0.00	4.67	6.67	0.00	0.00	0.00
UWOE	0.00	0.00	0.00	14.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
UWOW	0.48	0.43	0.57	65.00	3.00	1.00	13.00	24.00	1.43	0.89	0.75
UWWE	0.00	0.06	0.12	15.00	0.00	0.00	1.00	2.50	0.00	0.00	0.00
UWWW	0.00	0.03	0.17	13.00	0.00	0.00	0.50	3.50	0.00	0.00	0.00

Appendix I, Table 2 (continued): Data set used in most analyses .

Station	LNIRACWO	CO1	CO2	CO3	DENTRPL4 (per ha)	SDHT (m)	SDDBH (cm)	OLDIND	OLDIND2	VEG1	VEG2	VEG3
UBB	1.01	0.08	1.00	0.00	11.11	11.37	23.78	-0.50	-0.45	-0.90	1.42	-0.25
UBO	0.46	0.47			44.44	22.17	31.75	1.26	1.56	1.18	-0.30	2.34
UBTS	0.00		0.00		22.22	16.99	56.90	1.81	1.80	2.27	-0.18	-1.14
UCASU	0.25	0.67	0.00	0.00	33.33	16.98	35.60	0.78	0.28	0.65	-0.08	-0.71
UCAW	0.44	0.70	0.67	0.00	33.33	10.17	31.82	-0.27	-0.47	-0.38	0.42	-0.75
UDO	1.25	0.57	0.39	0.40	33.33	15.53	23.36	0.01	-0.33	-0.75	1.11	0.73
UEWS	0.17	0.13	0.05	0.09	22.22	11.84	27.21	-0.28	-0.43	-0.42	0.66	-1.02
UEWW	0.43	0.00	0.33	0.00	44.44	11.56	28.10	-0.27	-0.03	-0.22	0.42	-0.21
UFA	0.88			0.32	44.44	15.48	31.41	0.39	0.07	-0.44	0.75	1.97
UFC	0.95	0.71	0.74	0.88	33.33	13.30	30.70	0.08	0.50	0.01	0.78	0.88
UFFN	0.44	0.63	0.00	0.48	11.11	7.48	17.57	-1.30	-1.43	-1.15	-1.47	0.42
UFFS	0.48	0.82	0.00	0.30	66.67	10.55	22.85	-0.65	-0.46	-0.94	0.46	0.87
UFH	0.29	0.27			55.56	9.18	17.55	-1.08	-0.41	-1.55	1.22	1.75
UGR	0.51	0.53			22.22	10.72	26.62	-0.45	-0.56	-0.66	0.53	-0.32
UHP3	0.88			0.28	33.33	8.35	40.56	-0.08	0.05	0.25	-0.32	-0.28
UHPW	0.07		0.00	0.07	0.00	13.08	42.77	0.63	0.22	0.60	0.15	-1.06
UID	1.31			0.37	44.44	14.62	33.63	0.39	0.85	0.27	0.94	0.99
UJSE	0.86		0.28		11.11	10.92	21.77	-0.66	0.05	-0.56	1.31	0.06
UJSW	0.82	0.40	0.50	0.33	66.67	15.10	37.52	0.63	1.33	0.92	0.25	1.31
ULJ	0.97	0.68	0.29	0.65	55.56	12.70	29.89	-0.04	0.40	-0.40	0.29	2.48
ULPS	0.00	0.00		0.00	0.00	11.13	20.28	-0.70	-1.17	-0.77	-0.58	-0.92
UMCE	0.65			0.50	44.44	11.48	20.02	-0.67	-0.71	-0.67	-0.14	-0.31
