BEHAVIOUR AND HABITAT SELECTION OF MARBLED

MURRELETS NESTING ON THE SUNSHINE COAST

by

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ABSTRACT

I studied the behaviour and habitat selection of Marbled Murrelets

(*Brachyramphus marmoratus*) nesting in late-successional forests on the Sunshine Coast

of British Columbia. Fifty-two nest trees were located from 1995-1997. Marbled

Murrelets attended inactive nests prior to breeding, after nest failure, or in years following

a previous breeding attempt. These visits were most frequent in July. Nesting success was

33% and evidence of predation was found at 86% of failed nests. Nest trees were re-used

between years (11%) and rarely within a breeding season. Nineteen percent of nest trees

contained multiple nest sites indicating re-use over several years.

Marbled Murrelets selected for structural characteristics of their nesting habitat at

three spatial scales, microsite (nest site), element (nest tree), and patch (0.2 ha around nest

trees). Murrelets selected large diameter limbs with epiphytes and cover above the branch

at a microsite scale. Nest trees used by murrelets were larger in diameter and had more

potential nesting platforms than available trees. Murrelets selected nest trees adjacent to

canopy gaps, and they used these gaps to access their nests. Nest patches had higher

densities of large diameter trees, lower densities of small diameter trees, higher densities of

platforms, and a higher proportion of platforms with moss pads than available patches. At

all scales, selectivity was expressed most strongly for the availability of platforms, which

are a basic structural requirement of nesting murrelets.

On the Sunshine Coast, high densities of platforms and mossy platforms were

associated with occupied habitats and high activity of Marbled Murrelets. Sites occupied

by murrelets were at higher elevations, had higher densities of platforms, and had less gap

area than sites where murrelets were not-detected. Use of high elevation forests and

yellow-cedar trees likely occurred because late-successional forests are rare at low-elevations on the Sunshine Coast. Coarse forest classifications, such as biogeoclimatic variants, were not associated with the structural characteristics important to Marbled Murrelets and were not useful for identifying their habitat on the Sunshine Coast.

Management of nesting habitat for Marbled Murrelets on the Sunshine Coast should include landscape level planning to retain large patches of high quality nesting habitat for murrelets. These patches must be large enough to provide interior forest conditions. Managers should also consider long-term recruitment of future nesting habitat to ensure a supply of nest sites for Marbled Murrelets.

Acknowledgements

Table of Contents

List of Tables

List of Figures

Figure

General Introduction

Marbled Murrelets (*Brachyramphus marmoratus*) are seabirds of the family Alcidae that occur along the Pacific Coast of North America from central California to western Alaska (Nelson 1997). Like other alcids, Marbled Murrelets are highly adapted to their marine environment. The reduced area of their wings and position of their legs far back on their body help them dive and pursue their aquatic prey (Nelson 1997). Marbled Murrelets forage in nearshore coastal waters throughout their range and feed largely on small schooling fishes and invertebrates (Carter and Sealy 1990, Burger 1995a, Burkett 1995). The nesting habitat of Marbled Murrelets is unique from that of other alcid species. Most alcids nest in dense colonies on offshore islands (Gaston and Jones 1998). Marbled Murrelets nest inland in the crowns of coniferous trees throughout most of their range from Alaska south to California (Nelson 1997). Murrelets also nest on the ground in the northern portion of their range in Alaska (Nelson 1997).The murrelets' nesting strategy has been difficult to study, and consequently relatively little was known about this species until recently.

The nesting ecology and habitat of Marbled Murrelets have been investigated recently because of concerns about the conservation of this species and management of its nesting habitat. Marbled Murrelets are listed as threatened or endangered throughout their range, with the exception of Alaska (Rodway 1990, Ralph *et al.* 1995). Loss of nesting habitat due to forest harvesting is perceived as a major threat to the species (Rodway 1990, Carter and Morrison 1992). Studies of the activity of Marbled Murrelets, show that late-successional coastal forests are used for nesting throughout the murrelet's range, but the tree species and specific habitat characteristics used vary regionally (Burger 1995b, Hamer 1995, Hamer and Nelson 1995b, Kuletz *et al.* 1995, Naslund *et al.* 1995). For most studies, researchers' ability to evaluate habitat selection has been limited by small samples of nest sites.

In British Columbia, most studies of Marbled Murrelets have occurred on Vancouver Island (Manley *et al.* 1992, Savard and Lemon 1994, Burger 1995b, Rodway and Regehr 1998a, 1998b, 1998c) and the Queen Charlotte Islands (Rodway *et al.* 1993a,

1993b) where large areas of intact late-successional forests remain. Few nest sites and active nests have been located. On the southern mainland coast of B.C., potential nesting habitat of murrelets has been modified by extensive forest harvesting at low elevations. In this area, habitats used by murrelets may differ from other locations because of differences in availability of habitat types. The goal of my study is to examine the nesting behaviour, nest site selection and habitat use of Marbled Murrelets. This information provides a basis for management of murrelet habitat.

In Chapter 1, I describe the behaviour of murrelets at their nests and their patterns of activity at nesting stands. In Chapter 2, I describe the characteristics of murrelet nests and examine selection of nesting habitat. In Chapter 3, I examine habitat use by murrelets and the suitability of habitats on the Sunshine Coast. In Chapter 4, I provide management recommendations for the nesting habitat of Marbled Murrelets.

Study Area

The study area was located within the Sunshine Coast Forest District, which extends along the mainland coast of southwestern British Columbia from Howe Sound to Bute Inlet (Fig. 1). Study sites differed among years (see Chapter 3 for details). These sites spanned a distance of 105 km along the coast from the Salmon Landscape Unit and the Caren Range in the south, to Cortez and West Redonda Islands in the north. They extended 25 km inland to the upper reaches of Powell Lake. The study area included parts of the Georgia Lowland Ecosection of the Lower Mainland Ecoprovince and the Southern Pacific Ranges, Northern Pacific Ranges and Outer Fiordlands Ecosections of the Pacific and Cascade Ranges Ecoprovince (Demarchi 1996). The Sunshine Coast is divided by a series of long inlets. Low mountain ranges rising to 1200 m in elevation occur near the coast. Inland, the Coast Mountains dominate the topography with many peaks above 2500 m.

The Coastal Douglas-fir (CDF), Coastal Western Hemlock (CWH) and Mountain Hemlock (MH) biogeoclimatic zones occur in the study area (Meidinger and Pojar 1991). The CDF is limited to a narrow strip along the coast and was not investigated because late-successional forests (>250 yr) are rare. Biogeoclimatic variants represented at sites included; CWH very dry maritime (CWHxm), CWH dry maritime (CWHdm), CWH very wet maritime montane (CWHvm2), and the MH moist maritime (MHmm1) (Green and Klinka 1994).

The driest coastal forests occur in the CWHxm that extends from sea level to 200 m in elevation. Tree species in this variant include Douglas-fir *(Pseudotsuga menziesii)*, shore pine *(Pinus contorta)*, western hemlock *(Tsuga heterophylla)*, and western redcedar *(Thuja plicata)*. Dominant shrubs species include salal *(Gaultheria shallon)* and ocean spray *(Holodiscus discolor)*. The CWHdm occurs above CWHxm up to 600 m and at sea level along inlets. Tree species are similar to those in the CWHxm and shrubs include red huckleberry *(Vaccinium parvifolium)* and salal.

The CWHvm2 variant occurs from 600 to 1000 m elevation. Western hemlock and Pacific silver fir *(Abies amabilis)* are common in this variant. Douglas-fir and western

3

BU   Bunster Landscape Unit
❶   Monitoring Site 1
❷   Monitoring Site 2
BR   Brittain Landscape unit
SE   Sechelt Landscape Unit
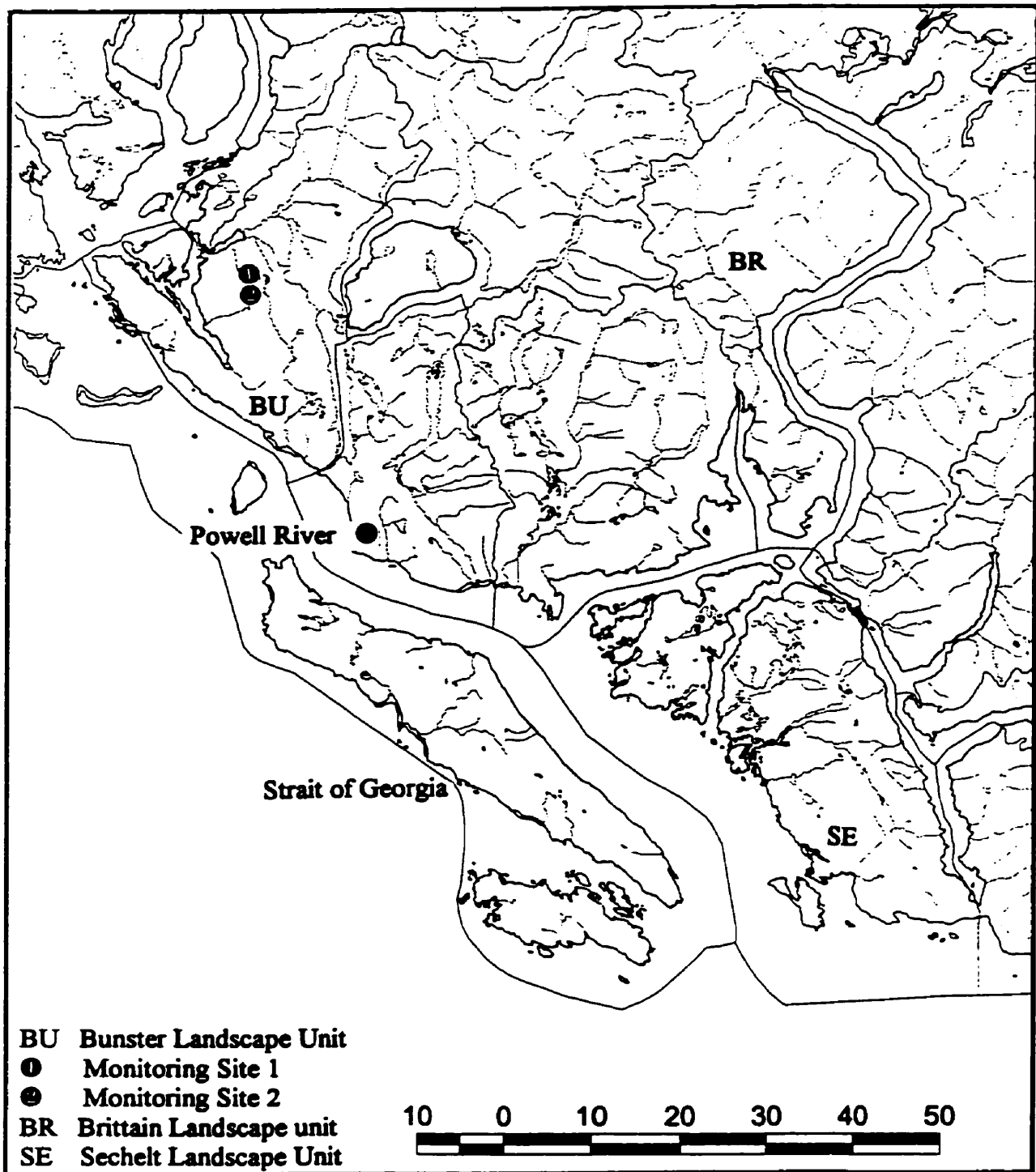
Figure 1. Map of the study area showing landscape units surveyed for murrelet activity and monitoring sites in the Bunster Range.

redcedar occur at lower elevations and yellow-cedar (*Chamaecyparis nootkatensis*) and mountain hemlock (*Tsuga mertensiana*) predominate at high elevations. Oval-leaved and Alaska blueberry (*V. ovalifolium* and *V. alaskaense*) dominate the shrub cover. The MHmm1 variant occurs in sub-alpine areas above 1000 m. Tree species in these stands include Pacific silver fir, mountain hemlock, western hemlock and yellow-cedar.

In the past, forest harvesting in the study area was concentrated in low elevations along the coast and in valley bottoms that were most accessible. Late-successional forests are now uncommon at low elevations. Estimates of forest cover for the Sunshine Coast District indicate that 2.4% of the CWHxm and 5.3% of the CWHdm forested area are late-successional forest. Forest harvesting is occurring in the CWHvm2 and the MHmm1. Late-successional forests comprise 26.7% and 28.1% of the forested area in these variants respectively (I. Blackburn unpub. data).

Forests in the study area fall under several jurisdictions including, Tree Farm License 41, Timber Supply Area, Indian Reservation, Protected Areas and Ecological Reserves. Many of the study sites are within the Sliammon First Nation traditional territory including the Bunster Range, Theodosia River valley and the Forbes Creek valley.

Locations of Murrelet Nests

Nest sites of Marbled Murrelets described in this thesis were located in three areas; the Bunster Range, Theodosia valley and the Brittain valley. The Bunster Range and Theodosia valley occur in the Bunster Landscape Unit. This landscape unit has a forested area of 35,404 ha, has 4,874 ha (13.8%) late-successional forest, and is adjacent to Desolation Sound. During the breeding season, Desolation Sound supports one of the highest densities of Marbled Murrelets in southern B.C. (Burger 1995a). An estimated 2,500 to 4,300 murrelets forage in this area (Drever *et al.* 1998). Murrelets use Theodosia Inlet as a flight corridor between marine habitat and inland forests (Kaiser *et al.* 1995).

The Brittain River is located on the north side of Jervis Inlet. This Landscape Unit contains 28,809 ha of forested area and has 8,859 ha (30.8%) of late-successional forest. Murrelet populations in Jervis Inlet have not been well-studied during the breeding season (Vermeer 1989).

Chapter 1. Activity and Behaviour of Marbled Murrelets at Nest Sites

Introduction

Nest sites are an important component of habitats used by birds. Quality of the nest site affects fitness through influences on reproductive success and adult survival (Martin and Roper 1988, Martin 1992). Relationships between habitat features and nest sites have been documented for many species (Martin 1998) but they may not reveal the ecological factors that drive habitat selection. An understanding of ecological processes that influence habitat selection is needed to derive approaches for management of habitat (Gavin 1989, Martin 1992).

Nesting behaviour provides a basis to interpret the importance of habitat features selected for nests. Bird behaviour and attendance at nests offers insights into how and why habitat features influence choice of nest sites. Intensity of habitat use and density are not always indicators of habitat quality (Van Horne 1983). Ecological information, such as nesting success, causes of nest failure and re-use of nest sites, is needed to determine how nesting habitat contributes to reproduction and survival at both individual and population levels.

Nesting behaviour and ecology are poorly documented for the Marbled Murrelet (*Brachyramphus marmoratus*), largely because of difficulties in locating their nests. Marbled Murrelets are alcid seabirds, but they nest inland in old-growth forests (Binford *et al.* 1975, Ralph *et al.* 1995). This contrasts with most alcids that nest in colonies on offshore islands (Gaston and Jones 1998). Although Marbled Murrelets may nest in excess of 50 km inland, they feed largely on small schooling fish in nearshore marine waters (Carter and Sealy 1990) or occasionally on salmonids at inland lakes (Carter and Sealy 1986, Hobson 1990). Marbled Murrelets lay a single egg clutch like most alcids (DeSanto and Nelson 1995). Their chicks are semi-precocial and are brooded for 1-3 days following hatching. Parents provision chicks by making repeated trips between marine foraging areas and inland nest sites. At fledging, murrelet chicks must make their initial flight from nests to marine habitat. Unlike most other forest nesting birds, murrelets are seabirds. Their use of marine foraging habitats and their adaptations for diving likely influence their nesting behaviour and use of inland habitats.

6

Behaviour of Marbled Murrelets at a tree nest was first observed in 1990 (Singer *et al.* 1991, Naslund 1993a). More recently, nesting behaviour has been documented at 9 nests in Oregon (Nelson and Peck 1995), 3 nests in California (Kerns and Miller 1995, Singer *et al.* 1995) and 2 nests in Washington (Hamer and Cummins 1991). Prior to my study, murrelet nesting behaviour had been observed at one nest site in British Columbia (Jones 1993).

Several aspects of nesting behaviour by murrelets are adaptive for avoiding predation, which is the most common cause of nest failure (Nelson and Hamer 1995a). Murrelets visit their nests at dawn and dusk and they are quiet and secretive during these visits (Nelson and Hamer 1995b). Reproductive success and causes of nest failure for murrelets have not been documented in B.C. This information is needed to understand the demography and status of murrelet populations. Causes of nest failure may indicate how features of nesting habitat may contribute to reproductive success.

Murrelets exhibit seasonal and daily patterns of inland activity (Naslund and O'Donnell 1995, O'Donnell *et al.* 1995), but the significance of these patterns is poorly understood. A seasonal peak in activity occurs from mid-July to early August (O'Donnell *et al.* 1995). On a daily basis, activity is concentrated within a 2-hour period, centered at sunrise (Naslund and O'Donnell 1995). Surveys conducted at dawn ("dawn surveys") were developed to inventory murrelets during these active periods (Ralph *et al.* 1994, RIC 1995). These surveys provide an index of habitat use by murrelets, but little is known about how much of this activity is related directly to nesting birds. Murrelets sometimes land in trees that do not contain active nests (Naslund 1993a, Naslund *et al.* 1995). This behaviour may represent nest prospecting, nest site defence, pair-bonding, resting or roosting (Naslund 1993a). Information on behaviour at active nests and visits to inactive nests could improve our understanding and interpretation of inland activity by murrelets.

My goal for this chapter is to describe how murrelets behave in their nesting habitat. I describe seasonal and daily patterns of inland activity for comparison with other locations in B.C. and elsewhere in the murrelet's range. I present data on incubation, chick feeding, and fledging behaviour at active nests, and nest attendance at inactive nests. I also present data on nesting chronology, nesting success, causes of nest failure, and re-use of

nest trees by Marbled Murrelets. This information provides a behavioural framework for understanding the characteristics and selection of murrelet nesting habitat presented in Chapter 2.

Methods

General Inland Activity

Inland activity by murrelets was assessed at two permanent monitoring sites in the Bunster Range (Fig. 1). Surveys at these monitoring sites were used to characterise seasonal and daily patterns of activity for comparison with seasonal patterns at-sea in Desolation Sound and with other inland locations in B.C. I established the monitoring sites in areas that had substantial murrelet activity during preliminary surveys in 1995 and were accessible from our base camp. The monitoring sites were located 1 km apart on a logging road adjacent to stands of late-successional forest. The sites were 5 km inland at elevations between 870 and 890 m. Monitoring Site 1 (MS1) was located next to Nest 1 (active in 1995). Monitoring Site 2 (MS2) was near Nests 11 and 5 (both active in 1996).

Murrelet activity at inland habitats was determined from dawn activity surveys following a standard protocol (Ralph *et al.* 1994, RIC 1995). Monitoring sites were surveyed weekly from May 20 to August 14, 1996. Both sites were surveyed on the same morning when possible or on consecutive mornings. Observers recorded murrelet "detections" during a 2-h period, centered at sunrise, when murrelet flights and vocalizations at inland areas are consistently greater than at other times of the day. A "detection" is defined as the sighting or hearing of a single murrelet or group of murrelets acting in a similar manner (Ralph *et al.* 1994). Three types of detections were recorded based on whether birds were heard only (auditory), seen only (visual), or heard and seen (both) (Fig. 2). The following data were recorded for each murrelet detection: time (PST), number of murrelets, the direction and closest distance from observers, height of detection, behaviour, type of flight path, and vocalization type (Ralph *et al.* 1994).