UMCW	0.00			0.00	22.22	15.02	27.13	0.12	1.12	1.03	0.16	-0.97
UMSE	0.71	0.45	0.57	0.37	100.00	12.46	54.23	1.10	1.25	0.98	-0.65	2.70
UMSW	0.31	0.32	0.08	0.33	11.11	14.04	45.43	0.88	0.76	0.75	0.87	-0.41
UNA	0.00		0.00		33.33	23.18	39.59	1.76	0.58	0.87	0.24	0.02
UNBS	0.39		0.40		33.33	23.18	39.59	1.76	0.58	0.95	0.14	-0.20
UNV	0.14			0.08	11.11	8.50	27.23	-0.70	-0.90	-0.07	-2.37	-0.49
UOAS	0.48	0.00	0.00	0.25	33.33	9.73	13.75	-1.19	-1.22	-1.57	1.15	-0.57
UONE	0.91	0.45	0.33	0.42	33.33	18.73	49.58	1.68	1.58	1.58	0.36	0.84
UONW	1.51		1.00	0.58	11.11	14.92	45.83	1.01	1.23	1.13	0.35	0.46
UOY	0.00	0.00			22.22	10.23	21.61	-0.75	-0.64	-0.40	-1.20	0.05
UOY2	0.80			0.17	33.33	10.29	24.55	-0.60	-0.72	-0.60	-0.47	0.22
URC	0.46	0.46			22.22	16.31	55.19	1.64	1.94	2.25	-0.12	-0.66
URJS	0.39		0.40		55.56	21.49	26.52	0.92	0.33	0.28	0.70	-0.31
URK	0.24			0.15	0.00	11.37	11.80	-1.08	-1.29	-1.01	-0.28	-1.22
USC	0.66	0.55	0.00	0.00	0.00	2.18	5.19	-2.57	-2.32	-2.93	1.76	-1.00
USL	0.31	0.07			22.22	13.56	42.25	0.67	0.98	1.15	-0.04	-0.86
USVN	0.87	0.35			44.44	15.05	31.00	0.31	0.23	0.08	0.64	-0.34
USVS	0.75	0.00	0.13	0.38	22.22	17.77	32.43	0.73	1.32	1.15	0.63	-1.11
UTC	0.00	0.00			11.11	10.63	30.25	-0.29	-0.06	-0.06	0.35	-0.89
UTCW	1.26		1.00	0.13	44.44	13.57	48.37	0.96	0.29	0.61	0.18	-0.19
UTHB	0.35		0.35		0.00	19.05	34.75	1.00	0.84	0.79	0.98	-0.90
UTOE	0.00			0.00	0.00	6.60	14.53	-1.55	-1.81	-1.13	-2.05	-0.33
UTOW	0.00			0.00	22.22	10.82	21.54	-0.68	-1.20	-0.62	-1.11	-0.64
UWCJ	0.84		0.27		66.67	18.47	31.83	0.79	0.88	0.73	0.52	-0.11
UWG	0.00			0.00	44.44	10.39	24.01	-0.62	-0.16	0.04	-1.42	0.18
UWOE	0.00	0.00			0.00	7.59	23.52	-1.00	-0.99	-0.21	-1.92	-0.50
UWOW	0.56	0.60			33.33	12.25	14.85	-0.82	-0.83	-0.67	-2.23	1.52
UWWE	0.00			0.00	0.00	10.74	16.24	-0.95	-1.11	-0.67	-0.62	-0.90
UWWW	0.00			0.00	11.11	4.97	18.78	-1.56	-1.33	-0.77	-2.18	-0.23

Appendix II - Correlation Matrices

Appendix II

Appendix II, Figure 1: Pearson correlation coefficient matrix comparing measures of Marbled Murrelet activity. "Significant" correlations (*P* < 0.05) are bolded, "highly significant" correlations (*P* < 0.01) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower *N* of column and row.

	N	LNIRADET	LNIRAOCC	LNIRASUB	LNIRA100	LNIRA150	LNIRACO	LNIRACWO	LNOCC1	LNOCC2	LNOCC3	CO1	CO2	CO3
N		49	49	49	49	49	49	49	26	25	32	26	25	32
LNIRADET	49	1	**0.329**	0.187	***0.749***	***0.865***	0.342	**0.300**	0.302	0.011	***0.511***	0.127	-0.038	0.343
LNIRAOCC	49	**0.329**	1	***0.895***	***0.710***	***0.633***	***0.762***	***0.581***	***0.885***	***0.777***	***0.848***	***0.780***	0.322	***0.752***
LNIRASUB	49	0.187	***0.895***	1	***0.543***	***0.458***	***0.652***	***0.491***	***0.738***	***0.683***	***0.791***	***0.741***	0.279	***0.739***
LNIRA100	49	***0.749***	***0.710***	***0.543***	1	***0.966***	***0.576***	***0.506***	**0.490**	**0.411**	***0.712***	0.314	0.100	***0.547***
LNIRA150	49	***0.865***	***0.633***	***0.458***	***0.966***	1	***0.555***	***0.473***	**0.471**	0.314	***0.704***	0.303	0.078	***0.523***
LNIRACO	49	**0.342**	***0.762***	***0.652***	***0.576***	***0.555***	1	***0.836***	***0.770***	***0.681***	***0.643***	***0.802***	***0.791***	***0.771***
LNIRACWO	49	**0.300**	***0.581***	***0.491***	***0.506***	***0.473***	***0.836***	1	**0.461**	**0.472**	***0.628***	**0.463**	***0.735***	***0.679***
LNOCC1	26	0.302	***0.885***	***0.738***	**0.490**	**0.471**	***0.770***	**0.461**	1	0.170	**0.577**	***0.871***	0.053	**0.569**
LNOCC2	25	0.011	***0.777***	***0.683***	**0.411**	0.314	***0.681***	**0.472**	0.170	1	0.164	0.278	***0.565***	0.429
LNOCC3	32	***0.511***	***0.848***	***0.791***	***0.712***	***0.704***	***0.643***	***0.628***	**0.577**	0.164	1	0.450	-0.048	***0.790***
CO1	26	0.127	***0.780***	***0.741***	0.314	0.303	***0.802***	**0.463**	***0.871***	0.278	0.450	1	0.087	0.435
CO2	25	-0.038	0.322	0.279	0.100	0.078	***0.791***	***0.735***	0.053	***0.565***	-0.048	0.087	1	0.166
CO3	32	0.343	***0.752***	***0.739***	***0.547***	***0.523***	***0.771***	***0.679***	**0.569**	0.429	***0.790***	0.435	0.166	1

Appendix II, Figure 2: Pearson correlation coefficient matrix comparing measures of Marbled Murrelet activity with habitat variables. “Significant” correlations (*P* < 0.05) are bolded, “highly significant” correlations (*P* < 0.01) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower *N* of column and row.