Murrelet behaviour was classified as "occupied below" (birds landing or flying below canopy), "occupied circling" (birds seen circling above canopy), not occupied (birds

8

Detection type

Behaviour categories

Nest visit type

Detection
sighting or hearing a bird or group of birds behaving in a similar manner

Visual Detection
or
Auditory and Visual Detection

Auditory Detection

Not Occupied Behaviour
direct flights above canopy

Occupied Behaviour
flying below canopy or circling above canopy

Occupied Behaviour
call from stationary point

Unknown Behaviour
keer calls, other vocalisations, wingbeats

Occupied Circling Behaviour
circle above canopy

Occupied Below Behaviour
flying below canopy

Circle Below Canopy

Direct Flight Below Canopy

Land/Depart

Fly-by
near tree
near branch

Nest Attendance
Inactive nest

Feeding Visit

Incubation Exchange

Land/Depart

Stall-out
attempt to land

Touch&Go
momentary
landing

Land

Land

Rest

Feed

Depart

Exchange/
Vocalize

Depart

Figure 2. Hierarchical classification for activity and behaviour of Marbled Murrelets. This scheme describes detection types, behaviour categories and behaviours at active and inactive nests.
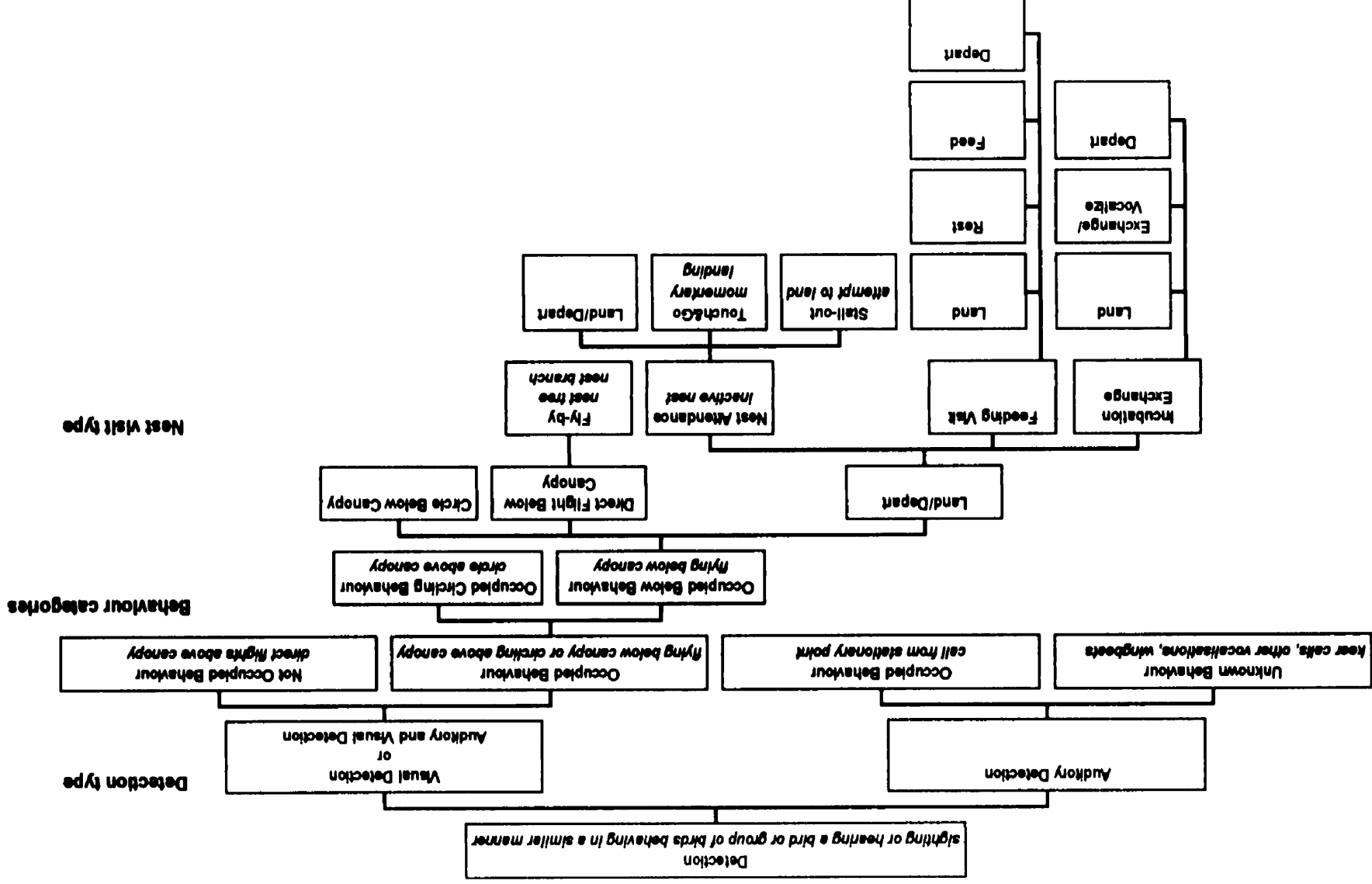
seen flying straight, directly above canopy) and unknown (auditory detections where bird behaviour is unknown) (Fig. 2). 'Occupied' behaviour includes occupied below, occupied circling behaviour, and birds calling from a stationary point (Ralph *et al.* 1994). Group size was recorded for all detections when murrelets were seen.

Seasonal activity patterns were described at monitoring sites by plotting total detections and occupied behaviour for surveys between May and August 1996. Frequencies of detection types (auditory, visual and both) were calculated for each monitoring site. Frequencies of each group size and behaviour were plotted for 10-min periods from 60 min before sunrise to 60 min after sunrise. I tested for differences in total detections and occupied behaviours between the two monitoring sites using a Wilcoxon paired sample test with data pairs consisting of surveys at each site on the same or consecutive days. Spearman rank correlation was used to test for correlation in activity between sites and amongst types of activity within sites. I used a Chi-square test to examine independence of detection types between the two monitoring sites. All tests were considered significant at alpha < 0.05.

Locating Nests

A variety of methods were used by field crews from 1994-1997 to find nests of Marbled Murrelets as part of the Marbled Murrelet Research Project (Simon Fraser University) and the Sunshine Coast Marbled Murrelet Inventory Program (B.C. Ministry of Environment Lands and Parks, MELP). Radio-telemetry was used in 1994 to locate nests of birds caught in Desolation Sound (Derocher *et al.* 1996). In 1995-1996, a combination of dawn activity surveys and tree climbing was used to locate nests (Naslund 1993a, Lougheed *et al.* 1998a). To locate nests, I focused on areas where I detected occupied behaviours (birds flying below or into the canopy and landing in trees). Survey effort was increased in the immediate area of the occupied behaviour to locate trees where murrelets were landing. When occupied behaviours were observed but we could not locate a nest from the ground, we returned to these areas at the end of the breeding season and climbed trees to search for nest sites. Locations with occupied behaviour were searched by climbing trees that exhibited potential nesting structures (limbs at least 15 cm in diameter).

In 1997, variable radius plots in edge and interior forest were climbed and searched for nests (see Manley 1998 for methods).

In 1995, 5 sites were surveyed for murrelet activity from June 1-July 31 and 89 trees were climbed and searched for nests from August 3-29 (Lougheed *et al.* 1998a). In 1996, 36 sites in the Bunster Range were surveyed from May 13-August 5 (Drever *et al.* 1998). We also scanned trees to look for murrelet nests and searched under potential trees for eggshell fragments during vegetation plots (n =36), transects (n =27) and other field work. MELP inventory crews surveyed 20 stands at other locations in the Sunshine Coast Forest District (Manley and Jones 1996). During 1996, 355 trees were climbed in the Bunster Range and 12 trees were climbed in the Brittain River Watershed. In 1997, 17 sites were surveyed in the Bunster Range at which 11 trees were climbed to search for nests (Lougheed *et al.* 1998b). During the MELP inventory in 1997, 48 sites were surveyed and 343 trees were climbed to search for nests in plots (Manley 1997). Nest trees were numbered in order of their discovery. When nest trees contained more than one nest cup each nest cup within a tree was given a different letter (e.g., Nest 15a).

Nesting Activity

Nesting chronology

Nesting chronology was estimated at nests where laying or hatching dates could be derived from nest observations. Laying and hatching dates were estimated assuming a 30-day incubation period and a 28-day nestling period (Hamer and Nelson 1995a).

Nesting behaviour

Nesting behaviour was monitored during dawn (60 min before to 60 min after sunrise) and dusk (60 min before to 60 min after sunset) survey periods. All behavioural observations were made from the ground using a spotting scope 25-50 m from nest trees. Incubating murrelets were not monitored intensively to avoid disturbing them. Behaviour of adults at the nest branch could only be determined when light intensities were sufficient to allow observations with the spotting scope. However, adult arrivals and departures were determined from observations without the assistance of the spotting scope during all light conditions. I determined flight paths that adult murrelets followed near nests by

surveying along their entrance and departure routes to nest trees.

I collected data on three types of nest visits made by adult murrelets: incubation exchanges, when adults arrived at nests to exchange incubation duties; chick feeding visits, when adults brought food to nests; and nest attendance, when adult birds visited nests that did not contain an egg or a chick, including visits to old nests. I differentiated nest attendance from incubation exchanges or feeding visits based on one of the following criteria; 1) birds were not remaining at the nest or feeding a chick, or 2) when landing, behaviour did not conform to a regular pattern as expected for incubation or feeding chicks (e.g., days missed or multiple landings by a pair of birds). Landings at trees where nest status could not be confirmed (Nests 16, 28) were not included in analyses of inactive nests.

Data collected at all visits included time (min ± sunrise or sunset) and duration (length of time between arrival and departure). For chick feeding visits, I calculated feeding frequency at dawn and dusk as the number of feeding visits per 2-h survey. Daily feeding frequency was estimated as number of feeding visits per 4-h survey on days when consecutive dusk and dawn surveys were completed at the same nest. Because multiple feeding visits occurred during a single survey, I used the following terms to describe the distribution of feedings during the survey. Each feeding visit was numbered from earliest to latest. 'Feeding visit interval' was defined as the time between the departure of one adult and the arrival of the next adult. 'Feeding return time' was the time between an individual adult's departure from its first feeding visit and its arrival for an additional feeding. Return time represents the time required for a murrelet to fly to the ocean, catch a fish, and return to the nest. For this calculation, I assumed that adults alternated feeding visits to their nest. I think this assumption is valid because of the short period between feedings relative to the duration of feeding visits. I recorded the behaviour and vocalizations of adult murrelets during nest visits. I also described the behaviour of chicks prior to fledging.

I summarized information on timing and duration of incubation exchanges, feeding visits, and nest attendance. I tested for differences in feeding frequency and feeding duration during dawn and dusk surveys using a Wilcoxon 2 sample test. The frequency of

12

surveys with nest attendance was calculated for surveys in May, June and July. I tested
for independence of nest attendance and month using a Chi-square test. Spearman rank
correlation was used to determine if the frequency of landings was correlated with the
frequency of fly-bys at inactive nest trees. Behaviour and timing of chick feeding visits was
compared with nest attendance visits. I used a Mann-Whitney U-test to compare the
number of occupied below behaviours recorded during surveys with chick feeding and
surveys with nest attendance. The time and duration of chick feeding visits were compared
with nest attendance visits using Mann Whitney U-tests.

Nesting Success

Nesting success was determined by monitoring nesting activity or collecting
nesting evidence. Nests were considered successful if fledging was observed or if a fecal
ring and down were present at the nest. At unsuccessful nests, the chick or egg was
abandoned, the chick died, un-faded eggshells were present in nest cups without fecal
rings, or predation was documented. Nests were assumed to have been depredated if
predation was observed, if I saw puncture marks on eggs or found remains of adult or
juvenile murrelets. Nest outcome and causes of nest failure are summarized for all nests
over the 3 years of my study.

Re-use of Nest Trees

Nest trees were monitored in years following their discovery (1996-97) to
determine if murrelets re-used the nest tree. Nest trees were surveyed a minimum of 3
mornings, at least once in each of May, June and July and were climbed at the end of the
breeding season to look for evidence of re-use such as eggshells, feathers and fecal rings.
The percentage of nest trees re-used was calculated based on the number of nest trees
where it was possible to observe re-use. Nest trees that were surveyed 3 times and
climbed at the end of the season were considered as opportunities to observe re-use. At
many nest sites, I observed occupied behaviours but landings did not occur. Because
occupied behaviours may indicate interest in a nest tree, the proportion of nest trees with
occupied behaviours was also calculated. The presence of multiple nest cups within a tree

13

indicates that the tree has been used for more than one breeding attempt. It is not possible to date murrelet nest sites unless evidence such as eggshells are present, but nest cups may remain visible for 4 or more years (I. Manley unpub data, A. Burger pers. comm.). I used the proportion of nest trees with >1 nest as a measure of nest tree re-use over multiple years. This measure would not detect re-use of the same nest, or detect multiple nests used within a single year.

Results

General Inland Activity

There were few detections of Marbled Murrelets and no occupied behaviours at Monitoring Site (MS) 1 prior to June 18 (Fig. 3). At MS2, murrelets were detected during all surveys in May and June and there was an minor peak in total detections on May 25. Both monitoring sites showed a maximum peak in total detections and occupied behaviour between July 4-21 followed by a sharp decline to no detections by the first week of August. A maximum of 43 total detections was recorded at MS1 on July 10; this is about half the maximum of 84 total detections recorded at MS2 on July 16. Total detections and occupied behaviour at MS2 were approximately twice those at MS1 during surveys paired by date (Table 1). Throughout the season, the number of total detections recorded during concurrent surveys at MS1 was positively correlated to that at MS2 (Spearman rank correlation, r_s=0.72, P= <0.001, n =12). At both monitoring sites, number of total detections was highly correlated with the number of occupied behaviours (Spearman rank correlation; MS1, r_s=0.76, P<0.01, n =12; MS2, r_s=0.89, P <0.001, n =12).

Table 1. Results of Wilcoxon paired sample test for total detections and occupied behaviour at Monitoring Sites 1 and 2 during 1996.

Activity	N	Mean ± (SE)/survey MS1	MS2	P
Total detections	12	17.2 (4.9)	33.9 (7.5)	0.02
Occupied behaviour	12	3.6 (1.5)	7.4 (2.1)	0.02
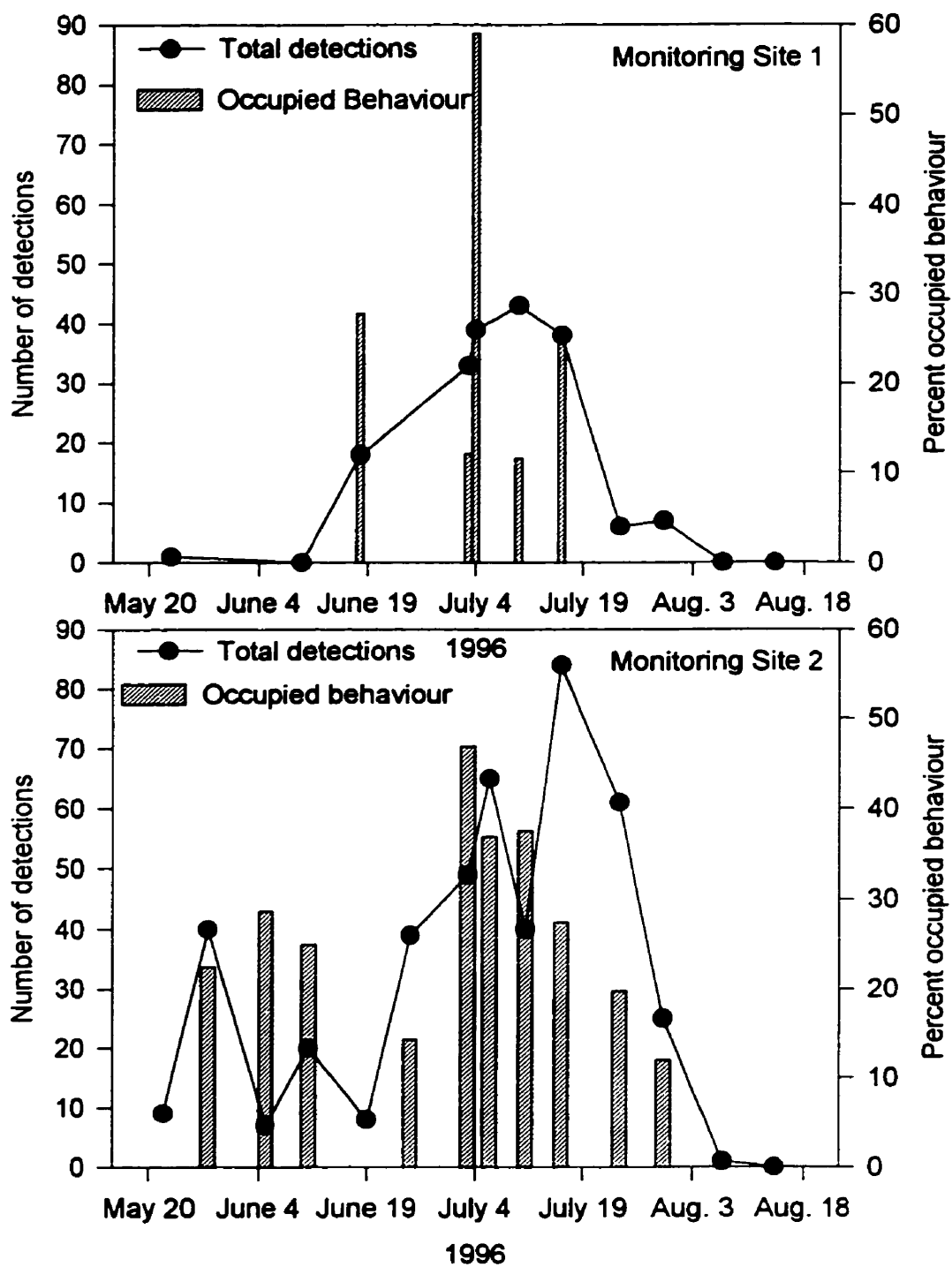
Figure 3. Murrelet detections and percent occupied behaviour at Monitoring Sites 1 and 2.

Proportion of visual and auditory detections

The majority of detections at MS1 and MS2 were auditory. Murrelets were heard calling but were not seen for 60.7% of detections at MS1 (n=453) and 56.1% of detections at MS2 (n=206). Visual detections of silent birds comprised 20.4% and 22.5% of activity at MS1 and MS2 respectively. Detections for which birds were seen and heard, comprised 18.9% and 21.4% of activity at MS1 and MS2, respectively. There were no differences in the proportions of auditory, visual and both auditory and visual detections between the two sites (χ^2=1.2, P=0.54, df=2). The proportions of detection types did not differ between pre-peak (May 20-June 15) or peak breeding (June 16-July 30) periods at MS2 (χ^2= 0.15, P= 0.93, df=2). Because there was only one detection at MS1 before June 15, I could not make a seasonal comparison at this site.

Group size

During inland surveys, murrelets were seen in groups of 1 to 6 birds. Pairs were the most common group size observed at both sites (Table 2). Single birds and pairs together comprised 64% of all observations. On a daily basis, single birds were observed earliest in the morning followed later by pairs and then larger groups (Table 2, Fig. 4). This trend was consistent at both sites, however, the times were later in the morning at MS1 than at MS2 (Fig. 4).

Type of behaviour

Overall, 26% of detections at both sites were occupied behaviour. Occupied behaviour included "occupied circling" (13%) and "occupied below" (13%). "Not occupied" behaviour (direct flights above canopy) comprised 32% of detections at both sites. Behaviour was unknown for 42% of detections. There was a higher proportion of "occupied below" behaviours and lower proportions of "occupied circling", "not occupied", and unknown behaviours at MS1 than at MS2 (Fig. 5). "Occupied below" behaviours were most frequent between 40-11 min before sunrise with another minor peak 11-20 min after sunrise. Other behaviours were distributed throughout the morning activity period (Fig. 5).

Table 2. Frequency and average timing of Marbled Murrelet groups seen during dawn surveys at Monitoring Sites 1 and 2, May 25 to Aug. 14, 1996.

	Group size					
	1	2	3	4	5-6	total
Site	Number of birds (% of birds)					
MS1	31	78	21	12	5	147
	(21.1)	(53.0)	(14.3)	(8.2)	(3.4)	
MS2	64	176	69	84	10	403
	(15.9)	(43.7)	(17.1)	(20.8)	(2.5)	
Total	95	254	90	96	15	550
	(17.3)	(46.2)	(16.4)	(17.5)	(2.7)	

Site	Time (min $\pm$ sunrise) mean (SE)				
MS1	-13.4	-3.0	24.6	8.3	7.0
	(20.1)	(20.8)	(28.8)	(9.5)	
MS2	-20.6	-12.5	-7.3	-1.2	-4
	(13.5)	(19.3)	(13.5)	(18.8)	(0.0)
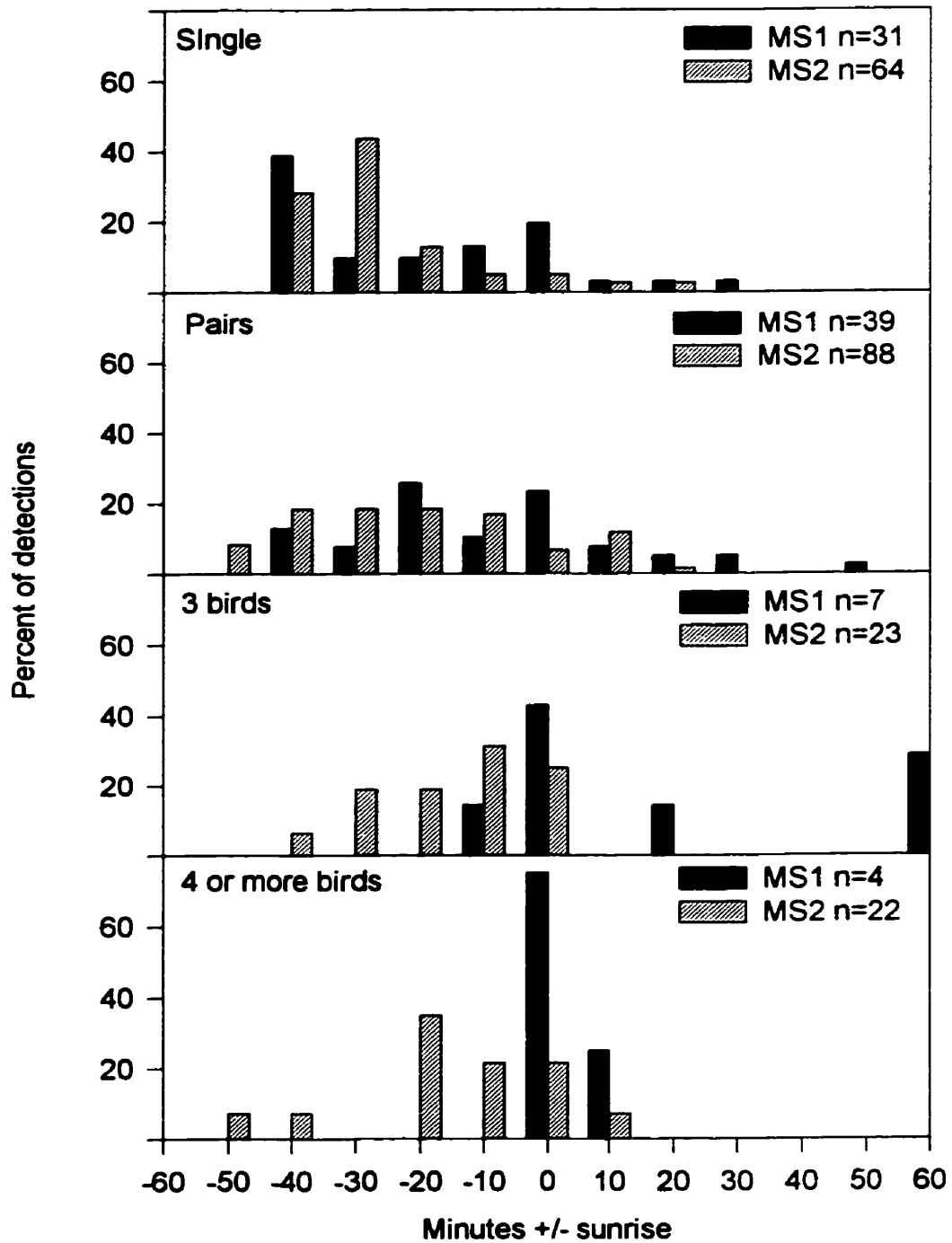
Figure 4. Time of detection for group sizes of Marbled Murrelets at Monitoring Sites 1 and 2, May 25 to Aug. 14, 1996. Times are in 10-min periods beginning at the times shown on the label.
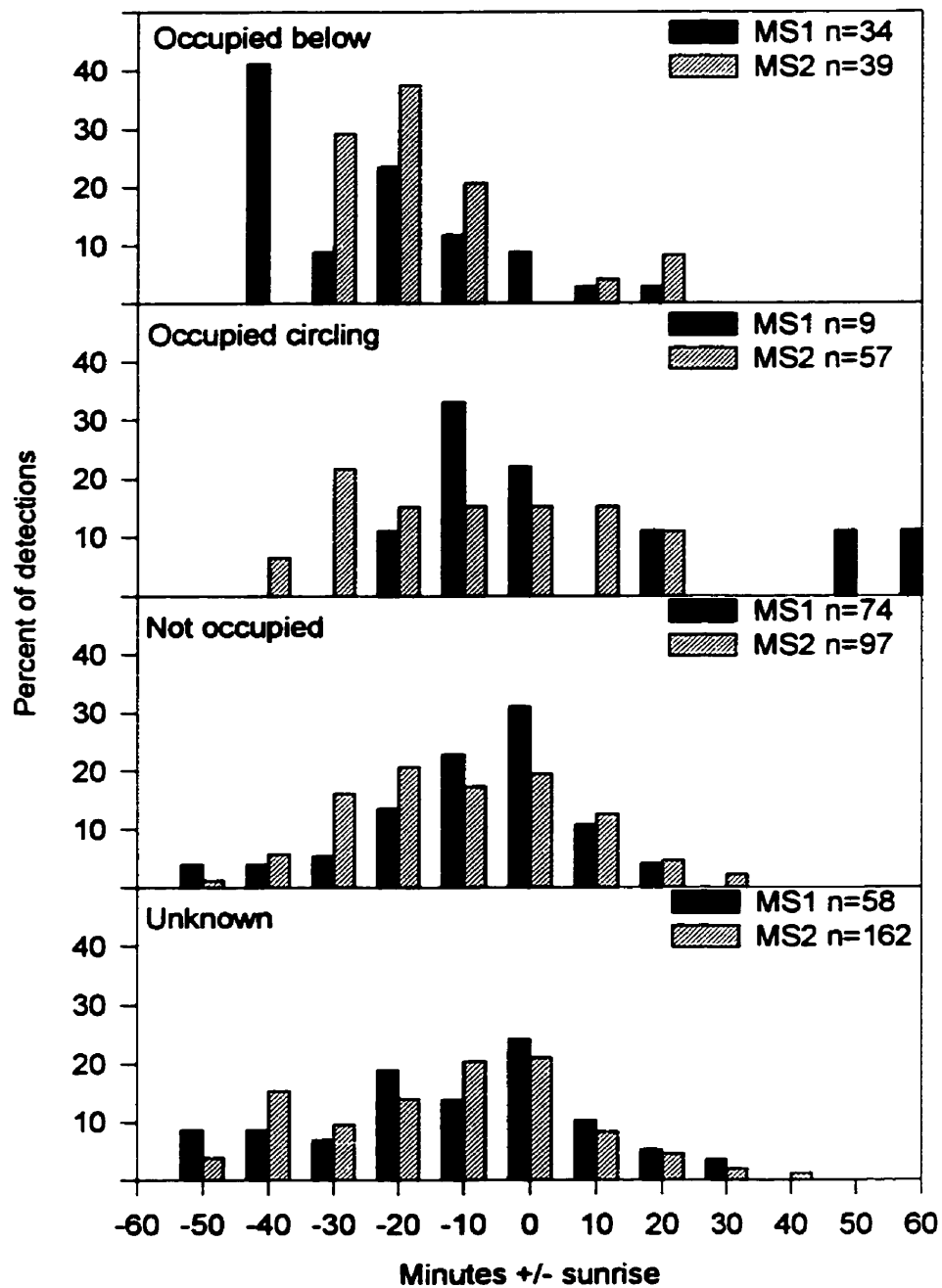
Figure 5. Time of detection for 4 behaviours of Marbled Murrelets recorded at Monitoring Sites 1 and 2, May 25 to Aug. 14, 1996. Times are in 10-min periods beginning at the times shown on the label.

Locating Nests

Fifty-two nest trees of Marbled Murrelets were located during the study from 1994-1997. Seven nests were active (nests where birds were incubating or feeding chicks) when they were located in 1995 and 1996. Active murrelet nests were found by scanning branches in trees from the ground (n =1), observing birds landing in trees during surveys (n =3), climbing trees in areas with occupied activity (n =1), checking known nests from the previous year for re-use (n =1) and with radio-telemetry (n =1) (Table 3). Nest visitation was observed at 6 nest trees where birds were not actively incubating or feeding a chick (inactive nests). Four of these trees were identified as nest trees following landing, one was a nest tree from the previous year, and one had been an active nest earlier that year. Forty-one nest trees were discovered after the breeding season during tree climbing. I had no information on behaviour for these nests but evidence at these nests was used to assess nesting success.

Nesting Behaviour

Nesting chronology

The nesting season of Marbled Murrelets on the Sunshine Coast extended a minimum of 128 days from May 11 to September 15 based on estimates from 7 active nests (Table 3). Egg laying was concentrated in May, with 4 nests having eggs laid before May 24. Egg laying also occurred later in the season on June 23 (Nest 3) and between July 5 and 19 (Nest 15a). I think that the late egg-laying attempt at Nest 15a was re-laying within a nest tree that was used and failed earlier in summer (see Nest Re-use). Hatching dates were estimated to span the period between June 15-July 23 but could extend as late as August 18. Fledging was observed on July 13 and August 20 but could extend as late as September 15 based on estimated laying dates.

Incubation exchanges

Incubation exchanges by Marbled Murrelets were observed on 4 occasions at 3 different nests listed in Table 3. At Nest 1, incubation exchanges were monitored on June 2 and 3, 1995. Incubation exchanges at Nests 5 and 11 were observed on May 13, 1996.

Table 3. Active nests of Marbled Murrelets found 1994-1996 and estimates of nesting chronology.

Nest	Date nest found	# days nesting observed	Date egg laid	Date chick hatched	Fate
Nest 5	May 12, 1996	1	<May 12	n/a	Adult flushed May 13, due to Common Raven
Nest 11	May 12, 1996	1	< May 12	n/a	Adult flushed May 13, due to Common Raven
Nest 1	June 1, 1995	6	~ May 13	~ June 15	Fledged July 13
Nest 32	July 16, 1996	1	~ May 16-June 15		Fledged between July16 -Aug 16
Nest 3	August 9, 1995	4	~ June 23	~ July 23	Fledged August 20
Nest 4	June 26, 1994	1[A]	< June 26		Evidence of fledging in 1994
Nest 15a	July 19, 1996	1 [A]	July 5- July 19	n/a	Failed ~ July 22

[A] daytime observation only

21

All incubation exchanges occurred between 28 and 25 min before sunrise and were less than 10 s in duration. Behaviour of murrelets during exchanges consisted of: 1) the arriving adult lands on the nest branch; 2) the incubating adult departs; and 3) the arriving adult moves on to the egg and begins incubating. Murrelets approached the nest tree at heights 1 to 5 m above the ground and swooped up into a stall flight at the nest branch. Soft wingbeat sounds and 'swooshing' wing sounds were heard as adults approached and landed at nests. At one incubation exchange, 3 soft "eh-eh" calls were heard when the adult landed.

Feeding visits

Feeding of chicks was observed at nests during a total of 18 surveys: Nest 1 (4 dawn surveys, 6 dusk surveys in 1995), Nest 3 (3 dawn surveys, 4 dusk surveys in 1995) and Nest 32 (1 dawn survey in 1996). Prey items were identified for 11 of 35 recorded feeding visits. During these 11 visits, single Pacific sand lance (*Ammodytes hexapterus*) were delivered to chicks.

Murrelets fed their chicks more frequently at dawn (mean = 2.6 ± 0.3 SE feedings/2 h, range 2-4, n = 7) than at dusk (mean = 1.8 ± 0.2 SE feedings/2 h, range 0-2, n = 9) (Wilcoxon test, Z=-3.8, P<0.001). A maximum of 4 and 2 feeding visits/survey were recorded at dawn and dusk surveys, respectively. Daily feeding frequency estimated from 6 consecutive dawn and dusk surveys was 4.5 ± 0.4 feedings/4 h. This is a minimum daily estimate because occasionally murrelets feed chicks during the day and we did not monitor nests during the whole day. However, a feeding was observed at Nest 3 incidentally at 11:29, August 12, 1996. There was a storm the previous evening, which may have prevented the adult from making a dawn visit.

Timing of feeding visits

During dawn surveys, Marbled Murrelets arrived to feed nestlings between 43 min before and 8 min after sunrise (Table 4, Fig. 6). Feeding times during dawn were similar at both Nest 1 and Nest 3 (mean = -21.1 min ± 4.8 SE and mean = -29.2 min ± 4.7 SE, respectively). Evening feeding occurred predominantly after sunset (mean $=14.1$ min ± 2.6

Table 4. Times that Marbled Murrelets arrived at nests to feed nestlings during dawn and dusk observation periods and times of nest attendance visits at inactive nests during dawn observations. Times are in minutes before or after sunrise or sunset. Data are from Nests 1 and 3 during 1995 and from 6 inactive nest trees surveyed in 1996.

	Time of Chick feeding visits (min)			Time of Nest attendance visits (min)
	Nest 1	Nest 3	Nests 1 and 3	
Dawn				
Mean ±SE	-21.1 ± 4.8	-29.2 ± 4.7	-23.8 ± 3.6	-22.1 ± 2.7
Range	-43.3 to -8.3	-41.1 to -11.1	-43.3 to -8.3	-43.3 to 9.0
n	12	6	18	26
Dusk				
Mean ±SE	18.8 ± 2.0	6.1 ±4.8	14.1 ± 2.6	-
Range	6.0 to 30.3	-15.1 to 17.3	-15.1 to 30.3	-
n	10	6	16	-
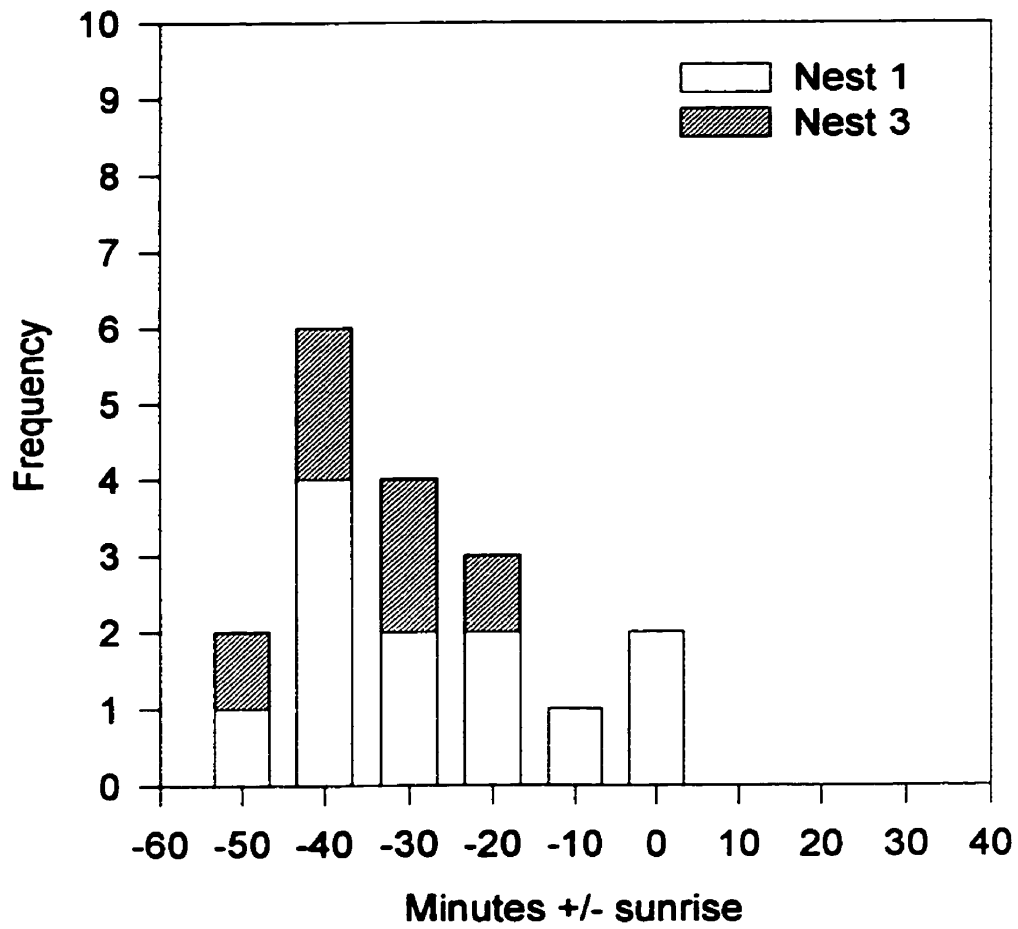
Figure 6. Timing of dawn feeding visits by Marbled Murrelets at Nest 1 and Nest 3 during 1995. Times are grouped in 10-min periods beginning at the times shown on the label.
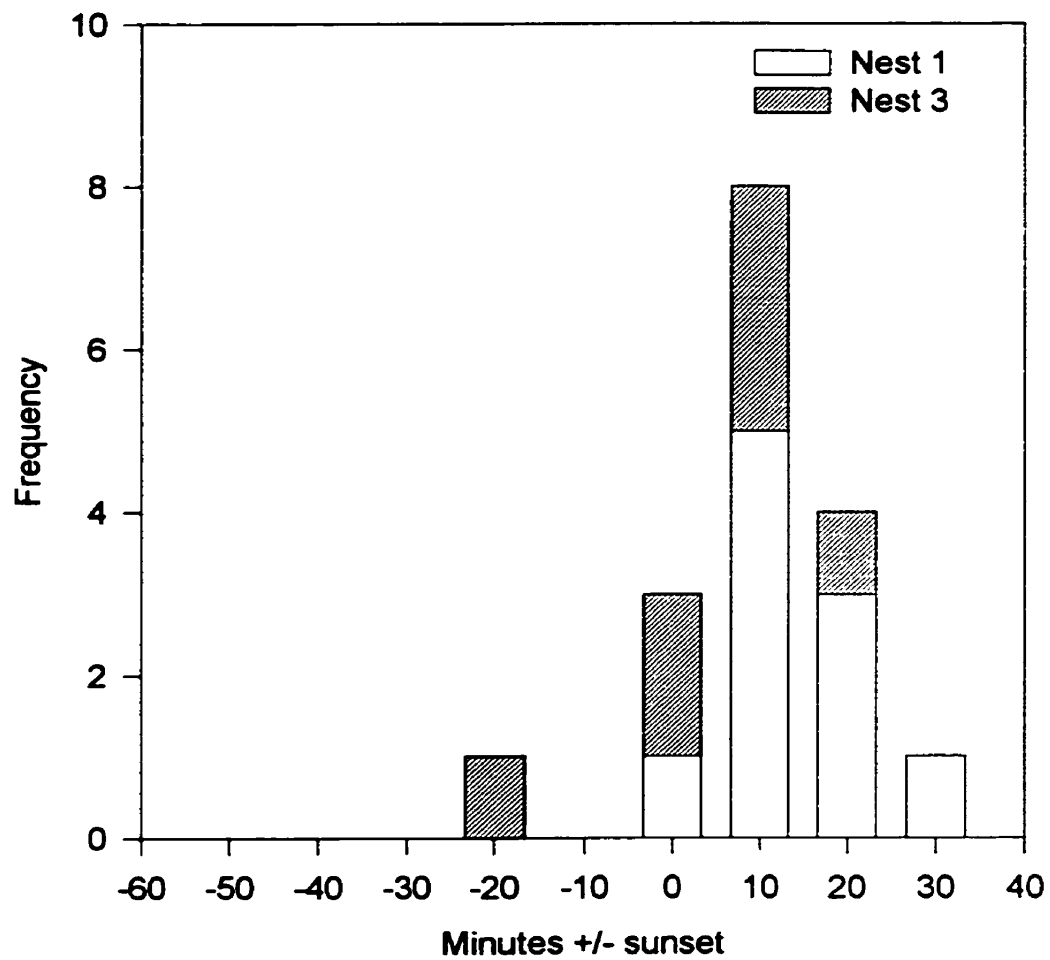
Figure 7. Times murrelets arrived at Nest 1 and Nest 3 for feeding visits during dusk surveys. Times are grouped in 10-min periods beginning at the times shown on the label.

SE, n = 16) and ranged from 15 min before to 30 min after sunset (Table 4, Fig.7).

Duration of feeding visits

The length of time Marbled Murrelets remained at the nest during dawn and dusk feeding visits ranged from 38 s to 22 min (Fig. 8). Dusk feedings were significantly shorter than dawn feedings for Nest 1 and Nest 3 combined (Wilcoxon 2-sample test, Z=-2.2, P=0.03; Table 5). The one diurnal feeding that I observed was a minimum of 53 min in duration but not included in analyses because the total duration was unknown.

Interval between feeding visits

Marbled Murrelets arrived at and departed from nests individually during feeding visits. Time between arrivals of consecutive adults (interval time) ranged from 6.3 to 17.9 min. Interval time between first and second feeding visits at Nest 1 were similar at dawn and at dusk (Table 6). Interval time increased with order of feeding visit. The interval time between second and third feeding visits and the interval time between third to fourth feeding visits were 4 and 12 min longer, respectively, than the interval time between first and second feeding visits (Table 6).

Duration of feeding visit also increased with feeding order at Nest 1. Second feeding visits were on average 4 min longer than first feeding visits at dawn and dusk (Table 6). Third and fourth feeding visits were observed only during dawn at Nest 1 but lasted on average 8 min longer than first feeding visits.