	N	LNIRADET	LNIRAOCC	LNIRASUB	LNIRA100	LNIRA150	LNIRACO	LNIRACWO	LNOCC1	LNOCC2	LNOCC3	CO1	CO2	CO3
N		49	49	49	49	49	49	49	26	25	32	26	25	32
EPIMEAN	49	0.149	***0.584***	***0.507***	***0.406***	**0.343**	***0.627***	***0.666***	***0.562***	0.337	***0.609***	0.378	**0.487**	***0.593***
EPITHMEA	49	0.170	0.267	**0.298**	0.266	0.215	0.153	0.211	0.366	-0.088	0.299	0.086	-0.108	0.254
POPPLAHA	49	0.130	0.267	0.263	0.263	0.241	***0.402***	**0.290**	0.268	0.179	***0.533***	**0.436**	0.098	**0.417**
REPLAHA	48	0.184	0.250	**0.337**	0.211	0.209	**0.333**	0.213	0.118	0.354	**0.406**	0.367	0.068	**0.396**
DENTRPL4	49	0.111	**0.355**	***0.378***	**0.335**	**0.286**	***0.448***	***0.398***	0.346	0.209	***0.496***	**0.482**	0.066	**0.383**
TIMBVOL	49	0.174	***0.601***	***0.518***	***0.496***	***0.433***	***0.559***	***0.563***	***0.690***	0.187	***0.683***	**0.489**	0.111	***0.616***
SDHT	49	-0.005	***0.395***	**0.313**	**0.282**	0.203	**0.316**	0.199	0.373	0.032	**0.380**	0.273	-0.154	**0.410**
SDDBH	49	0.172	0.275	0.191	***0.369***	**0.343**	0.277	0.256	0.365	-0.087	**0.416**	0.193	0.126	0.339
OLDIND	49	0.098	***0.386***	**0.290**	***0.377***	**0.316**	**0.342**	0.263	**0.423**	-0.035	***0.456***	0.262	-0.013	**0.420**
OLDIND2	49	0.238	***0.443***	**0.356**	***0.493***	***0.437***	***0.366***	**0.342**	0.378	0.120	***0.534***	0.213	0.057	***0.504***
DBHMEAN	49	**0.295**	**0.355**	0.259	***0.451***	***0.422***	**0.286**	**0.315**	0.329	0.156	***0.555***	0.182	0.180	***0.486***
DENWH	49	-0.023	-0.005	0.061	0.096	0.061	0.213	***0.374***	0.018	-0.168	0.148	-0.029	0.060	0.325
DENLARGE	49	0.099	**0.314**	0.226	***0.378***	**0.335**	0.234	0.208	0.360	0.031	**0.417**	0.339	-0.083	**0.369**
DENSTEM	49	0.013	-0.136	-0.040	-0.086	-0.034	-0.033	-0.179	-0.005	-0.092	-0.278	0.180	-0.179	-0.253
CANCLVEG	49	0.078	0.017	-0.078	0.246	0.208	0.187	0.104	0.184	0.044	0.011	0.153	0.240	0.237
HTMEAN	49	0.281	***0.419***	***0.395***	***0.481***	***0.428***	**0.313**	**0.329**	0.236	0.247	**0.428**	0.102	-0.032	***0.461***
DISSEA	49	-0.256	-0.067	-0.078	-0.083	-0.128	-0.226	-0.234	-0.081	-0.264	-0.253	0.115	-0.349	**-0.445**
SLOPE	48	0.000	**-0.288**	**-0.299**	-0.083	-0.088	-0.260	-0.250	-0.214	-0.135	***-0.553***	-0.190	-0.168	**-0.433**
VEG1	49	0.130	0.196	0.153	**0.284**	0.252	0.131	0.061	0.156	0.152	0.216	-0.035	0.144	0.259
VEG2	49	0.194	***0.369***	**0.341**	***0.409***	***0.377***	***0.385***	***0.481***	0.074	0.150	0.207	0.018	0.099	0.273
VEG3	49	0.107	***0.434***	***0.408***	0.256	0.222	***0.511***	***0.451***	***0.481***	0.355	***0.655***	**0.454**	0.296	***0.617***

Appendix II, Figure 3: Pearson correlation coefficient matrix comparing habitat variables. “Significant” correlations (*P* < 0.05) are bolded, “highly significant” correlations (*P* < 0.01) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower *N* of column and row.

	N	EPIMEAN	EPITHMEA	POPPLAHA	REPLAHA	DENTRPL4	TIMBVOL	SDHT	SDDBH	OLDIND	OLDIND2	DBHMEAN	DENWH	DENLARGE	DENSTEM	CANCLVEG	HTMEAN	DISSEA	SLOPE
N		49	49	49	48	49	49	49	49	49	49	49	49	49	49	49	49	49	48
EPIMEAN	49	1	***0.509***	**0.301**	0.148	***0.378***	***0.662***	***0.394***	***0.496***	***0.515***	***0.577***	***0.540***	0.264	**0.364**	**-0.332**	0.155	***0.434***	-0.182	***-0.374***
EPITHMEA	49	***0.509***	1	0.075	0.063	0.127	***0.478***	0.200	0.246	0.258	**0.327**	**0.295**	0.181	0.032	-0.162	0.180	**0.313**	-0.134	-0.165
POPPLAHA	49	**0.301**	0.075	1	***0.614***	***0.808***	***0.466***	0.137	0.066	0.117	0.172	0.174	0.131	0.120	***0.429***	**0.359**	0.181	-0.099	-0.052
REPLAHA	48	0.148	0.063	***0.614***	1	***0.593***	**0.292**	0.197	0.070	0.152	0.174	0.134	0.065	0.140	0.241	0.122	0.181	0.022	0.186
DENTRPL4	49	***0.378***	0.127	***0.808***	***0.593***	1	***0.539***	0.248	0.219	**0.340**	0.270	**0.296**	**0.354**	**0.298**	0.252	0.233	**0.337**	-0.071	-0.064
TIMBVOL	49	***0.662***	***0.478***	***0.466***	**0.292**	***0.539***	1	***0.503***	**0.311**	***0.469***	***0.528***	***0.405***	0.207	**0.351**	-0.134	0.231	***0.505***	-0.159	**-0.324**
SDHT	49	***0.394***	0.200	0.137	0.197	0.248	***0.503***	1	***0.497***	***0.862***	***0.716***	**0.325**	0.199	***0.588***	-0.261	0.135	***0.570***	0.199	-0.034
SDDBH	49	***0.496***	0.246	0.066	0.070	0.219	**0.311**	***0.497***	1	***0.869***	***0.823***	***0.724***	0.256	***0.792***	***-0.481***	**0.304**	***0.435***	0.085	-0.211
OLDIND	49	***0.515***	0.258	0.117	0.152	**0.340**	***0.469***	***0.862***	***0.869***	1	***0.891***	***0.609***	0.264	***0.799***	***-0.431***	0.255	***0.580***	0.163	-0.142
OLDIND2	49	***0.577***	**0.327**	0.172	0.174	0.270	***0.528***	***0.716***	***0.823***	***0.891***	1	***0.861***	0.280	***0.830***	***-0.479***	**0.350**	***0.835***	-0.075	-0.283
DBHMEAN	49	***0.540***	**0.295**	0.174	0.134	**0.296**	***0.405***	**0.325**	***0.724***	***0.609***	***0.861***	1	0.099	***0.720***	***-0.547***	**0.349**	***0.689***	-0.258	***-0.376***
DENWH	49	0.264	0.181	0.131	0.065	**0.354**	0.207	0.199	0.256	0.264	0.280	0.099	1	**0.304**	0.056	0.236	**0.358**	-0.065	0.066
DENLARGE	49	**0.364**	0.032	0.120	0.140	**0.298**	**0.351**	***0.588***	***0.792***	***0.799***	***0.830***	***0.720***	**0.304**	1	***-0.376***	**0.292**	***0.588***	0.127	-0.182
DENSTEM	49	**-0.332**	-0.162	***0.429***	0.241	0.252	-0.134	-0.261	***-0.481***	***-0.431***	***-0.479***	***-0.547***	0.056	***-0.376***	1	0.102	-0.246	0.210	0.273
CANCLVEG	49	0.155	0.180	**0.359**	0.122	0.233	0.231	0.135	**0.304**	0.255	**0.350**	**0.349**	0.236	**0.292**	0.102	1	**0.326**	-0.145	-0.075
HTMEAN	49	***0.434***	**0.313**	0.181	0.181	**0.337**	***0.505***	***0.570***	***0.435***	***0.580***	***0.835***	***0.689***	**0.358**	***0.588***	-0.246	**0.326**	1	-0.224	-0.262
DISSEA	49	-0.182	-0.134	-0.099	0.022	-0.071	-0.159	0.199	0.085	0.163	-0.075	-0.258	-0.065	0.127	0.210	-0.145	-0.224	1	***0.406***
SLOPE	48	***-0.374***	-0.165	-0.052	0.186	-0.064	**-0.324**	-0.034	-0.211	-0.142	-0.283	***-0.376***	0.066	-0.182	0.273	-0.075	-0.262	***0.406***	1

Appendix II, Figure 4: Spearman correlation coefficient matrix comparing measures of Marbled Murrelet activity with non-normal distributed habitat variables. "Significant" correlations (*P* < 0.05) are bolded, "highly significant" correlations (*P* < 0.01) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower *N* of column and row.