Return times for multiple feedings

During 3 dawn surveys at Nest 1, more than 2 feedings were observed when one or both adults returned to the nest for a second feeding. Return times for these birds were calculated assuming that adults in the pair alternate feeding visits, i.e., the adult making the first feeding was also the adult making the third feeding. Return times for individual birds ranged from 15.1 min to 34.7 min (mean = 24.1 ± 3.9 SE min, n =4). Surveys with 3-4 feeding visits occurred between 10-13 days prior to fledging on June 30, July 2 and July 3, 1995.
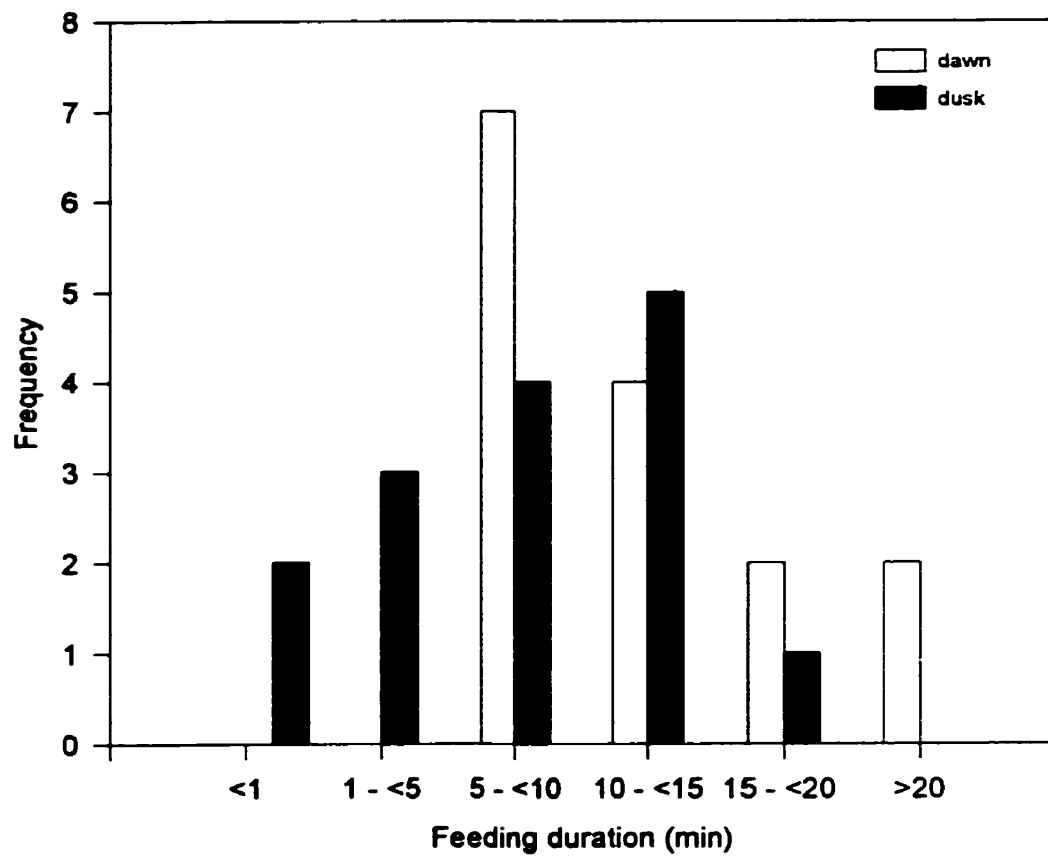
Figure 8. Duration of dawn and dusk feeding visits at Nest 1 and Nest 3, 1995.

Table 5. Duration of dawn and dusk feeding visits and nest attendance visits by Marbled Murrelets. Data are from Nests 1 and 3 during 1995, and from 6 inactive nest trees surveyed in 1996.

| | Duration of Chick feeding visits (min) | | Duration of nest attendance visits (min) |
	Nest 1	Nest 3	Inactive nests
Dawn			
Mean ±SE	12.5 ● 1.4	13.0 ● 2.4	3.3 ● 2.4
Range	6.1 – 21.8	6.1 - 16.6	0.2 - 13.0
n	12	4	5
Dusk			
Mean ±SE	6.9 ● 1.3	10.7 ± 1.6	-
Range	0.6 – 11.6	6.0 - 15.3	-
n	8	5	-

Table 6. Intervals between feedings and feeding visit duration in relation to feeding order. Data are from dawn and dusk surveys at Nest 1 during 1995. Interval between feeding visits is the time between the arrival of consecutive birds.

| | Interval time between feeding visits (mean ± SE min) | | |
	1st to 2nd	2nd to 3rd	3rd to 4th
Dawn	12.0 ± 2.0	16.2 ± 3.6	24.0
n	4	3	1
Dusk	11.1 ● 1.7		
n	4		

| | Duration of feeding visits (mean ± SE min) | | |
	1st	2nd	3rd and 4th
Dawn	8.6 ● 1.1	12.6 ± 3.0	16.2 ± 1.2
n	4	4	4
Dusk	6.1 ± 1.1	10.1 ± 0.7[a]	
n	4	3	

[a] Mean was calculated without one very short feeding observed immediately prior to fledging. With this feeding the mean and SE are 7.7 ± 2.5 min.

Overlap of nest visits

During 7 of 13 surveys with multiple feeding visits, both adults spent brief periods together on the nest branch. This occurred when a second adult with a fish arrived while the first adult was still feeding the chick. The arrival of the second adult resulted in the first adult allowing the chick to take the fish and then departing the nest immediately. Both adults were observed on the nest together for between 15 and 34 sec. The occurrence of both adults at the nest branch was the only time that adults were heard to vocalize during chick feeding. During 3 of the 7 surveys when both adults were present, vocalizations were heard as one adult left the branch. These vocalizations were either 3 soft 'Q' calls, 3 short alternate calls, or 1 sharp 'keer' call. Vocalizations were heard at Nest 3 (n=3 surveys) but not at Nest 1 (n=4 surveys).

Behaviour during the feeding visit

Adult murrelets were observed resting prior to feeding the chick during 8 of 10 visits where adult behaviour was observed on the nest branch. After landing on the nest branch, adults remained still at the landing site for between 2.6 and 15.9 min (mean = 8.2 min ± 2.0 SE, n =8) before approaching the chick. On average, these rests comprised 68% (range 27-98%) of time spent at the nest during feeding visits. During these initial resting periods, adults breathed heavily, presumably from the exertion of the flight. On one of the visits when adults did not rest, the adult was alert and looking in several directions before and during the feeding. This adult may have been vigilant towards a predator or disturbed by us because this was our first survey at this nest. On the other visit, the adult immediately brooded the chick for 3 min before feeding it.

Adult birds at Nest 1 always entered and exited the nest from the south. They approached the nest flying low (1-3 m above the ground) along a logging road located 30 m from the nest. Surveys along the approach route to the nest revealed that the birds were flying along a creek to its junction with the road 150 m south of the nest. Birds were heard making 'swooshing' or quiet wing-beat sounds during all landings and departures from Nest 1.

Murrelets approached Nest 3 by flying through a bog clearing, then along a 5-m wide path in the forest uphill for about 40 m to the nest tree. Nest 3 was located on the

north edge of the path. The path remained from mining exploration approximately 15 to 25 years ago and is covered in *Vaccinium sp.* and conifer saplings. Birds flew as low as 7-10 m above the ground when approaching and leaving the nest tree. Wingbeats were heard on one half of flights to and from Nest 3.

Fledging behaviour

Fledging was observed at Nest 1 on July 13, 1995 and at Nest 3 on August 20, 1995. Fledging occurred 24 and 22 min after sunset at Nests 1 and 3, respectively. The chick at Nest 1 began removing its down on the morning of July 13, had completely removed its down feathers by 1 h before sunset, and was very active, preening and stretching its wings during the 90 min that it was observed before fledging. The chick was fed twice at 6 and 19 min after sunset. The last feeding took only 23 s and was the shortest feeding we observed at any nest. After this feeding, the chick continued preening and stretching its wings for another 15 min before leaving the nest. When the chick left the nest it dropped only 1-2 m below the height of the nest and then flew above the canopy directly to the southwest. The chick did not follow the logging road at a low height like its parents did when they left the nest.

The chick at Nest 3 removed its down between 11:00 and 19:00 PST on August 19. Between 19:00 and 20:30 the chick was very active preening, opening its bill and flicking its tail. Two feedings occurred from 7 to 17 min and 17 to 23 min after sunset, but the chick did not leave the nest that evening. Observations on the following evening were made 40 m down slope from the nest to ensure that our presence would not interfere with fledging. The adults did not return to feed the chick before it fledged 22 min after sunset on August 20. When leaving the nest, the chick flew above the canopy to the southwest and did not follow the clearing that its parents used.

Nest Attendance

Marbled Murrelets landed at 6 inactive nest trees during my study. Twenty-six landings were recorded during 16 of 37 dawn surveys (Table 7). Nest attendance occurred from May 25 to July 30, 1996. Attendance varied significantly among months at the 3 nest

trees surveyed throughout the season (Nests 1, 11, and 15; χ^2 = 6.78, df=2, P=0.03).
Surveys with nest attendance were most frequent in July (81%, 13 of 16 surveys) and
lowest in May (25%, 1 of 4 surveys). Attendance was recorded at nest trees that were
successful the previous year (n=1), that failed during the current year (n=4) and in a nest
tree with an old nest cup (n=1).

Nest attendance was associated with below canopy flights near the nest branch or
tree in 94% of dawn surveys (15 of 16). Below canopy flights included "fly-bys" (flights
by single or pairs of birds near the landing branch; Fig. 2, Naslund 1993a) and either direct
or circling flights past the landing tree (mean = 5.4 detections/survey, range 0-17). The
number of landings and the number of below canopy flights were not correlated (r_s=0.01).
Landings (mean =1.2 detections/survey) were less frequent than fly-bys and below canopy
flights. I recorded single landings (66% of surveys) or multiple landings, ranging from 2 to
5 per survey (44% of surveys). Both single birds (58% of landings) and pairs of birds
(42% of landings) landed at inactive nests. Thirty-eight percent of surveys had landings
only by single birds, 31% had landings only by pairs of birds, and 31% had landings by
both single and pairs of birds.

I observed the following landing behaviours as defined by Naslund (1993a).

Land/depart: 42% of landings -bird(s) are seen both landing and departing. The length of
stay is recorded.

Land: 27% of landings - bird lands on the branch and may or may not be seen departing.

Touch and go: 23% of landings - bird(s) approach similar to a stall-out and land
momentarily on the branch.

Stall-out: 8% of landings - bird(s) approach the branch from below and stall their flight at
the branch as if they were going to land there. This results in the birds hovering
briefly near the nest branch before they dive and regain their flight speed.

Stationary point: 4% of landings - bird(s) call from a branch in the tree.

Table 7. Landing frequency at 6 inactive nest trees monitored in 1996.

Nest	History	Dates surveyed in 1996	No. of surveys	No. of surveys with landings	No. of landings
Nest 1	Active in 1995	May 23-Aug. 14	11	2	3
Nest 11	Failed early in 1996	May 22-Aug. 14	14	5	5
Nest 13	Old nest cup	Jun. 15-19	2	2	5
Nest 28	Failed in 1996	July 14	1	1	1
Nest 15	Failed early in 1996	May 25- July 30	8	5	11
Nest 16	Failed	Jun. 27	1	1	1
Total			37	16	26

Pairs of murrelets approaching nest trees often exhibited several combinations of landing behaviours. For example, one bird might stall-out at a branch while the other does a touch and go landing. Other combinations of behaviours observed included: one bird landing while the other circled the tree; and one bird landing and calling form the branch while the other bird flew past the nest tree.

Murrelets were observed landing only in the nest tree in all cases except one. At Nest 13, on June 19, both birds landed briefly at the nest branch. Following this observation, a single bird landed and another single bird stalled-out over a branch in a neighbouring tree. Most landings (61%) were brief lasting from 1 to 4 s. The remaining 39% of landings ranged from 7 s to 13 min in duration. The 13-min landing occurred at Nest 1, when both birds landed and remained on the branch together. Bird behaviour during this landing was not observed.

Comparison Between Types of Nest Visits

Nest attendance occurred between 43 and 9 min before sunrise (mean = 22.2 min before sunrise ± 2.7 SE, Table 4) and did not differ significantly from the time of chick feeding visits (t = 0.38, df =42, P =0.71, Table 5). Landings at inactive nests ranged from 1 s to 13 min in duration and were significantly shorter than chick feeding visits (Wilcoxon 2-sample test; Z=-2.2, P=0.02). The number of occupied behaviours recorded during surveys with nest attendance and those with chick feeding were similar (mean = 5.11 detections ± 0.71 SE during chick feeding, mean = 6.69 detections ± 1.29 SE during nest attendance, Mann-Whitney, U=55, P=0.81).

Nesting Success

Nest outcome was assessed for 68 nesting attempts at 52 nest trees from 1994-1997. Nesting attempts included 4 re-used nests and 10 trees with multiple nest cups. Nesting success was determined for 21 nests, and outcome was not determined for the remaining nests (n=47) due to timing of discovery, limited evidence or inadequate monitoring (Table 8).

Two-thirds of the observed nests failed (14 of 21) and predation of eggs was the

Table 8. Outcomes of Marbled Murrelet nesting attempts on the Sunshine Coast 1994-1997.

Year	Number of nests	Outcome		
		Successful	Failed	Unknown
1994	1	0	0	1
1995	8	2	1	5
1996	33	2	8	23
1997	26	3	5	18
Total	68	7	14	47

most frequent cause of nest failure (12 of 14, Table 8). Eggs were depredated and eaten at 4 nests, leaving entire eggshells at or beneath the nest (Table 9). This type of predation is most likely caused by Steller's Jays (*Cyanocitta stelleri*) or Gray Jays (*Perisoreus canadensis*). Very few, small fragments of eggshells were found at 8 nests where the egg had presumably been removed by Common Ravens (*Corvus corax*). Additional evidence that predators remove eggs and eat them elsewhere included a depredated egg located on the ground away from a known nest site. Trees in the stand where the egg was found were searched but no nest site was located.

Evidence at nest sites does not indicate how predators obtained access to murrelet eggs. Murrelet eggs may have been abandoned due to predators or for other reasons. Interactions between murrelets and predators were observed only once. A Common Raven flew over the forest near Nests 5 and 11 on May 13, resulting in two incubating murrelets flushing and leaving their eggs unattended. Predators, presumably a Common Raven took the eggs in these nests at a later time.

Re-use of Nest Trees

Inter-annual re-use of nest trees occurred at 12% and 11 % of nest trees in 1996 and 1997 respectively (Table 10). Nest trees with successful (Nest 1), depredated (Nest 16) and unknown status (Nests 5 and 13) nests were re-used. All re-use attempts failed and 2 nests had evidence of predation (Nests 5 and 13). Nest attendance was observed at 3 nest trees in the year prior to re-use (Nests 1, 13 and 16; Table 7). Re-use attempts occurred in the same nest site (Nests 5 and 13) or on different limbs in the same tree (Nests 1 and 16). Details of attendance and re-use attempts at these trees are described in Appendix 1.

Nineteen percent of nest trees had more than one nest site within the tree, indicating that these nest trees had been used for more than one nesting season (Table 11). Nest trees with multiple nests had either 2 nest sites (n=9) or 3 nest sites (n=1). Most old nest cups did not contain evidence of use, but some cups had adult feathers, old eggshell fragments, and small amounts of chick down. Re-use of the same nest site may not be detectable without monitoring bird behaviour at the nest, because evidence of the most recent use may cover evidence of previous use.

Table 9. Evidence of predation and fledging success used to classify the outcomes of Marbled Murrelet nests on the Sunshine Coast 1994-1997.

Evidence	Proposed cause	n
Nest with fecal ring; down and eggshells in nest, or eggshell and membrane on ground below nest branch	Fledged current year	7
Few eggshell fragments, < 2 mm in size unfaded from the current year	Egg removed from nest, possibly by Common Raven	8
Almost entire eggshell with pecked holes on nest branch	Jay predates egg at nest site	2
Entire eggshell on ground below nest branch	Egg depredated at nest site (jays)	2
Tufts of adult feathers on branch above nest site	Adult depredated at nest site	1
Dead chick found on ground below nest site	Fell from nest	1
Eggshell on ground with blood and albumen stains; nest site not located	Common Raven ate egg away from nest site	1[A]
Feathers of nearly fledged juvenile on ground; nest site not located	Chick depredated before or after fledging	1[A]
Nest without fecal ring; faded eggshells and/or membrane in or below nest, small amounts of down in nest cup	Old possibly successful nest	3
Nest cup empty or with adult feather	Old nest cup , outcome unknown	44

[A] Evidence of predation where nest site was not located

Table 10. Inter-annual re-use and occurrence of occupied behaviours at Marbled Murrelet nest trees monitored during 1995-1997 on the Sunshine Coast.

Year	Number of nest trees		
	Monitored	Re-used (%)	Occupied behaviour (%)
1995	1	0 (0)	0 (0)
1996	8	1 (12)	5 (63)
1997	27	3 (11)	14 (52)
Total	36	4 (11)	19 (57)

Table 11. Multiple nests within nest trees used by Marbled Murrelets on the Sunshine Coast, 1994-1997.

| Year | Number of nest trees | | Nests |
	Total	With multiple nests (%)	Total
1994	1	0 (0)	1
1995	8	0 (0)	8
1996	23	7 (30)	31
1997	20	3 (15)	23
Total	52	10 (19)	63

Within year re-use was observed at one nest site (Nest 11) and one nest tree (Nest 15) in 1996. Both the initial and re-use nest attempts failed during incubation at these nest trees. Re-use of Nest 15 was the latest date of incubation by a Marbled Murrelet in my study (Table 3). Both re-used nests were attended following failure of the first nesting attempt and Nest 15 was attended following failure of the second attempt (see Appendix 1 for details of attendance).

Discussion

Activity Patterns

The peak in activity observed in the Bunster Range is consistent with seasonal patterns of activity observed elsewhere in the Marbled Murrelet's range. Peaks in activity have been observed from the last week in June (Manley *et al.* 1992) to the first week in August (Nelson 1989) and may vary between years and locations. An early secondary peak in activity occurred during late May at MS2. This early peak has been observed also at sites in Oregon and Alaska (O'Donnell *et al.* 1995) and may correspond to nest prospecting behaviour during the early breeding season. In all locations, activity declines to zero detections within 2-3 weeks after peak activity (O'Donnell *et al.* 1995). The absence of detections at inland sites from August to October corresponds with a flightless period during the murrelet's remigial moult.

The proportion of visual detections recorded at monitoring sites in the Bunster Range (42%) is higher than those in the Queen Charlotte Islands (19-26%, Rodway *et al.* 1993a) or California and Oregon (10-15%, Paton and Ralph 1988, Nelson 1989). Trees in the Bunster Range are approximately half the height (30-40 m) of low elevation old-growth stands (60-80 m) where murrelets have been studied on the West Coast of Vancouver Island. The greater proportion of visual detections in the Bunster Range may be due to the lower heights of birds flying at or below canopy or due to differences in canopy opening at the survey locations (Burger 1995b, Rodway and Regehr 1998a).

Occupied behaviours include 4 types of behaviours associated with nesting birds: nesting; landing in trees; below canopy flights; and circling above canopy (Ralph *et al.* 1994, Paton 1995). Proportions of below canopy occupied behaviours are 25% in northern California (O'Donnell 1993) and 6-21% at nests in central California (Naslund

40

1993a), similar to the 9.9% and 19.4% recorded and MS2 and MS1, respectively. Circling above canopy was only recently included as an occupied behaviour and its link to nesting behaviour is controversial. In the Bunster Range, below canopy occupied behaviours and circling above canopy occupied behaviour did not occur in similar proportions at the two sites I surveyed. Both sites had a similar proportion of all occupied behaviours (24.5% MS1 and 26.0% MS2), but MS1 had a higher proportion of below canopy flights and a lower proportion of circling flights while the opposite occurred at MS2. Occupied circling behaviour occurred later in the morning than below canopy occupied flights. Combining these behaviours could obscure behavioural differences between sites. Circling behaviour has been considered less indicative of active nesting than below canopy behaviours. However, circling behaviour was more prevalent at MS2, which has more known nest sites and higher nest density than MS1. Research on the number and types of behaviours related to nesting density is needed to understand the relevance of both types of occupied behaviours.

Daily variation in behaviour and group size during general activity surveys are consistent with aspects of murrelet nesting behaviour that are observed at nest sites. The early timing of single birds and occupied behaviours coincide with the times that murrelets exchange incubation duties, feed chicks and visit inactive nests (40-10 min before sunrise).

The biological significance of the seasonal peak in activity of Marbled Murrelets is not well understood. Occupied behaviour is highly correlated with total activity (Fig. 3) and comprised between 10-60% of the peak activity recorded in my study. Not-occupied behaviours contribute the remaining 40-90% of peak activity. The peak in activity could result from presence of immature birds, changes to the social behaviour of nesting birds or increased activity by nesting birds. In many Alcid species, immature birds attend colonies late in the breeding season during years prior to their first breeding attempt (Sealy 1976, Gaston 1990). The presence of non-breeding birds at colonies is typical of long-lived species that first breed between 2-6 yr (Gaston and Jones 1998). Alternatively, nesting birds may exhibit occupied behaviours in the vicinity of their nests, but engage in other behaviours and form larger groups once they are away from their nests (Nelson and Peck 1995). The seasonal increase in activity might result from increases in foraging trips by

adult birds (Hamer and Cummins 1990) or from increased activity associated with fledging (Paton and Ralph 1990).

Observations of murrelet behaviour at active and inactive nests may provide some insight to the significance of seasonal increases in activity. At dawn, murrelets make successive feeding trips to their chicks in relatively short periods. These trips would not allow much time for other activities between feedings. Murrelets that were feeding chicks returned with food within 15-34 min of leaving their nest suggesting that adults fly directly between their nests and foraging sites without socializing or grouping with other birds. Rests by adults at nests that I observed and the seasonal loss in mass that occurs in birds flying inland (L. Lougheed pers. comm.) may indicate that chick feeding trips are energetically costly for adults. Other alcids undergo an adaptive mass loss to reduce the energetic cost of foraging trips to feed their chicks (Croll *et al.* 1991). The increased duration of feedings and interval between feedings with increased feeding frequency that I observed may be a result of fatigue. Increases in feeding trips by breeding murrelets may contribute to seasonal increases in occupied behaviours. However, based on the frequency and timing of feedings and their apparent energetic cost, I think that breeding birds alone do not account for seasonal increases in not-occupied behaviours.

Non-breeding murrelets are not constrained by chick feeding and may benefit from visiting nesting areas during the breeding season. Murrelets are active at nesting areas from October to February during the non-breeding season (Naslund 1993b, O'Donnell *et al.* 1995). Winter activity at nest stands may function to maintain familiarity with flight routes and nesting habitat, to maintain pair-bonds, to prospect for nests or mates, or to defend nests (Naslund 1993b). Non-breeding birds may gain similar benefits from activity at inland sites during the breeding season. In my study, I documented murrelet attendance at failed nests and old nests from previous years. Although my sample size is small, the majority of attended nests were re-used in the same or following seasons. This evidence suggests that the activity of non-breeding birds may be important for securing future nesting attempts. Attendance at these nests was highest in July, which corresponds to the peak in total activity. High rates of nest failure in my study and others (Nelson and Hamer 1995a) could free a large proportion of birds from nesting duties and increase the number

42

of birds at inland sites during the peak activity period. These birds may return to breeding areas after nesting failure to secure nests or mates for future nesting attempts the following year or rarely within the same season. If failed breeders attempt to secure nests for future breeding, then I expect that other non-breeding birds, including immature birds and unpaired birds, would be present for similar reasons.

Evidence from murrelets captured in Desolation Sound indicates that unpaired birds may visit inland areas during the breeding season. Murrelets flying between forest areas and marine areas have a male biased sex ratio (2:1), but murrelets caught in marine areas have normal 1:1 sex ratio (Vanderkist *et al.* in press). This bias could indicate that more males than females visit inland areas. Marbled Murrelets participate equally in incubation and chick feeding duties (Naslund 1993a) suggesting that the male bias is not a result of males being responsible for a greater proportion of nesting duties. The excess of males visiting inland areas may result if male birds exhibit more territorial and nest prospecting behaviours than do females. This behaviour may contribute to the seasonal peak in activity observed in the Bunster Range and elsewhere. Alternative hypotheses for male-biased sex-ratio are that males are more susceptible to capture in mist nests (Vanderkist 1999).

Nesting Chronology

Marbled Murrelets have a lengthy and asynchronous breeding period. The murrelets' breeding season in the Bunster Range, estimated to occur from May 10 to September 15, was longer than an estimate derived for B.C. from records of stranded fledglings and fledglings observed at-sea (Hamer and Nelson 1995a). My observation of a bird incubating on July 19, was 2 weeks later than the end of incubation estimated for the province (Hamer and Nelson 1995a). This incident of egg-laying later in the breeding season was associated with re-nesting within a tree that had failed earlier in the year. It provides evidence that the extended breeding season may result from re-nesting as suggested by Hamer and Nelson (1995a). In Oregon and California, the long breeding season (149 and 170 days respectively) consists of two distinct periods of chick fledging separated by 2-4 weeks during which chick fledging has not been recorded (Hamer and

Nelson 1995a). Accurate knowledge of length of the murrelet's breeding season is important for the timing of at-sea surveys used to measure the proportion of juvenile birds in the population. Estimates of the murrelet's fledgling period can be used to determine the proportion of juveniles that have fledged and are available to be surveyed during an at-sea census. As well, forest harvesting or other disturbances in or adjacent to nesting habitat can be concentrated outside of the breeding period to minimize disturbance to nesting birds.

Nesting Behaviour

Murrelets in my study area used flight paths along openings in the forest canopy to access nests as has been observed in other locations (Naslund *et al.* 1995, Nelson and Peck 1995, Singer *et al.* 1995). Openings may be required by murrelets to approach nests from below and stall-land at the nest. Observations of murrelets crashing into tree limbs and aborting landings to re-approach the nest suggest that landing can be difficult for this species, probably due to their high flight speeds (Nelson and Peck 1995). The landing behaviour of murrelets may influence selection of nesting habitat and is discussed in relation to canopy openings in Chapter 2.

Many aspects of murrelet nesting behaviour observed in the Bunster Range are similar to observations of nesting murrelets in other regions. Murrelet incubation exchanges in my study area and elsewhere occur between 30 and 10 min before sunrise (Nelson and Hamer 1995b). Feeding and fledging behaviour are consistent with observations from California, Oregon, Washington and Alaska (Naslund *et al.* 1995, Nelson and Hamer 1995b, Nelson and Peck 1995, Singer *et al.* 1995).

Adult Marbled Murrelets rested at the nest branch before feeding their chicks (Nelson and Peck 1995, Nelson and Hamer 1995b, my study). Adults may remain motionless after landing to avoid attracting predators to their nests (Nelson and Peck 1995). However, murrelet chicks begin begging when the adult lands (Naslund 1993a, Nelson and Peck 1995, my study). Therefore, resting at a branch could prolong chick begging which could increase predation risk (Haskell 1994). Perhaps the exertion of feeding flights causes adults to rest before feeding chicks. To bring fish from the ocean in

44

my study area, murrelets flew a minimum of 5 km with an elevation gain of between 800 to 1000 m. Differences in the duration and timing of feeding visits also indicate that feeding trips could fatigue birds. This hypothesis could be tested by measuring adult resting periods and feeding frequency for nests located at different distances inland and elevations. The energetic cost of nesting long distances inland or at high elevations may affect habitat selection at the landscape level and this topic requires further research to assess and quantify its effect.

Feeding Visits

Murrelet chicks in the Bunster Range were fed between 3-6 times per day (mean = 4.5). This is more frequent than averages reported for Oregon nests (mean = 2.2; Nelson and Peck 1995) and North American nests overall (mean = 3.2; Nelson and Hamer 1995b). Feeding frequency in the Bunster Range and in the nearby Caren Range were the highest values reported for murrelets, although both estimates are based on a small sample of nests. Both the Bunster Range and Caren Range are located within 5 km of marine foraging areas whereas feeding rates in Oregon were based on nests between 25 and 40 km inland. Distance inland may influence nest provisioning, chick growth and adult energetic costs. Feeding frequency may also influence length of the nestling period which has been as long as 40 days in Oregon (Hamer and Nelson 1995a). The location of nesting habitat relative to feeding locations may affect many aspects of the nesting behaviour of murrelets. There is a need for more research on the potential costs and benefits of the distribution of nesting habitat at a landscape level because forest management alters this distribution.

The high frequency of feeding that I observed resulted from multiple feeding visits by adult birds. Adults arrived singly, at consistent intervals and avoided spending time together at the nest. The spacing of feedings at a nest site may result from differences in when members of a pair catch fish or it may be a deliberate strategy to minimize activity and maximize adult attendance at nests. Intensive observations at-sea could determine if pairs of murrelets feeding chicks obtain fish at different times or if one of the pair waits at-sea holding a fish after its partner departs to avoid overlap at the nest.

Comparison Between Types of Nest Visits

Nest attendance (visits to empty and old nests) by Marbled Murrelets resembled chick feeding visits. The daily timing of both types of visit was similar and both types of visit resulted in similar numbers of occupied detections during dawn surveys. Activity by murrelets must be monitored carefully to determine the type of nest visit. Nest attendance visits were shorter in duration and were associated with the following behaviours: landings by paired birds; stall out landings; multiple landings within a short time period; and frequent fly-bys in association with landings. However, some of these behaviours were observed at active nests and were associated with the time of chick hatching (Naslund 1993a). In general, there is considerable overlap in the amount of activity, the timing of activity and the types of behaviours observed at active nests and inactive nest trees. Below canopy occupied behaviours can indicate active nests or nest attendance. Occupied behaviours are used to identify nesting locations of Marbled Murrelets but these behaviours may indicate not only active nesting, but past nesting, or future nesting. Occupied behaviours are probably not a good index of the relative proportions of breeding and non-breeding birds. The proportion of non-breeding birds is an important variable in murrelet demography and other methods to assess this should be developed and monitored in response to changes in habitat availability (Beissinger 1995).

Trees where murrelets land should be considered nest trees even if active nesting is not confirmed. Almost all landing trees in my study area contained nests when they were subsequently climbed and searched. Landings may occur before or after a nesting attempt or in seasons following nesting (Naslund 1993a, Nelson and Peck 1995, my study). Even if a nest site or nesting evidence is not visible, the landing tree may be a location of past or for future nests. Based on the frequency of nest tree re-use in my study, a breeding pair may require many nest trees over their reproductive life. Protection of only active nests would not provide sufficient nest trees over the long term. Landing trees are similar in structure and characteristics to nest trees (Naslund et al. 1995), and their retention may provide future nest sites for murrelets.

46

Nesting Success

Predation appears to be the most frequent cause of nest failure throughout the range of the Marbled Murrelet (Nelson and Hamer 1995a; my study). Predation and failure at nests are higher for Marbled Murrelets than for other alcid species and other forest nesting birds (Nelson and Hamer 1995a, DeSanto and Nelson 1995). Marbled Murrelets exhibit morphological and behavioural characteristics that appear to contribute to avoidance of predation. Both adult and juvenile plumages are cryptic at the nest site (Carter and Stein 1995). The following behaviours may also function to minimize detection by predators: crepuscular nest visits; direct silent flights to and from nests; long incubation shifts; quiet and few vocalizations at nests; and avoiding the presence of both adults at the nest. Although predation of adults has been reported (Marks and Naslund 1994, Nelson and Hamer 1995a, my study), predation of eggs is higher than that of chicks or adults. In my study, predation by corvids was associated with nest failure during incubation. In most cases, I do not know how predators obtained access to murrelet eggs. Two murrelets flushed from their nests when a Common Raven flew over. Common Ravens are predators of adult murrelets, and in this case the murrelets may have abandoned their eggs in favour of their own survival. Murrelets may defend their egg or chick from Steller's Jays (Naslund 1993a). Jays may have gained access to murrelet eggs if they were abandoned or left unattended. I attributed egg removal at nests to Common Ravens, but mammalian predators may also remove murrelet eggs. Mammals including squirrels, mice and marten (*Martes americana*) are reported as predators of artificial murrelet nests (Marzluff *et al.* 1998). More information on nest failure and predation of adult murrelets is needed to understand the importance of these factors to Marbled Murrelets.

Nest Site Re-use

Marbled Murrelets in my study re-used nest trees within years, between years and over multiple years. The majority of re-used nest trees were attended prior to re-use and most re-use occurred after nest failure. Inter-annual re-use of both successful (n =2) and failed (n =2) nest trees has been observed in other studies of Marbled Murrelets (Nelson and Peck 1995, Singer *et al.* 1995, Jones 1993). Within year re-use of nest trees has not

been documented previously. The re-use of nest trees and nest sites indicates that these structures are important resources for up to several breeding attempts by Marbled Murrelets. I did not identify individual birds in my study and therefore the nest tree re-use that I observed may represent site fidelity by the same individuals or use of the same tree by different birds. Different individuals may re-use failed nests because nest sites are limiting for the population, or because these individuals are somehow precluded from using better habitats (e.g., by social status, Holmes *et al.* 1996). Genetic analyses of feathers could be used to determine if the same individuals are re-using nests. It is important to distinguish if re-use reflects site fidelity or habitat limitation because these factors have implications for the management of nesting habitat. Re-use of nest trees could be investigated in landscapes with different amounts of remaining habitat. This approach could determine if re-use of nest trees is associated with habitat availability.

Alcids typically exhibit high nest site fidelity, especially at successful nests (Nettleship and Birkhead 1985, DeSanto and Nelson 1995, Harris *et al.* 1996). Common Guillemots (*Uria aalge*) have about 85% re-use of nest sites and when they do change nest sites they generally move short distances (Harris *et al.* 1996). Nest re-use by Marbled Murrelets may be lower than estimates for other seabirds because, as less colonial, forest nesters they could express site fidelity at a larger spatial scale than that observed for colonial seabirds. If murrelets returned to the same area but used trees within 100 m from their nests they may not be detected, especially when the birds are not individually marked. My estimates of nest tree re-use may be conservative because of difficulties detecting re-use of the same nest cup. Re-use of nest trees by murrelets in my study ranged from a very small proportion within a year to 20% over multiple years. More estimates of nest tree re-use are needed, particularly for individually marked murrelets and in different landscape contexts, e.g., different amounts of late-seral forest. These data would allow researchers to assess the significance of this behaviour and its consequences for habitat management and conservation.

Conclusion

Most monitoring and research on Marbled Murrelets in terrestrial environments is

based on inland activity recorded during dawn surveys. Inland activity shows consistent seasonal and daily patterns in the timing and number of detections. Activity is useful for describing murrelet distribution inland and patterns of habitat use at appropriate spatial scales (Rodway and Regehr 1998b). The biological significance of activity patterns and behaviours is poorly understood and this limits the use of activity as an index for population monitoring. However, I expect that specific nesting behaviours such as nesting success, nest attendance, nest site re-use and feeding frequency would respond quickly to factors affecting murrelet populations such as habitat modification. Measures of nesting behaviour could be used to monitor population status (e.g., source and sink populations), to monitor saturation of habitat, or to determine the relative proportion of non-breeders in a population. Changes to behaviour would be observed likely before decreases in the population are evident. Although nesting behaviour is more difficult to monitor than activity, long-term studies should be done to determine the effects of habitat loss. Long-term studies of the nesting behaviour and ecology of Marbled Murrelets could yield important information for the conservation of this species. Effects of habitat loss and modification of nesting behaviour need to be determined to understand how these factors affect murrelet populations.

Murrelet nesting behaviour indicates that both cover at the nest site for protection from predation and openings near the nest site for flight access could affect selection of nest sites. I examine the Marbled Murrelets requirements for cover and nest access in a scale dependent habitat framework in Chapter 2.

Chapter 2. Characteristics and Selection of Nests by Marbled Murrelets

Introduction

The major topic of research on Marbled Murrelets has been the study of nesting habitat. Loss of nesting habitat was identified as the primary threat to this species and was cited in its listing as an endangered species in the United States (Ralph *et al.* 1995) and a threatened species in Canada (Rodway 1990). The identification of habitats and habitat characteristics used for nesting by Marbled Murrelets is key to development of appropriate habitat management.

Habitat studies of Marbled Murrelets focus mostly on the characteristics of habitat at landscape and stand levels (Rodway *et al.* 1993b, Burger 1995b, Kuletz *et al.* 1995, Miller and Ralph 1995), and, in some cases, the selectivity of habitats at these scales (Grenier and Nelson 1995, Raphael *et al.* 1995). These studies indicate that the availability of large diameter trees within mature and old-growth stands is important to nesting murrelets.

Within a region, habitats vary at different spatial scales. There can be many types of coarse habitats in a landscape, e.g., forest and ocean. Each of these habitats is comprised of smaller units that differ in specific characteristics: e.g., a stand dominated by Douglas-fir. These stands are not homogenous but are comprised of patches. Each patch consists of an assemblage of elements. These elements (e.g., a tree) can be complex structures which contain specific microsites, e.g., a large mossy branch.

In analyses of habitat selection, use of habitats or habitat features is evaluated in relation to their availability (Johnson 1980). Selectivity is examined at several hierarchical levels which range from coarsest to finest; landscape, stand, patch, element and microsite levels (Johnson 1980; Lofroth 1993). For the Marbled Murrelet, habitat selection could occur at a landscape level when murrelets select marine locations at which to feed, and watersheds or groups of watersheds in which to nest. Stand level selectivity could occur when murrelets select stands within the watershed. Patch level selectivity could occur when specific patches are selected within the stand. Element level selectivity could occur if murrelets select a particular structure (e.g., a tree) required for survival or reproduction.

50

When murrelets select a particular limb within the tree on which to place their nest, this is the finest level of selectivity, microsite (or nest site) selection.

The finer scales of habitat selectivity have rarely been evaluated for the Marbled Murrelet because of difficulties in locating a sufficiently large sample of nests. In Alaska, murrelet nest trees were larger in diameter and had more potential nest platforms than other available trees (Naslund *et al.* 1995). In Oregon, selectivity analyses at the patch level revealed that nest patches have fewer large diameter trees than did other available patches (Grenier and Nelson 1995). These results are difficult to interpret because of regional differences in forest types and differences in scale of the analyses. A multi-scale approach identifies key habitat characteristics and the scale at which they are important. More recent habitat management strategies also incorporate a multi-scale approach with different strategies applied at different scales (B.C. Ministry of Forests and B.C. Ministry of Environment Lands and Parks 1995). My goal in this chapter is to identify habitat characteristics that affect nest site selection at patch, element and microsite scales. I hope to identify more specific habitat features associated with nesting than can be achieved from stand and landscape level studies alone. In Chapter 3, I address patterns of habitat use at the stand and landscape levels. Information about nesting habitat selectivity at a fine scale will contribute to our understanding of the murrelets' nesting biology and identify specific habitat features that can be incorporated into multi-scale strategies for forest management.

Methods

Locating Nests

A variety of methods to find nests of Marbled Murrelets were used by several field crews from 1994-1997 as part of the Marbled Murrelet Research Project (Simon Fraser University) and the Sunshine Coast Marbled Murrelet Inventory Program (B.C. Ministry of Environment Lands and Parks, MELP). Radio-telemetry was used in 1994 to locate nests of birds caught in Desolation Sound (Derocher *et al.* 1996). In 1995-1996, a combination of surveys and tree climbing was used to locate nests (Naslund 1993a, Lougheed *et al.* 1998a). To locate nests, I focused on areas with occupied behaviours (birds flying below or into the canopy and landing in trees). Survey effort was increased in

the immediate area of an occupied behaviour to locate trees in which murrelets were landing. When occupied behaviours were observed but we could not locate a nest from the ground, we returned to these areas at the end of the breeding season and climbed trees to search for nest sites. Locations associated with occupied behaviour were searched by climbing trees that exhibited potential nesting structures (limbs at least 15 cm in diameter). In 1997, trees in variable radius plots in edge and interior forest were climbed and searched for nests (see Manley 1997 for methods).

In 1995, 5 sites were surveyed for murrelet activity from June 1-July 31 and 89 trees were climbed and searched for nests from August 3-29 (Lougheed *et al.* 1998a). In 1996, 36 sites in the Bunster Range were surveyed from May 13-August 5 (Drever *et al.* 1998). We also scanned trees to look for murrelet nests and searched under potential trees for eggshell fragments during vegetation plots (n =36), transects (n =27) and other field work. MELP inventory crews surveyed 20 stands at other locations in the Sunshine Coast Forest District (Manley and Jones 1996). During 1996, 355 trees were climbed in the Bunster Range and 12 trees were climbed in the Brittain River Watershed. In 1997, 17 sites were surveyed in the Bunster Range at which 11 trees were climbed to search for nests (Lougheed *et al.* 1998b). During the MELP inventory in 1997, 48 sites were surveyed and 343 trees were climbed to search for nests in plots (Manley 1997). Nest trees were numbered in order of the date of their discovery. When nest trees contained more than one nest cup, each nest cup within a tree was given a different letter (e.g., Nest 15a).

I examined habitat selection by nesting Marbled Murrelets at scales ranging from patch level to microsite level. For analyses of selection at the patch level, I compared tree and forest characteristics in nest patches to those in paired, random patches within the same stands. For element level analyses, I compared the trees that murrelets used for nesting to trees that were available within nest patches. At the microsite level, I compared nest limb characteristics to those of unused limbs within nest trees.

My ability to evaluate selectivity at the level of stands and landscapes by using nest sites is constrained by methods that I used to locate murrelet nest sites. Efforts to locate nests with radio-telemetry did not yield sufficient nests. Hence the stand and landscape

level characteristics of nest sites are limited to stands and areas where I searched for nests. Selectivity at larger scales such as a stand and landscape level are investigated using murrelet activity and occupancy which were sampled over a larger area than that for which nest sites were obtained (Chapter 3). Selectivity for a required structure (e.g., nest platforms (microsite level) and nest trees (element level) often results in the strongest expression of selectivity at fine scales (Weir 1995, Davis 1996). Higher levels of selectivity commonly reflect patterns established at fine levels. Examination of nest site characteristics allows detailed patterns of habitat selection to be determined at microsite to patch scales. Murrelet activity and occupancy reflect nest locations at a stand and landscape level, but do not resolve selectivity at finer scales.