	N	LNIRADET	LNIRAOCC	LNIRASUB	LNIRA100	LNIRA150	LNIRACO	LNIRACWO	LNOCC1	LNOCC2	LNOCC3	CO1	CO2	CO3
N		49	49	49	49	49	49	49	26	25	32	26	25	32
ALTNEW	49	-0.282	***-0.687***	***-0.572***	***-0.588***	***-0.549***	***-0.570***	***-0.642***	**-0.391**	**-0.476**	***-0.707***	-0.183	**-0.466**	***-0.678***
CANCL	49	0.129	-0.270	**-0.353**	0.092	0.098	-0.184	-0.077	**-0.481**	-0.340	-0.209	**-0.495**	-0.051	-0.196
DENAF	49	0.060	0.260	0.227	0.217	0.227	**0.283**	0.099	0.256	0.107	-0.036	**0.449**	-0.038	-0.039
DENLAF	49	-0.196	0.242	0.265	0.081	0.028	0.112	-0.066	0.339	-0.047	0.108	***0.522***	-0.247	0.027
DENLMH	49	**-0.283**	**-0.292**	-0.248	**-0.308**	**-0.290**	-0.277	**-0.292**	-0.256	.	-0.210	-0.256	.	-0.203
DENLRC	49	0.262	-0.046	-0.150	**0.320**	**0.322**	-0.094	0.011	-0.227	-0.299	0.011	-0.276	-0.175	-0.057
DENLSS	49	0.097	***0.457***	***0.504***	0.261	0.223	***0.485***	***0.502***	**0.486**	0.255	***0.603***	**0.466**	0.271	***0.585***
DENLWH	49	-0.060	***0.484***	***0.394***	**0.309**	0.224	**0.348**	**0.339**	***0.532***	0.150	**0.383**	**0.490**	0.147	0.327
DENLYC	49	-0.152	**-0.311**	**-0.308**	-0.239	-0.213	-0.195	-0.177	-0.154	.	-0.215	-0.219	.	-0.099
DENMH	49	**-0.303**	***-0.538***	***-0.450***	***-0.615***	***-0.538***	***-0.499***	***-0.561***	**-0.417**	.	***-0.493***	-0.328	.	***-0.513***
DENRC	49	***0.372***	-0.226	-0.264	0.127	0.181	-0.242	-0.181	**-0.400**	-0.283	-0.185	-0.354	-0.269	-0.271
DENSS	49	0.093	***0.461***	***0.507***	0.263	0.223	***0.492***	***0.506***	***0.500***	0.284	***0.609***	**0.478**	0.283	***0.604***
DENYC	49	-0.230	***-0.572***	***-0.492***	***-0.592***	***-0.502***	***-0.419***	***-0.472***	-0.344	-0.272	***-0.510***	-0.285	-0.271	**-0.430**
DISSTRM	46	0.075	***-0.390***	**-0.336**	-0.208	-0.096	**-0.372**	**-0.371**	**-0.461**	-0.385	-0.304	***-0.506***	-0.189	-0.322
SURVNO	49	0.233	0.272	0.268	0.271	0.278	**0.313**	***0.464***	0.327	0.019	***0.563***	0.242	0.189	***0.527***

Appendix II, Figure 5: Spearman correlation coefficient matrix comparing non-normal distributed habitat variables. “Significant” correlations ($P < 0.05$) are bolded, “highly significant” correlations ($P < 0.01$) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower N of column and row.