Habitat Data

Microsite level

Nest trees were climbed to search for nests and document nest site characteristics. Measurements of other platforms within nest trees were obtained for a sample of 9 nest trees climbed in 1995. Platforms are limbs or structures that are large enough for murrelets to nest on, or limbs >15 cm in diameter at the tree bole. I measured the following characteristics of all platforms within these trees: height of limb, limb diameter near the bole, platform area (length and width of the flat surface of a limb), depth of epiphytes on the limb, and orientation of the limb relative to the bole (degrees). Cover above platforms was categorized as exposed (<1/3 covered), partly covered (1/3-2/3 covered) and covered (>2/3 covered).

Measures of other limbs in nest trees were time consuming, hence, assessments of these platforms were simplified for the larger sample of nest trees found in 1996 and 1997. In these years, climbers recorded the following data for all platforms in nest trees: total number of platforms (limbs or structures >15 cm in diameter); epiphyte substrate on the platform; cover above the platform; and platform type. Platform epiphyte categories were: None, Lichen/litter, Moss1 (patches of moss <2 cm thick) and Moss2 (continuous moss pad >2 cm deep). Platform types included the following 4 categories: 1) lateral limb, limbs >15 cm in diameter (large enough to create a platform on their own); 2) limb with moss, limbs that together with moss cover are >15 cm in diameter; 3) mistletoe, multiple branch

formation resulting from mistletoe infestations; and 4) multiple leader, large limbs that grow vertically.

Element level

I used data from 37 nest patches to examine selectivity at the element level. Tree and forest characteristics were measured in a 25-m radius circular plot centered on the nest tree (nest patch). Within these plots, species, diameter, height, number of potential nest platforms, canopy stratum and top condition were recorded for all trees and snags >10 cm in diameter. Tree height was measured for a few canopy trees within the plot using a clinometer and then estimated to the nearest metre for other trees using these trees as a reference. Number of potential nest platforms, epiphyte substrate, overhead cover and platform type categories were estimated from the ground for all trees in nest plots. Element level selectivity was evaluated by comparing characteristics of nest trees to those of available trees within the nest patch. Available trees were defined as trees with at least one potential platform.

The amount of canopy opening was determined for nest plots by identifying and measuring each canopy gap within the nest plot. Canopy gaps were defined as openings in the canopy greater than 3x3 m, not including sub-canopy trees. Gaps were identified and sketched on a map and gap area was estimated only for the portion of the gap within the nest plot. Gap area was estimated by measuring the length and the width of the gap and using the formula for an ellipsoid to calculate the area. Each gap was classed into one of four types based on their origin: edaphic gap (Lertzman *et al.* 1996) - resulting from lack of growing conditions (rocky or wet); riparian gap - around streams or water bodies; tree gap - resulting from tree mortality; industrial gap - resulting from removal of trees by humans (logging road, mining exploration road, clearcut). Although riparian gaps are a type of edaphic gap (Lertzman *et al.* 1996), I considered these seperately because murrelets use creeks and streams as flight paths in the forest (Manley *et al.* 1992, Rodway and Regehr 1998a). The sizes and types of gap used for nest access were compared to gaps available in the nest plot. Gaps used for nest access were determined from observation of birds or orientation of the nest branch and landing pads at the nest.

Patch level

For selectivity analyses at the patch level, I defined a patch as the area of 25-m radius circular vegetation plots (0.196 ha). Tree and forest characteristics measured at the nest patch (see element level above) were also measured at a random patch centered on a random point within 60-200 m from the nest tree. I located random patches at a randomly selected distance and direction from the nest tree. At each such point, I selected the nearest canopy tree for the plot center. Characteristics of nest patches and their paired random patches were obtained for 34 nest trees. Slope and aspect were measured at the center of each plot. The amount of canopy opening was determined for each plot by summing individual gap measurements. Nest plots and random plots were classified to biogeoclimatic site association using indicator plant species analysis (Green and Klinka 1994). With this method, the percent cover of indicator species in the tree, shrub, herb and moss layers are estimated and matched with classification tables to determine site associations.

Selectivity Analyses

Microsite level

I assessed microsite selectivity for two different samples. The first sample is measurements of limb diameter, height, platform area and orientation for all platforms in 9 nest trees. I compared measurements for nest limbs and unused limbs in nest trees using Mann-Whitney U-tests. I converted nest height to percent of total tree height (100 x height of nest/height of tree) to account for differences in nest placement in different sized trees. To test for selectivity of limb orientation, I grouped orientations into 4 categories: north (316-45 °); east (46-135 °); south (136-225 °); west (226-315°). I then tested for differences in the use and availability of orientation categories with a Fisher's exact test.

The second sample is primarily ordinal data collected for 52 nest trees found from 1995-1997. For these trees, I examined microsite selectivity for categories of platform epiphyte substrate and platform overhead cover. I compared the frequency of these categories for nest limbs and unused limbs with Chi-square tests, Fisher's exact tests, and Bonferroni confidence intervals.

Element level

   At the element level, I compared the mean diameter of nest trees to the mean diameter of other available trees within nest patches. I restricted this comparison to platform trees because trees without platforms were not suitable for nesting. I grouped nests by tree species for this analysis. For tests involving height, number of platforms and platform characteristics, I grouped nest trees into 4 species-diameter classes: yellow-cedar (*Chamaecyparis nootkatensis*) 60-89 cm dbh; yellow-cedar 90-120 cm dbh; western hemlock (*Tsuga heterophylla*) 90-120 cm dbh; yellow-cedar >120 cm dbh. Analyses within these groups ensured that species and diameter differences did not confound selectivity. I did not evaluate selectivity for Douglas-fir (*Pseudotsuga menziesii*) and mountain hemlock (*Tsuga mertensiana*) nest trees because I found only one nest in each species. I compared continuous variables with Mann-Whitney U-tests and categorical variables with Chi-square tests and Fisher's exact tests. Categories were considered preferred when they were used significantly ($P<0.05$) more than expected based on availability and avoided when they were used less than expected (Nue *et al.* 1974). I determined selectivity for tree species using all dbh classes combined. I used a Chi-square test and Bonferroni Confidence intervals to examine differential use of three species groups; yellow-cedar, western hemlock, and Douglas-fir and mountain hemlock combined. I assessed selectivity for canopy gaps at the element level by comparing the size and types of gaps used by murrelets to access nests with other gaps available within the nest plot. I compared the areas of nest access gaps and available gaps using a Mann-Whitney U-test.

Patch level

   To assess patch level selectivity, I compared habitat variables including densities of trees of different diameters, total gap area, numbers of platforms, and slope for each nest patch with its paired random patch using Wilcoxon rank sum tests for paired samples (SAS 1990). Stand level selectivity did not confound patch level selectivity because nest patches were compared to a paired random patch within the same stand. Patch level analyses involving numbers and characteristics of platforms were done both with and without the nest tree included in the nest patch. I made this adjustment because element

level analyses revealed that nest trees dominated nest patches in terms of these characteristics.

Selectivity for canopy gaps was assessed at the patch level by comparing the total gap area in nest plots with total gap area in paired random plots. Selectivity for aspect was evaluated using a Chi-square test. Aspects were grouped into four 90°categories and the frequencies of these categories were compared between nest and random plots. I compared the frequency of site associations at nest patches to those available in random plots using a Chi-square test.

Nest Characteristics

I summarize nest patch, nest tree and nest site characteristics in my study for comparison with similar data from other locations in the range of Marbled Murrelets. I determined forest cover classification for nest stands from 1:20 000 forest cover maps because this data is often used to make preliminary assessments of habitat. I measured stand size, the contiguous area of suitable murrelet habitat, using a planimeter on 1:20 000 maps. I determined nest elevation and distance inland using 1:50 000 topographic maps. I calculated the distance between nests located in the same stand as an indication of nest clustering. I present estimates of nest density for nest sites located during climbing plots conducted in the area (see Manley 1997, 1998 for methods).

Results

Microsite Level Use and Selectivity

I detected selectivity for the size and specific features of nest limbs at the microsite level. Nest limbs were significantly larger in diameter and had a greater platform area (flat surface) than other limbs in nest trees (Table 12). Nest limbs did not differ from available limbs in height or moss depth. The orientation of nest limbs did not differ from available limbs (Table 13; Fisher's exact test, 2-tail, $P= 0.61$). Murrelets exhibited selectivity for cover above platforms (Table 14; $\chi^2=50.4$, df=2, $P=0.001$). Covered platforms were preferred, while exposed platforms were avoided (Table 14). Epiphyte cover also influenced nest site selectivity by murrelets (Table 15). Overall 98% of platforms available

57

Table 12. Characteristics of platforms with Marbled Murrelet nests and platforms without nests for 9 nest trees. A platform is defined as a limb or structure >15 cm in diameter. P values are from Mann-Whitney U-tests.

Variable	Platforms without nests			Platforms with nests			
	Mean	SE	n	Mean	SE	n	P
Limb diameter (cm)	19.7	1.1	35	30.7	5.7	9	0.02
Platform area (cm^2)	349.7	86.2	35	663.4	175.3	9	<0.001
Height (m)	18.4	0.9	35	19.7	1.5	9	ns
Moss depth (cm)	4.2	0.5	35	4.9	0.7	9	ns

Table 13. Orientation of nest platforms and platforms without nests (other) within 9 nest trees of Marbled Murrelets.

Type of platform	Number of platforms			
	North	East	South	West
Other	16	6	8	5
Nest	2	2	3	2
Total	18	8	11	7

Table 14. Overhead cover above platforms at 52 Marbled Murrelet nest trees. Chi-square test, P = 0.001. (-) and (+) indicate categories that were significantly avoided or preferred as indicated by Bonferroni confidence intervals P<0.05.

	Other platforms	Nest platforms	Selectivity
Exposed (%)	17	2	-
Partly covered (%)	61	33	
Covered (%)	22	65	+
Total platforms	390	60	

Table 15. Epiphyte cover on limbs used for nesting by Marbled Murrelets. Fisher's exact test, P = 0.01, (-) and (+) indicate categories that were significantly avoided or preferred as indicated by Bonferroni confidence intervals P<0.05.

	Other platforms	Nest platforms	Selectivity
None (%)	1	0	-
Lichen/litter (%)	1	3	+
Moss 1 (%)	20	7	-
Moss 2 (%)	78	90	
Total platforms	386	61	

in nest trees had moss as a substrate. Bare platforms were not used and platforms with thin moss were avoided (Table 15). Platforms with Lichen/litter substrate were rare but were used more frequently than expected (Table 15). Most nests occurred on platforms with thick moss (Moss2) as a substrate, and this category was used in proportion to its availability.

Element Level Use and Selectivity

Selectivity analyses at the element level were highly significant. Murrelets selected nest trees that were significantly larger in diameter than other trees with platforms in nest plots (Table 16, P<0.001 for all species combined). Differences in diameter between nest and available trees were significant within species for yellow-cedar and western hemlock (Table 16). Differences in diameter were not significant within mountain hemlock and Douglas-fir trees. Both of these species were relatively uncommon and there was only one nest for each species.

Marbled Murrelets selected nest trees with a large number of potential nesting platforms. For all three size classes of yellow-cedar trees, nest trees had significantly more platforms than available trees (Table 17, Fig. 9). Numbers of platforms are highly correlated with diameter (Chapter 3), and for yellow-cedar trees numbers of platforms increase with increasing dbh (Fig. 9). Western hemlock nest trees had more platforms than available trees but the difference was not significant probably due to small sample sizes. Mountain hemlock and Douglas-fir trees had few platforms compared to other species. In the Douglas-fir tree used for nesting, the nest platform was the only suitable nest site available in the tree.

Nest trees tended to be slightly taller than available trees (Table 18). However differences in height were only significant for all tree species combined. The magnitude of the difference in height was only 1-2 m, which does appear to be biologically relevant.

Murrelets used tree species for nesting disproportionate to their availability (χ^2=13.9, df=3, P=0.003; for all dbh classes). Yellow-cedar trees were the most frequently used tree species (92%) and the most frequent tree species with platforms in nest plots (72%) (Table 19). Western hemlock trees and all other tree species combined

60

Table 16. The dbh of 52 nest trees used by Marbled Murrelets and 204 available trees. Available trees are trees with platforms within nest plots. P values are from Mann-Whitney U-tests.

Nest tree species	Available trees dbh (cm)			Nest trees dbh (cm)			
	Mean	SE	n	Mean	SE	n	P
Yellow-cedar	85.9	2.1	140	99.8	2.7	47	<0.001
Western hemlock	71.3	2.1	30	106.8	7.5	3	<0.001
Mountain hemlock	75.7	3.8	13	79.0	-	1	Ns
Douglas-fir	91.2	6.8	3	86.0	-	1	Ns
Western redcedar	94.4	9.8	9	-	-	0	-
Pacific silver fir	65.1	4.8	9	-	-	0	-
All species	82.8	1.6	204	99.6	2.5	52	<0.001

Table 17. The number of potential nest platforms in nest trees of Marbled Murrelets and available trees. P values are from Mann-Whitney U-tests.

Dbh size class (cm)	Tree species	Platforms in available trees			Platforms in nest trees			
		Mean	±SE	n	Mean	±SE	n	P
61-90	Yellow-cedar	2.8	0.3	73	7.5	0.8	14	<0.001
	Mountain hemlock	2.7	0.9	9	2.0	-	1	-
	Douglas-fir	2	-	1	1.0	-	1	-
91-120	Yellow-cedar	4.5	0.6	39	8.9	1.1	29	<0.001
	Western hemlock	6.0	4.0	2	10.7	1.8	3	
>120	Yellow-cedar	4.9	1.0	14	16.0	5.0	4	<0.01
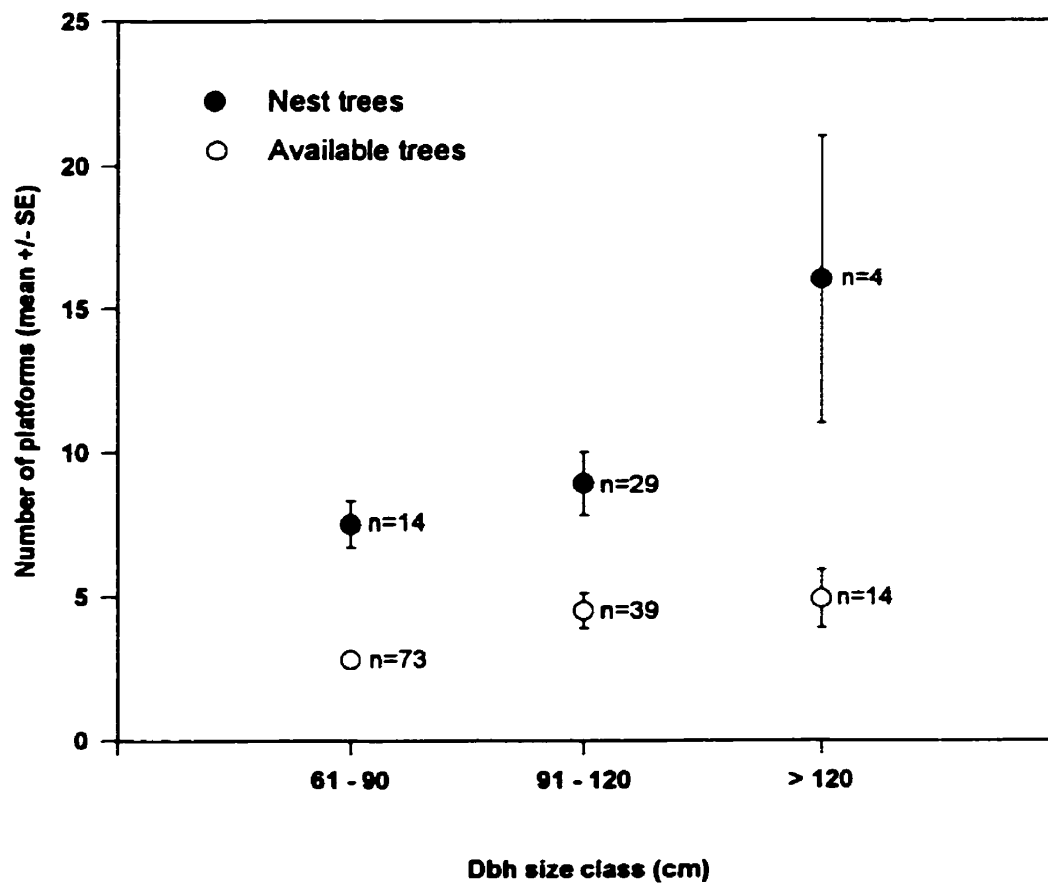
Figure 9. Number of platforms in nest trees of Marbled Murrelets and in available trees for 3 dbh size classes. Data are for yellow-cedar nest trees (n=47) and available trees (n=126).

Table 18. The heights of trees containing nests of Marbled Murrelets and available trees. P values are from Mann-Whitney U-tests.

Tree species	Height of available trees (m)			Height of nest trees (m)			P
	Mean	±SE	n	Mean	±SE	n	
Yellow-cedar	26.3	0.4	140	27.7	0.7	47	0.06
Western hemlock	24.3	1.5	30	33.9	6.7	3	0.06
Mountain hemlock	25.2	1.1	13	25.0	-	1	ns
Douglas-fir	26.7	0.9	3	24.0	-	1	ns
Western redcedar	28.8	2.9	9	-	-	0	-
Pacific silver fir	26.7	1.1	9	-	-	0	-
All species	26.0	0.4	204	28.2	0.8	52	0.02

Table 19. Frequency of tree species used for nesting by Marbled Murrelets and of available trees by diameter size classes.

Dbh size class (cm)		Tree species					
		Western redcedar	Pacific silver fir	Douglas -fir	Mountain hemlock	Western hemlock	Yellow- cedar
61-90	Available	2	3	1	9	20	73
	Nest	0	0	1	1	0	14
91-120	Available	5	1	2	3	2	40
	Nest	0	0	0	0	3	29
>120	Available	1	0	0	0	0	14
	Nest	0	0	0	0	0	4
All classes	Available	8	4	3	12	22	127
	Nest	0	0	1	1	3	47

(western redcedar, Douglas-fir and Pacific silver fir) were used less frequently than expected based on their availability (Bonferroni confidence intervals P<0.05). Marbled Murrelets did not nest in western redcedar and Pacific silver fir in my study. Western hemlock trees were used for nesting in the 91-120 cm dbh size class. In the plots, only yellow-cedar and western redcedar trees had dbh >120 cm and of these only yellow-cedar was used for nesting. At the element level, selectivity for platform cover and epiphyte substrate occurred but not as strongly as at the microsite level. Selectivity for platform cover categories was significant for all classes of yellow-cedar nest trees and for western hemlock nest trees (Table 20). For both of these species, murrelets selected nest trees with fewer exposed platforms and more covered platforms. However, selectivity for platform cover was not apparent for the 3 size classes of yellow-cedar trees separately. Reduced sample sizes or interactions between size class and platform cover may have influenced this result.

I did not detect selectivity for epiphyte substrate at the element level within yellow-cedar trees (Table 21). Both used and available yellow-cedars had predominantly mossy platforms (nest trees, 17% Moss1 and 83% Moss2; available trees, 16% Moss1 and 82% Moss2). Murrelets selected western hemlock nest trees with predominantly Moss2 platforms and avoided trees with a high proportion of Lichen/litter platforms. This result contrasts with the preference for Lichen/litter covered platforms at the microsite level within western hemlock (Table 15). Murrelets selected western hemlock with a large number of mossy platforms as nest trees, but nested on relatively uncommon Lichen/litter platforms within these western hemlocks.

At the element level, I detected selectivity for the type of canopy gap that murrelets used to access nest sites. Murrelets used types of canopy gaps disproportionate to their availability (χ^2=13.9, df=3, P=0.003; Fig. 10). Industrial gaps were preferred while tree gaps were avoided (Bonferroni confidence intervals, P<0.05). Differential use of canopy gaps is related to the size of different gap types. Nest access gaps were significantly larger in area than other gaps available in nest plots (mean=267 m² ● 49.5 SE for nest access gaps; mean= 59.04 m² ± 4.8 SE for other gaps; Mann Whitney U= 1316.5, P<0.001 for all gap types). Gap size also differed amongst gap types, with industrial gaps

Table 20. Percentage of platform cover categories in nest trees and available trees. P values are from Chi-square tests. (+) and (-) indicate categories that are preferred and avoided for nesting according to Bonferroni 95% confidence intervals.

Dbh size class (cm)	Tree species		Platform cover (%)			n total platforms	P
			Exposed	Partly covered	Covered		
60-90	Yellow-cedar	Available	26.1	59.6	14.3	203	>0.10
		Nest	18.4	61.2	20.4	98	
91-120	Yellow-cedar	Available	19.8	61.9	18.2	176	>0.10
		Nest	13.5	63.1	23.4	244	
91-120	Western hemlock	Available	70.0 (-)	20.0	10.0 (+)	10	<0.001
		Nest	12.5	43.8	43.8	32	
>120	Yellow-cedar	Available	24.6	58	17.4	69	>0.10
		Nest	14.1	57.8	28.1	64	
All Classes	Yellow-cedar	Available	23.4 (-)	60.3	16.3 (+)	448	<0.001
		Nest	14.8	61.8	23.4	406	

Table 21. Element level selectivity for categories of platform epiphyte in nest trees and available trees. P values are from Chi square tests. (+) and (-) indicate categories that are preferred and avoided for nesting according to Bonferroni 95% confidence intervals.

Dbh size class (cm)	Tree species		None	Lichen /litter	Moss1	Moss2	n total platforms	P
60-90	Yellow-cedar	Available	0.5	0.1	8.0	91.0	202	>0.10
		Nest	1.0	0	15.0	84.0	98	
91-120	Yellow-cedar	Available	1.1	1.1	16.9	80.9	177	>0.10
		Nest	0	0	16.3	83.7	239	
91-120	Western hemlock	Available	7.1	64.4	7.1	21.4	14	<0.001
		Nest	9.4	0 (-)	31.3	60.3 (+)	32	
>120	Yellow-cedar	Available	2.9	1.5	35.8	59.7	67	>0.10
		Nest	0	1.6	20.3	78.1	64	
All classes	Yellow-cedar	Available	1.1	0.9	15.7	82.3	446	>0.10
		Nest	0.2	0.3	16.7	82.8	401	
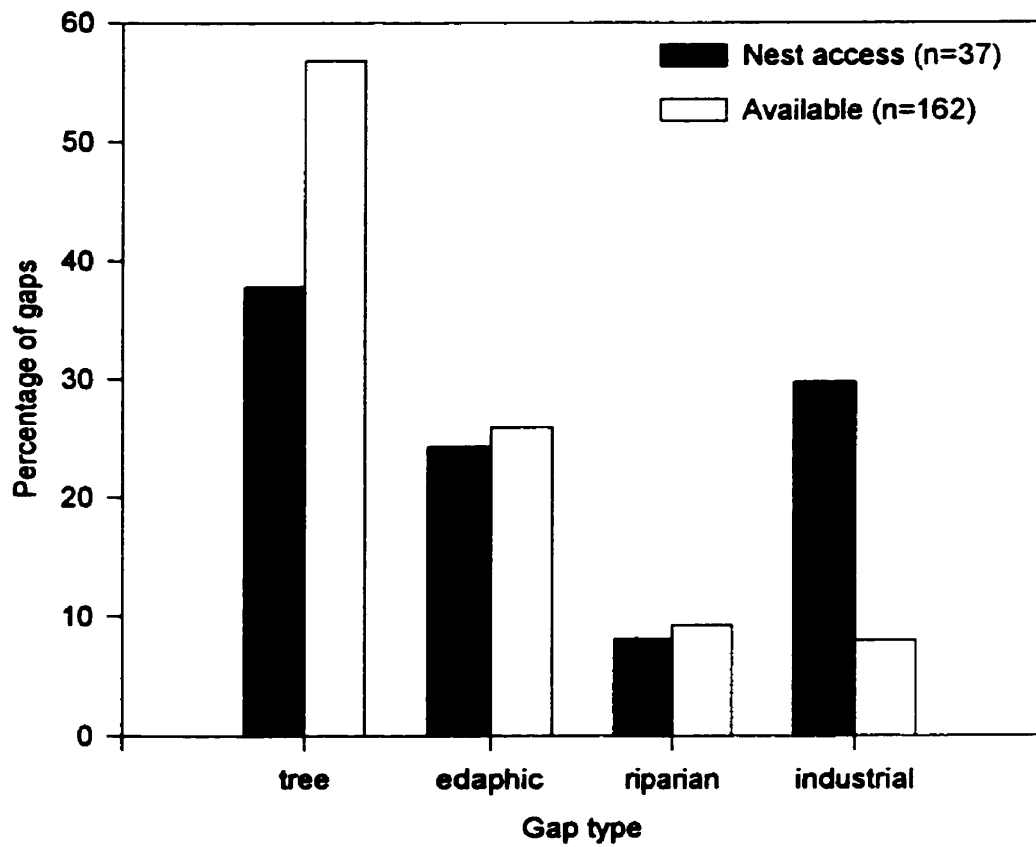
Figure 10. Percentage of gap types used by Marbled Murrelets to access nest sites and available within nest plots.

significantly larger than all other gap types (Kruskal Wallis Anova, P=0.002). Within each gap type, gaps used to access nests were larger in area than other gaps within nest plots (Fig. 11). Nest gaps were significantly larger for all types except riparian gaps (Mann-Whitney U-tests, P<0.05; Fig. 11).

Patch Level Use and Selectivity

Marbled Murrelets exhibit selectivity at the patch level for density of trees, number of nesting platforms, and the characteristics of these platforms. Nest patches had significantly fewer total trees and fewer trees in the 11-40 cm dbh category (Table 22). Trees in the 11-40 cm diameter category comprised between 76-82% of all stems. Thus the difference in this category accounts for the entire difference in total tree density observed between nest and random plots. Selectivity for trees in the 41-60 cm category was not observed. However, in diameter categories encompassing the range of observed nest tree diameters, 61-90 cm and >90 cm, nest patches had significantly higher densities of trees than did random patches (Table 22). Nest patches had fewer large snags than random patches, but this difference was not significant.

Selectivity at the patch level was apparent for nesting platforms. Murrelets selected nest patches with higher densities of trees with platforms (Table 23). The strongest selectivity occurred for numbers of platforms which were almost 3 times more frequent in nest patches (128.5/ha) than in random patches (47.4/ha). Differences in platform density were also significant when the nest tree and its platforms were not included in the nest plot. This demonstrates that even when selectivity for platforms at the element level is accounted for, nest patches have significantly higher densities of platforms. I compared numbers of platform trees and platforms calculated from yellow-cedar trees, the most frequent nest tree species, in the same diameter range as known nest trees (61-90 cm). Yellow-cedar trees of this size contributed 70% of platforms in both nest and random plots, and consequently selectivity for these trees and platforms was highly significant (Table 23).

Selectivity for platform epiphyte cover was apparent at the patch level ($\chi^2=36.3$, df=3, P<0.001; Fig. 12). In nest patches, platforms with None, Lichen/litter and Moss1

70
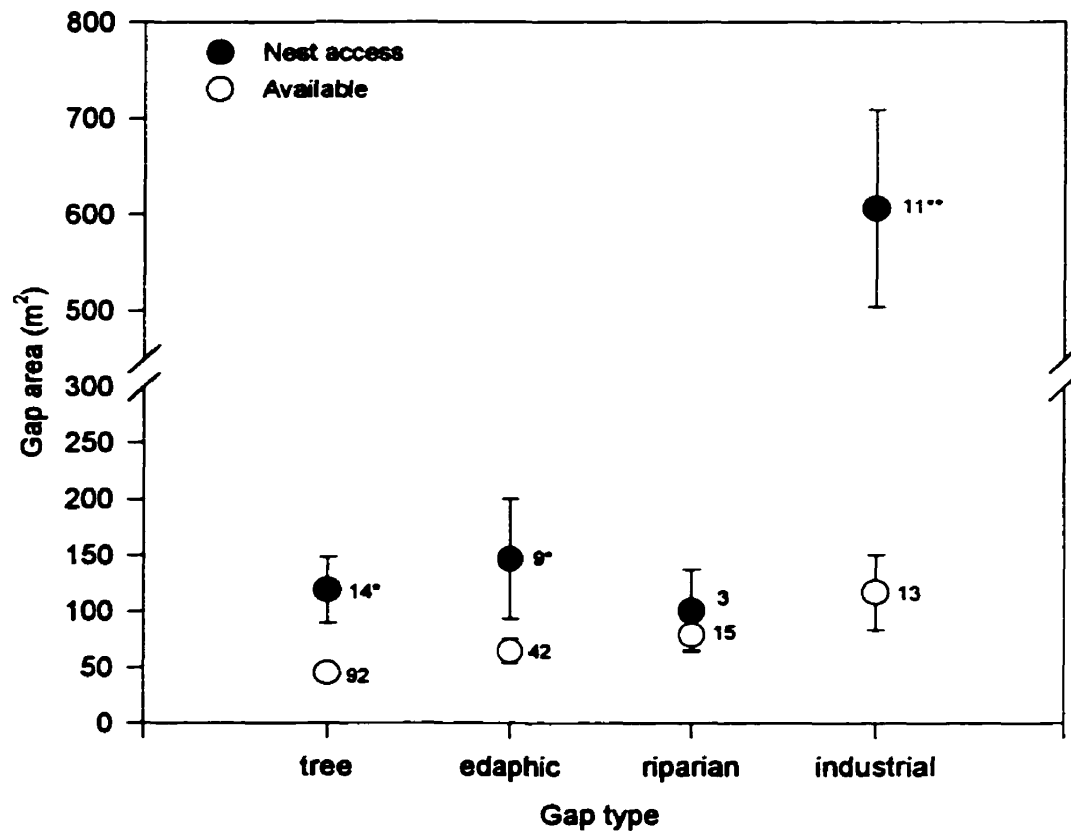
Figure 11. Area (mean ± SE) of gaps used by Marbled Murrelets to access nest sites and gaps available in nest plots. Significant differences between nest access and available gaps from Mann-Whitney U-tests are marked with **(P<0.05) and ***(P<0.01). Sample size is shown next to means.

Table 22. Tree densities by diameter size classes for 34 paired nest and random plots. P values are from Wilcoxon rank sum tests.

Dbh size class (cm)	Number of stems/ha		P
	Nest plot Mean ± SE	Random plot Mean ± SE	
11-40	521.2 31.1	694.6 46.4	<0.01
41-60	95.9 6.1	101.5 7.1	>0.10
61-90	53.0 4.6	37.7 4.1	<0.01
>50	106.6 7.7	87.7 7.1	<0.05
>90	14.8 2.0	8.7 2.0	<0.01
All live trees	684.9 33.7	850.2 44.4	<0.01
Snags >50	13.8 1.5	17.9 2.6	>0.10

Table 23. Numbers of platforms and platform trees for 34 paired nest and random plots. P values are from Wilcoxon rank sum tests.

Including nest trees	Tree species		Nest plot Mean ± SE		Random plot Mean ± SE		P
Yes	All	Platform trees/ha	32.1	3.6	18.4	2.6	<0.01
Yes	All	Platforms/ha	128.5	14.3	47.4	8.7	<0.001
Yes	Yellow-cedar	Platform trees/ha	20.9	2.0	11.2	2.0	<0.01
Yes	Yellow-cedar	Platforms/ha	101.5	11.7	33.7	7.1	0.001
No	All	Platform trees/ha	27.0	3.6	18.4	2.6	0.03
No	All	Platforms/ha	85.7	11.7	47.4	8.7	0.017
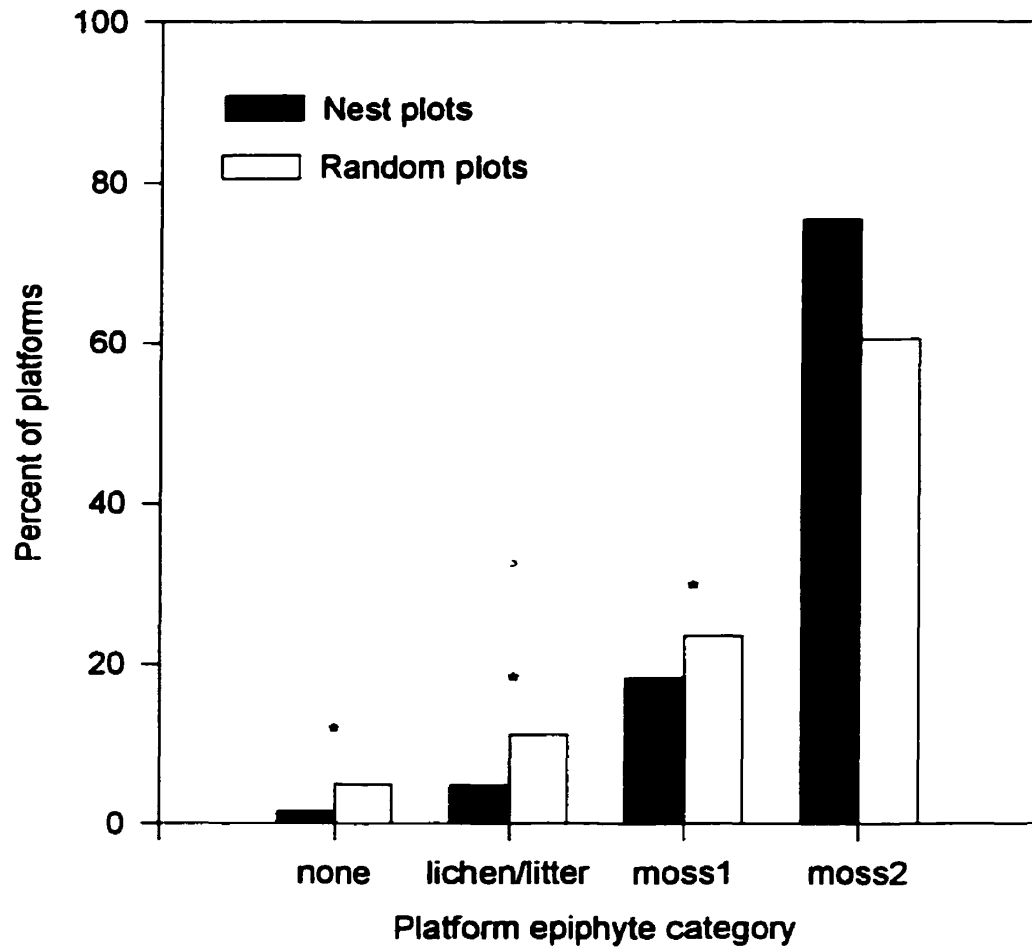
Figure 12. Percentage of 4 epiphyte cover categories for platforms in nest plots (n=34) and random plots (n= 34). * indicates categories significantly different (P<0.05, Bonferroni confidence intervals).

epiphyte categories occurred less frequently than expected (P<0.05, Fig. 12). Platforms with Moss2 epiphyte category were found at nest plots in proportion to their availability (Fig. 12). I did not detect selectivity for platform cover at the patch level. Platform epiphyte cover categories occurred with similar frequency at nest and random plots (χ^2=1.6, df=2, P=0.44).

At the patch level, I found no evidence of selection for size or types of gaps. Nest plots had a greater total gap area than random plots, but this difference was not significant (Table 24). The frequencies of 4 gap types were similar in nest and random plots (χ^2= 6.4, df=3, P=0.17). The size distribution of canopy gaps did not differ between nest and random plots (Kolmogorv-Smirnov maximum difference =0.09, P=0.51). Nest plots had slightly steeper slopes than random plots but the difference was not significant (Table 24). Nest and random plots did not differ in relative frequency of aspect categories (four 90° categories (χ^2=3.9, df=3, P=0.26).

There were no differences in the frequency of vegetation site associations used by nesting Marbled Murrelets compared to those available in random plots (Table 25). Site associations 01, 09 and 07 comprised 79.2% of nest plots (44.1%, 20.6% and 14.7%, respectively). Site associations 09, 01 and 03 were the three most common at random vegetation plots (35.3%, 26.5% and 14.7%, respectively).

Characteristics of Nest Trees and Stands

Nest trees of Marbled Murrelets in the Bunster Range were approximately half the dbh and height of other nest trees in B.C. and Washington, Oregon and California (PNW) and were more similar in size to nest trees in Alaska (Table 26). The height and diameter of nest branches were intermediate between nests in Alaska and nests from the U.S. Pacific Northwest. Nest sites in my study were located much closer to the tree trunk than nests in other regions. Nest trees in my study ranged from 688-1260 m in elevation. Most murrelet nest trees have been in lower elevation habitats (Table 26). Sizes of nest stands ranged from 2-566 ha and nest trees were located between 0-503 m from forest edges in my study area.

Forest cover classification was determined for nest stands from 1:20 000 forest

Table 24. Slope and total gap area at nest plots and random plots. P values are from Wilcoxon rank sum tests.

	Nest plot Mean ± SE	Random plot Mean ± SE	P	n
Slope (°)	23.5 2.6	19.9 2.6	ns	31
Total gap area (m²)	564 54.0	473 51	ns	29

Table 25. Percentage of nest trees and plots in BEC site associations. Random and nest plots were paired. Random plots were not obtained for 3 of the nest trees.

BEC variant	Site association	No. Nest trees n=37	Random plots % n=34	Nest plots % n=34
CWHvm2	01 HwBa-Blueberry	16	26.5	44.1
CWHvm2	03 HwCw-Salal	3	14.7	5.9
CWHvm2	05 BaCw-Foamflower	2	0.0	5.9
CWHvm2	06 HwBa-Deer fern	1	8.8	2.9
CWHvm2	07 BaCw-Salmonberry	5	11.8	14.7
CWHvm2	09 CwYc-Goldthread	7	35.3	20.6
CWHvm2	11 CwSs-Skunk Cabbage	2	2.9	5.8
MHmm1	04 HmBa-Bramble	1	-	-

Table 26. Tree and patch characteristics for Marbled Murrelet nests on the Sunshine Coast (my study) and from published data for nests in Alaska (Naslund *et al.* 1995), other areas in B.C., and the Pacific Northwest (PNW) (Hamer and Nelson 1995b).

Variable		Sunshine Coast	Alaska	Other B.C.	PNW[A]
Nest patches	n	32	14	9	45
Elevation (m)	mean ± SE range	886 ± 1 688-1260	96 ± 50	321 ± 310	332 ± 206
Stand size (ha)	mean ± SE range	224 ± 14 2-565	31 ± 26		206 ± 351
Distance to edge (m)	mean ± SE range	139 ± 21 0-503		92 ± 131 15-700	
Tree density (/ha)	mean ± SE range	684 ± 234 275-1110	575 ± 240	297 ± 136	182 ± 132
Platform density (/ha)	mean ± SE range	128 ± 14 5-321			
Platform tree density (/ha)	mean ± SE range	32 ± 4 5-66			
Canopy closure (%)	mean ± SE range	71 ± 0.3[1] 35-95	62 ± 15[2]		49 ± 23[2]
Nest trees	n	52	14	9	45
Dbh (cm)	mean ± SE range	100 ± 3 60-153	63 ± 18	212 ± 84	211 ± 91
Height (m)	mean ± SE range	28 ± 1 17-45	23 ± 4	58 ± 15	66 ± 13
Platforms/nest tree	mean ± SE range	9 ± 1 1-30	7 ± 1		
Nest sites	n	62	14	9	47
Nest height (m)	mean ± SE range	20 ± 1 12-30	13 ± 2	33 ± 8	45 ± 13
Nest branch diameter (cm)	mean ± SE range	25 ± 1 11-62	15 ± 5	32 ± 9	32 ± 11
Cover above nest (%)	mean ± SE range	75 ± 2 30-100	89 ± 5		85 ± 20
Distance from nest to trunk (cm)	mean ± SE range	8 ± 2 0-90	62 ± 66	134 ± 122	89 ± 132

[A] PNW refers to nest sites in British Columbia, Washington, Oregon, and California.
[1] Canopy closure estimated as: 100% minus mean % gap.
[2] Canopy closure = visual estimate.

cover maps (Table 27). Nests were located in stands with height classes 3 (19.5-28.4 m, 13.5%), 4 (28.5-37.4 m, 80.7%), and 5 (37.5-46.4 m, 5.8%). Canopy closure ratings for nest stands ranged from 4 (36-45% closed) to 8 (76-85% closed). Site index, or the potential height of 50-yr old trees growing on the site ranged from 9 - 19 m for nest stands. Murrelets nested in both the CWHvm2 (51 nests) and MHmm1 (1 nest) variants. Nests in the CWHvm2 were found in 7 site associations. Most nests were in the CWHvm2-01, vm2-09 and vm2-07 site associations (Table 25).

Thirty-one nest trees were in clusters associated with 1-2 other nest trees (Table 28). Four clusters were located in 1997 during climbing plots conducted as part of a B.C. Ministry of Environment Lands and Parks inventory (Manley 1998). Nest density at these sites ranged from 1.3-4.2 nests/ha. These sites were the highest nest density of the plots climbed in that study and average density for all plots was much lower (0.3-0.7 nests/ha; Manley 1998). Nest density for other nest clusters was not measured because a fixed area was not systematically searched for nests. At these sites the distance between nests is reported as an index of their density. For all clusters except two, it was not possible to determine if nests were active at the same time. Nest 47 and 48 both fledged chicks in 1997 and were active the same season. Nest 5 and 11 were both in the incubation stage on May 13, 1996, and were the two closest nests documented in my study.

Discussion

Murrelets exhibit selectivity for habitat characteristics at microsite, element and patch levels. The most basic need of nesting murrelets is a platform within the tree crown that is large enough to support an adult, its egg, and chick. Murrelets require this structure because unlike other forest nesting species they do not construct a nest or use cavities. I expected the availability and quality of nest sites to dominate habitat selection by Marbled Murrelets, because unlike typical forest-dwelling birds, murrelets are seabirds and use forest habitats only for nesting. Factors influencing the size of platform, epiphyte substrate, protective cover and access at nest sites may be important at specific scales of habitat selection. Because feeding occurs exclusively in aquatic areas, the relationship between marine areas and nesting habitat will influence habitat selection but most likely at

Table 27. Forest cover classification of 20 stands containing 51 ^ Marbled Murrelet nest trees on the Sunshine Coast.