	N	ALTNEW	CANCL	DENAF	DENLAF	DENLMH	DENLRC	DENLSS	DENLWH	DENLYC	DENMH	DENRC	DENSS	DENYC	DISSTRM	SURVNO
N		49	49	49	49	49	49	49	49	49	49	49	49	49	46	49
ALTNEW	49	1	0.210	0.043	-0.016	**0.292**	-0.060	***-0.559***	***-0.392***	***0.398***	***0.678***	0.266	***-0.563***	***0.752***	**0.327**	***-0.416***
CANCL	49	0.210	1	0.187	-0.163	0.185	***0.517***	***-0.527***	**-0.312**	**0.298**	-0.063	***0.472***	***-0.528***	0.134	***0.393***	-0.197
DENAF	49	0.043	0.187	1	***0.515***	-0.107	-0.084	-0.119	0.227	-0.091	-0.233	-0.175	-0.111	-0.117	-0.158	-0.177
DENLAF	49	-0.016	-0.163	***0.515***	1	-0.120	-0.051	-0.025	***0.461***	-0.223	-0.251	-0.276	-0.021	-0.268	**-0.336**	-0.180
DENLMH	49	**0.292**	0.185	-0.107	-0.120	1	-0.067	-0.136	-0.158	***0.542***	***0.476***	-0.061	-0.136	***0.422***	0.137	-0.011
DENLRC	49	-0.060	***0.517***	-0.084	-0.051	-0.067	1	-0.253	-0.179	0.027	**-0.282**	***0.643***	-0.254	-0.168	**0.305**	-0.048
DENLSS	49	***-0.559***	***-0.527***	-0.119	-0.025	-0.136	-0.253	1	0.226	-0.252	**-0.284**	***-0.436***	***0.999***	***-0.377***	***-0.422***	***0.509***
DENLWH	49	***-0.392***	**-0.312**	0.227	***0.461***	-0.158	-0.179	0.226	1	-0.250	***-0.490***	***-0.478***	0.224	***-0.488***	***-0.553***	0.255
DENLYC	49	***0.398***	**0.298**	-0.091	-0.223	***0.542***	0.027	-0.252	-0.250	1	0.276	0.049	-0.251	***0.644***	0.154	-0.099
DENMH	49	***0.678***	-0.063	-0.233	-0.251	***0.476***	**-0.282**	**-0.284**	***-0.490***	0.276	1	0.034	**-0.284**	***0.800***	***0.447***	-0.274
DENRC	49	0.266	***0.472***	-0.175	-0.276	-0.061	***0.643***	***-0.436***	***-0.478***	0.049	0.034	1	***-0.437***	0.146	***0.494***	-0.132
DENSS	49	***-0.563***	***-0.528***	-0.111	-0.021	-0.136	-0.254	***0.999***	0.224	-0.251	**-0.284**	***-0.437***	1	***-0.377***	***-0.423***	***0.512***
DENYC	49	***0.752***	0.134	-0.117	-0.268	***0.422***	-0.168	***-0.377***	***-0.488***	***0.644***	***0.800***	0.146	***-0.377***	1	***0.437***	**-0.308**
DISSTRM	46	**0.327**	***0.393***	-0.158	**-0.336**	0.137	**0.305**	***-0.422***	***-0.553***	0.154	***0.447***	***0.494***	***-0.423***	***0.437***	1	-0.122
SURVNO	49	***-0.416***	-0.197	-0.177	-0.180	-0.011	-0.048	***0.509***	0.255	-0.099	-0.274	-0.132	***0.512***	**-0.308**	-0.122	1

Appendix II, Figure 6: Spearman correlation coefficient matrix comparing non-normal distributed habitat variables with normal distributed habitat variables. "Significant" correlations ($P < 0.05$) are bolded, "highly significant" correlations ($P < 0.01$) are bolded and italicised. The significances are given for orientation only, they are not results of proper hypothesis tests. The sample size of each cell is the lower *N* of column and row.

	N	ALTNEW	CANCL	DENAF	DENSS	DENRC	DENMH	DENYC	DENLAF	DENLWH	DENLSS	DENLRC	DENLYC	DENLMH	DISSTRM	SURVNO
N		49	49	49	49	49	49	49	49	49	49	49	49	49	46	49
EPIMEAN	49	***-0.698***	-0.202	0.016	***0.510***	***-0.420***	***-0.510***	***-0.543***	0.073	***0.489***	***0.511***	-0.114	**-0.356**	**-0.306**	***-0.468***	0.192
EPITHMEA	49	-0.267	0.113	0.023	0.067	-0.013	**-0.318**	-0.212	-0.018	0.208	0.074	-0.077	-0.078	-0.038	-0.277	-0.110
POPPLAHA	49	-0.259	0.250	***0.395***	**0.316**	-0.079	***-0.398***	**-0.282**	0.136	0.055	**0.314**	0.037	-0.032	-0.015	**-0.346**	0.013
REPLAHA	48	-0.124	0.057	0.170	**0.308**	0.075	-0.235	-0.077	-0.017	0.055	**0.304**	0.111	0.082	0.051	-0.137	0.070
DENTRPL4	49	**-.311**	.125	**.311**	.403	-.131	***-.474***	***-.399***	.118	.176	***.405***	.023	-.061	-.034	***-.415***	.155
TIMBVOL	49	***-0.781***	-0.112	0.273	***0.482***	***-0.400***	***-0.657***	***-0.686***	0.232	***0.556***	***0.477***	-0.084	**-0.282**	-0.182	***-0.482***	**0.293**
SDHT	49	***-0.507***	-0.225	0.036	***0.384***	-0.118	***-0.541***	***-0.650***	***0.439***	***0.466***	***0.386***	0.188	***-0.516***	**-0.300**	***-0.397***	-0.005
SDDBH	49	***-0.466***	-0.105	-0.079	**0.318**	-0.127	***-0.574***	***-0.550***	0.222	***0.501***	**0.328**	***0.402***	-0.196	-0.144	**-0.338**	0.189
OLDIND	49	***-0.540***	-0.145	0.012	***0.378***	-0.140	***-0.655***	***-0.674***	***0.376***	***0.558***	***0.383***	**0.338**	**-0.355**	-0.239	***-0.453***	0.082
OLDIND2	49	***-0.635***	-0.093	-0.099	***0.436***	-0.138	***-0.660***	***-0.710***	0.214	***0.537***	***0.442***	**0.333**	**-0.349**	-0.190	***-0.424***	0.138
DBHMEAN	49	***-0.547***	-0.030	-0.198	***0.434***	-0.110	***-0.545***	***-0.515***	-0.001	***0.428***	***0.442***	**0.293**	-0.106	-0.050	**-0.301**	0.243
DENWH	49	**-0.336**	0.208	-0.108	0.157	0.068	***-0.513***	***-0.391***	-0.070	0.088	0.148	0.236	-0.058	-0.034	-0.135	0.209
DENLARGE	49	***-0.450***	-0.099	0.019	***0.373***	-0.124	***-0.572***	***-0.523***	**0.341**	***0.548***	***0.374***	***0.410***	-0.119	-0.047	***-0.426***	0.161
DENSTEM	49	***0.426***	***0.413***	***0.504***	***-0.391***	0.226	0.273	**0.341**	0.025	**-0.363**	***-0.402***	0.050	0.180	0.218	**0.336**	-0.227
CANCLVEG	49	**-0.292**	**0.338**	0.246	0.122	0.032	***-0.365***	**-0.287**	-0.160	-0.027	0.111	0.166	-0.013	0.051	0.022	0.060
HTMEAN	49	***-0.646***	0.015	-0.046	**0.351**	-0.063	***-0.612***	***-0.695***	0.082	***0.384***	**0.351**	**0.283**	**-0.354**	-0.146	**-0.310**	0.128
DISSEA	49	***0.381***	0.104	***0.375***	**-0.359**	0.071	0.066	0.094	***0.426***	0.146	**-0.352**	0.155	-0.063	-0.164	0.039	***-0.514***
SLOPE	48	***0.523***	**0.327**	0.123	***-0.397***	**0.331**	0.219	**0.336**	0.020	-0.274	***-0.397***	0.220	0.143	0.100	0.197	**-0.336**
VEG1	49	-0.278	-0.003	-0.123	0.230	-0.005	*0.400*	0.289	*0.465*	-0.210	*-0.417*	-0.034	0.280	*-0.450*	-0.209	-0.112
VEG2	49	*-0.740*	-0.043	0.227	0.177	-0.350	0.031	0.127	*0.364*	*-0.427*	*-0.717*	-0.079	0.132	*-0.750*	-0.204	0.296
VEG3	49	-0.349	-0.050	0.157	-0.023	0.064	-0.305	*0.590*	0.173	0.059	-0.116	*-0.484*	*0.593*	-0.091	-0.348	0.188

Appendix III - Maps (in the back cover pocket)

Hiermit versichere ich, daß ich die vorliegende Diplomarbeit selbständig angefertigt und keine anderen als die gegebenen Hilfsmittel verwendet habe. Alle wörtlich oder sinngemäß entnommenen Textstellen sind als Zitate gekennzeichnet und belegt.

Marburg, April 1998