Polygon number	No. of nest trees	Height class[1]	Canopy closure class[2]	Site index[3]	Contiguous forest area[4]
87	2	4	8	13	565.6
121	5	4	5	13	314.0
62	1	4	4	13	314.0
689	1	5	5	15	273.4
142	5	4	5	12	273.4
692	2	4	5	12	273.4
693	1	4	5	12	273.4
126	1	3	4	9	273.4
699	3	4	5	13	241.7[5]
519	3	3	5	12	240.4[6]
530	1	3	6	11	210.0
393	1	5	5	19	198.9[7]
538	8	4	5	13	193.4
541	2	4	5	13	193.4
532	5	4	5	12	193.4
673	5	4	5	12	193.4
516	2	3	6	12	137.0[8]
370	1	5	5	16	30.0
676	1	4	5	12	26.0
672	1	4	5	12	2.0

^ Nest 4 was located in TFL 39 where forest cover data is produced in a different format. The forest cover code for this stand was M 405 HB-448 which indicates a mature stand of hemlock and Pacific silver fir, with a volume of 448 m³/ha.

[1] canopy height class 3 (19.5-28.4 m), 4 (28.5-37.4 m), 5 (37.5-46.4 m)
[2] canopy closure class 4 (36-45%), 5 (46-55%), 6 (56-65%), 7 (66-75%), 8 (76-85%)
[3] projected height (m) of 50-year old trees
[4] forest area determined at time nest was discovered, subsequent modifications are noted
[5] current area 24.1 ha for 3 nests
[6] current area 0 for 2 nests, 210 ha for 1 nest
[7] current area 0 ha
[8] current area 0 ha for 1 nest, 126 ha for 1 nest

Table 28. Distance between Marbled Murrelet nests found in clusters of 2 or more nest sites. Nest density data is from (Manley 1998). Nest density for other nest clusters was not measured because a fixed area was not systematically searched for nests.

Nest clusters	Distance between nest trees (m)	Nest density (nests/ha)
N15abc, N34ab, N37		4.2
15-34	102	
34-37	44	
37-15	112	
N41, N42, N43		4.2
41-42	51	
42-43	46	
43-41	42	
N46ab, N47, N48		2.6
46-47	13	
47-48	58[2]	
N38, N39	43	1.3
N3, N6	52	
N5, N11	38[1]	
N7, N35ab, N24		
7-24	53	
7-35	40	
24-35	17	
N8, N23	~75	
N28ab, N29, N30		
28-29	43	
29-30	55	
30-28	78	
N16ab, N17ab	73	
N18, N19	53	
N21, N22	~100	
N32ab, N33ab	~100	

[1] nests both active and incubating at same time
[2] both nests fledged a chick in 1997

the landscape scale. Choice of nest site influences fitness through its effects on reproductive success and adult survival (Martin 1992). Predation at nest sites is a major factor influencing reproductive success of Marbled Murrelets (Chapter 1, Nelson and Hamer 1995a). Also, there is evidence that predation at nests can influence adult survival. Predation of adults at nests by hawks and ravens has been documented (Singer *et al.* 1991, Marks and Naslund 1994). Murrelet nesting behaviour and plumages show adaptations to predator avoidance suggesting that nest predation has been a strong selective pressure influencing the behaviour and nest site selection of Marbled Murrelets (Nelson and Hamer 1995a).

Microsite selectivity strongly reflects the murrelets' need for a suitable platform structure on which to nest. Element and patch level selectivity provides insights into structural characteristics of the trees and forests that provide these platforms. Nest trees and patches may also influence the quality of the nest microsite and their structure may be important for predator avoidance and access of murrelets to nests.

Microsite Level Use and Selection

The Marbled Murrelet's requirement for a nesting platform of suitable size was demonstrated by significant results of microsite selection. In the nest trees that I sampled, murrelets selected limbs larger in diameter and with a greater platform area than available limbs. Murrelets also preferred limbs with overhead cover and avoided limbs with bare or thin moss substrate.

The use of large diameter limbs for nesting platforms occurs consistently throughout the murrelets' range in North America. Nest limbs have similar average diameters in all regions with the exception of Alaska (Table 26). The minimum diameter for nest limbs is approximately 10-12 cm (Hamer and Nelson 1995b). The substrate available on the limb influences the size of limb required. Small limbs supporting heavy moss growth (typical of nests in Alaska) can provide a large enough surface for nesting (Naslund *et al.* 1995). Litter would not collect on limbs until they are large and have a relatively flat surface. Nest branches with litter used as a nesting substrate would probably be much larger than branches with moss substrate. I did not detect selectivity for either the

height of limbs or moss depth on limbs (measured as a continuous variable). Nest sites of murrelets are usually located within the lower 2/3 of the tree crown (average 54%-78% of nest tree height). The position of nests within the lower 2/3 of the tree crown may reflect that larger limbs usually occur lower in the crown, locations higher in the nest tree may be more exposed, or that limbs lower in the crown may be easier to access from below. Also branch and trunk movement during wind would be greatly diminished in the lower portions of trees. In terms of absolute nest height, nest sites have ranged from 10 m above ground in Alaska to 73 m in Oregon (Hamer and Nelson 1995b, Table 26).

I did not detect differences in the orientation of nest and available platforms. Although limbs with southerly orientations may provide a warmer microclimate for eggs and nestlings, moss on limbs may be deeper in northerly aspects. Exposure to direct sun may be stressful for murrelets. I have observed chicks and adults panting at nests exposed to direct sunlight. Other factors such as nest access may affect the choice of limbs used by murrelets. Nest limbs are associated with canopy gaps and this facilitates access to the nest. In my study area, murrelets always approached nests from downhill. Therefore both the aspect of the patch and the positioning of canopy gaps within the patch may affect the choice of nest limbs.

Overhead cover at nest limbs is an important variable affecting the selection of nest sites. Exposed platforms were avoided and only 1 of 62 nest sites was on an exposed platform. Platforms with >2/3 overhead cover were preferred. Nest sites in the Bunster Range have an average of 75% overhead cover (Table 26). Nest sites in other regions have on average 79 to 90% cover (Hamer and Nelson 1995a). Overhead cover at nest sites is thought to hide nests from predators, and reduce predator search efficiency. Nelson and Hamer (1995a) reported that successful nest sites had greater overhead cover (89% cover) than predated nest sites (69% cover). Preference for covered platforms by murrelets likely reflects the higher quality and potential benefits to fitness of a well concealed nest site. Overhead cover at nest sites may also provide protection from inclement weather and shade from direct sunlight.

Epiphyte substrate influenced selectivity at the microsite level. Platforms with no substrate and those with thin moss cover were avoided. Lichen/litter covered platforms

82

were preferred, but this preference resulted from a high percentage use (2 of 4) of this uncommon platform type. The majority of nest sites and available platforms had thick moss substrate. Moss substrate may have several beneficial functions to nesting murrelets. Moss may provide a suitable microclimate for incubating eggs and young chicks. There may be insulative benefits of nesting in moss especially when nesting begins early and in cold damp environments at high elevations and latitudes (Naslund *et al.* 1995). Moss may also confine the egg and chick better than other substrates. A deeper nest cup can be made within thick moss that would prevent an egg from rolling and help confine a young chick. Moss is also important because it increases the platform area available on a branch (see above). The use of Lichen/litter covered platforms appears to be associated with tree species. Data from the Bunster Range show that western and mountain hemlock trees in this region have fewer moss covered platforms than yellow-cedar (Chapter 3). In my study, both instances of murrelets nesting on Lichen/litter covered platforms occurred in western and mountain hemlock trees.

Element Level Use and Selection

Selectivity analyses at the element level revealed several differences between nest trees and other trees with platforms in nest plots (referred to as available trees). Murrelet nest trees were larger in diameter than available trees. Nest trees in the Bunster Range averaged 99.6 cm in diameter and were amongst the largest diameter trees present in the plots. These nest trees are larger than nest trees in Alaska but smaller than the average of 211 cm dbh reported for nest trees in the Pacific Northwest (Table 26, Hamer and Nelson 1995a). These differences indicate that the diameter of a suitable nest tree varies regionally. Differences in the growth of trees and epiphytes result in trees developing suitable platforms at different diameters in different regions. Within each region, nest trees are amongst the largest and oldest trees available. Because of these differences it is important that habitat managers use local information to identify nesting habitat for murrelets. For example, prior to my study, nest trees described in B.C. were on average 212 cm dbh based on a sample of low elevation nest trees (Nelson and Hamer 1995a). If high elevation areas like the Bunster Range were evaluated based on these data, most of

the trees would appear to be too small for nesting. The use of large diameter trees results from a strong correlation between tree diameter and platform availability (Naslund *et al.* 1995; Hamer 1995; Chapter 3). These relationships likely vary among regions.

The number of platforms in a tree yielded highly significant selection at the element level. Nest trees have more potential platforms than do available trees and this result is consistent within diameter categories. The number of platforms is an important characteristic of nest sites although few studies have presented data on the number of platforms in nest trees. Nest trees in Prince William Sound (Alaska) had an average of 7 platforms per tree (Naslund *et al.* 1995, Table 26). The Alaska study also documented that nest trees have more platforms than other canopy trees around the nest (Naslund *et al.* 1995). Murrelets may select nest trees with greater numbers of platforms because trees with more platforms are more likely to have some high quality nest platforms (i.e., those large enough and with sufficient cover). An alternative explanation is that trees with multiple potential nest sites diminish the search efforts of predators. The multiple nest site hypothesis proposes that by nesting in areas with large numbers of potential nest sites, predators have to search more places to locate nests (Martin and Roper 1988). These ideas are discussed further when I examine selectivity for platform availability across spatial scales.

Tree height is not correlated with the availability of nest sites and shows minor differences between nest trees and available trees. Many nest trees have dead or broken tops and are old, hence height is not a strong predictor of platforms.

Selectivity for tree species was not apparent at the element level. The high use of yellow-cedar trees for nesting may simply reflect that this species is the primary provider of platforms in the study area. Murrelets have been documented nesting in 7 tree species throughout North America (Hamer and Nelson 1995a). The potential of each tree species for nesting likely shows regional differences.

Platform characteristics were selected at the element level but selectivity was not as strong as that observed at the microsite level. Selection for cover above platforms was significant for western hemlock nest trees and for all yellow-cedar nest trees but not for separate diameter classes of yellow-cedar trees. Preference for epiphytes on platforms was

84

only detected for western hemlock nest trees. The slight differences in proportions for the diameter classes of yellow-cedar were not significant until all were combined in one sample. Western hemlock trees on the other hand had significant results with a small sample. I think that this results from the higher variability in the characteristics of western hemlock platforms. Because western hemlock platforms are less frequent in preferred categories (mossy or covered), selection for these categories is more pronounced.

Gaps

Murrelets selected nest trees located next to larger than average canopy gaps. Use of canopy gaps by murrelets to access nests has been observed at most nest sites (Manley and Kelson 1995, Naslund *et al.* 1995, Nelson and Peck 1995, Singer *et al.* 1995). Murrelets use these canopy openings to approach their nest from below nest height and make a stall landing. Birds not using a stall landing have been observed crashing into foliage and aborting landing attempts (Nelson and Peck 1995). No other studies of Marbled Murrelets have evaluated the use and availability of canopy openings in a scale dependent framework. Concern that murrelet use of openings results from a bias towards observing birds in more open areas has been expressed (Nelson and Peck 1995). In my sample, 7 nests were located on clearcut edges, and were probably easier to find using visual surveys than nests located within the forest. The preference for industrial gaps that I observed may be a result of nests being easier to locate in these gaps. However, even with these nests excluded, nest access gaps of all natural types are significantly larger than a random sample of available gaps. Murrelets may nest in trees adjacent to industrial gaps because they are large openings and provide easy access. Evidence from my study area and elsewhere in North America indicates that nest failure from predation is higher for nests within 50-100 m of edges (Manley and Nelson 1999, Nelson and Hamer 1995a). Because nests on edges may be easier to locate, nest searches in 1997 were structured in paired edge and interior plots (Manley 1997). The nest sites located in this manner were on average further from edges but were similarly associated with canopy gaps (Manley 1998).

Relationships between the nest site, nest tree, nest access gap, and nest patch

involve the consideration of several factors. For a canopy gap to be used, it must be positioned such that it allows birds access to the nest branch, and this will depend on the location of foliage surrounding the nest branch, especially from below. Murrelets in the Bunster Range have been observed approaching nests only from downhill. On steep slopes, it may be difficult to approach below nest height from the uphill side. Therefore the slope of the surrounding patch may influence which canopy gaps and nest branches can be used. Further analysis of the flight and landing routes of murrelets may offer some insight into the importance of access to the suitability of nest sites. For example, murrelets nest in trees ranging from 20-90 m in height. If birds need to approach the nest branch from at least 10 m below in order to stall, then I predict that canopy openings might be more crucial for murrelets in forests with low canopy heights. In taller forests, the gaps used may occur in different forest strata (e.g., between dominant and co-dominant strata). Observations of nesting behaviour indicate that murrelets may approach even very high nests (42 m) by swooping as low as 2 m above the ground (Manley and Kelson 1995). The degree that murrelet access to nests is constrained by flight behaviour is not known, but my data indicate that it is a factor in selection of nesting habitat.

Canopy gaps are characteristic of coastal old-growth forests (Lertzman *et al.* 1996, Wells *et al.* 1998), but are generally not included in descriptions of forest stands. Gaps are a product of stand dynamics and contribute to the structural complexity of forests. Canopy gaps in habitat transitional between CWHvm2 and MHmm1 had a median size of 41 m^2 and resulted from the mortality of on average 3 canopy trees (Lertzman and Krebs 1991). Although canopy gaps are not generally measured in assessments of forest stands, they appear to play an important role for access to nests by Marbled Murrelets.

Patch Level Use and Selection and Comparisons Among Scales

Platform availability was the most striking and consistent difference between nest patches and random patches. Large numbers of platforms were preferred strongly at both the element and patch level. Nest patches had significantly more platforms even when nest trees were excluded from the nest patch (i.e., even when element level selectivity was accounted for). I have considered three explanations for why murrelets would choose to

nest in both trees and patches with a high density of platforms. It is possible that murrelets chose areas with a high density of platforms because within these areas they are more likely to find a platform with the right combination of characteristics for a superior nest site. Murrelets need to find a platform that has overhead cover, a suitable substrate, that is large enough and that is accessible. Given the suite of characteristics that murrelets prefer, it follows that they may need to locate themselves in a patch with lots of potential platforms to choose from. This may be particularly important if murrelets return to breed in the same nest tree or stand for future nesting attempts (Chapter 1).

An alternative explanation comes from the multiple nest site hypothesis (Martin and Roper 1988) which proposes that birds reduce their risk of predation when they nest in an area with many potential nesting locations. These additional nest locations reduce the searching efficiency of avian predators, in particular corvids. I examined this hypothesis with nest sites in the Bunster range and found that successful nests had more platforms in the nest tree and the nest patch than did failed nests, but the difference was not significant (I. Manley unpub. data). A larger sample must be obtained before this hypothesis can be rejected. Whatever the underlying cause for the importance of nesting in areas of high platform density, it is clear that management strategies for murrelet habitat will need to focus on providing suitable platform densities at all spatial scales.

Canopy gaps and tree density

Canopy gaps and tree density are complementary representations of the degree of opening or closure in forests. Selection by murrelets for both openings and cover at different scales is key to understanding how murrelets meet their need for both access and protective cover at nest sites (Table 29). The importance of protective cover at the nest site is expressed clearly at the microsite level. At the element level, cover is compromised by the need for access to the nest. However, the requirement for a large canopy gap at the element level did not increase the total opening of the nest patch (Table 24). It appears that murrelets maintain cover in the nest patch through differential selection of tree density. Nest patches have a lower density of trees in the 11- 40 cm diameter class, which also results in a lower total tree density at nest sites. But, nest

87

Table 29. Comparison of element and patch level selectivity for tree diameter and platform availability on the Sunshine Coast, B.C.

Attribute	Element level	Patch level
	n=38 nest trees	n=34 nest patches
Tree diameter	> at nest trees	
11-40 cm		Less at nest patches
41-60 cm		
61-90 cm		More at nest patches
>91 cm		More at nest patches
Number of platforms	> at nest trees	> at nest patches
Gap area	> at nest trees	No difference
Gap type		
Industrial	Preferred	
Tree		
Riparian		
Edaphic		

patches also have a higher density of large diameter trees 61-90 and >90 cm in diameter. I propose that murrelets achieve access to nests by selecting patches with fewer small trees, but cover at the nest patch is not compromised because they select nest patches with a higher density of large trees. This compensation may occur as a result or their selectivity for a high density of platforms in nest patches, which correlates with a high density of large diameter trees. Small scale variance in forest characteristics may be an important feature of nesting habitat for Marbled Murrelets because it ensures juxtaposition of habitat elements which occur because of different and sometimes conflicting forest processes. This juxtaposition of large trees and canopy gaps and variance in tree and gap sizes enhances the likelihood of suitable nesting opportunities for Marbled Murrelets.

Patch level selectivity has been examined in one study of 10 nest trees in Oregon (Grenier and Nelson 1995). In their study, there was lower canopy closure at nest patches and lower density of large diameter trees at nest plots than at random locations. This contrasts with the results of my study. Relatively few studies of murrelet habitat measure the size and number of canopy gaps. The use of different techniques to estimate overall canopy closure in a plot, may obscure the importance of individual gaps. In my study selection for canopy openings was only apparent at the element level.

Overhead cover

Selection for overhead cover at platforms was highly significant at the microsite level, significant for 2 tree categories at the element level, and not significant at the patch level (Table 30). The decreasing significance of this variable with increasing scale indicates that cover above platforms is specific to nest sites and does not drive habitat selection at the patch level. Murrelets select patches based on numbers of platforms, then select a nest tree based on platform numbers and accessibility, and then, within this tree, they select a platform that has specific characteristics such as overhead cover.

Epiphyte substrate

Epiphyte substrate on platforms was selected for at all scales, but the preferred categories preferred varied with scale (Table 31). Bare platforms were avoided at all levels

Table 30. Comparison of microsite, element and patch level selectivity for cover above platforms on the Sunshine Coast, B.C. WH=western hemlock, YC=yellow-cedar.

	Microsite	Element level	Patch level
Platform cover	52 nest trees, 61 nests n=61 nest platforms n=386 unused platforms in nest trees	38 nest trees n=438 platforms in nest trees n=458 platforms in nest plots	34 nest trees n=829 platforms in nest plots n=324 platforms in random plots
Exposed	Avoided	Avoided (WH 91-120 cm dbh, all YC)	
Partly covered			
Covered	Preferred	Preferred (WH 91-120 cm dbh, all YC)	

Table 31. Comparison of microsite, element and patch level selectivity for epiphyte substrate on platforms on the Sunshine Coast, B.C. WH=western hemlock, YC=yellow-cedar.

Platform epiphyte substrate	Microsite level	Element level	Patch level
	52 nest trees, 61 nests n=61 nest platforms n=386 unused platforms in nest trees	38 nest trees n=438 platforms in nest trees n=458 platforms in nest plots	34 nest trees n=829 platforms in nest plots n=324 platforms in random plots
Bare	Avoided		Avoided
Lichen/litter	Preferred	Avoided (WH 91-120 cm dbh)	Avoided
Moss1	Avoided		Avoided
Moss2		Preferred (WH 91-120 cm dbh)	

of selectivity. Lichen/litter covered platforms were preferred at the microsite level (for western hemlock) but avoided at the element and patch levels. The preference for Lichen/litter covered platforms is based on a very small sample size and may reflect merely that only large platforms can collect litter. My results suggest that murrelets select patches and trees with a high proportion of mossy platforms and low proportions of bare, Lichen/litter covered platforms. They then preferred to nest on Lichen/litter covered platforms within these nest trees. However, the use of litter covered platforms was rare so their importance should not override the fact that most murrelets nested on platforms with deep moss. What is important, is that platforms require some type of substrate to make them suitable for nesting. Bare platforms and platforms with thin moss were consistently avoided across habitat selection scales. Evaluations of habitat suitability for murrelets must include the availability of suitable substrates on platforms.

Characteristics of Nest Stands

Murrelet use of high elevation old-growth stands that I observed in the Bunster Range has not been documented elsewhere in the murrelet's range. Other studies have indicated that in unlogged areas, low elevation habitats have higher murrelet activity and greater habitat suitability (Rodway *et al.* 1993a, Ralph *et al.* 1995). Because my research occurred in a highly modified landscape it is difficult to determine how habitat use and preference may have changed as a result of these modifications. The relative suitability of high and low elevation habitats may vary throughout the murrelet's range. The suitability of my study area is largely due to the presence of large diameter yellow-cedar trees. Other high elevation habitats, outside of the southern mainland coast of B.C. may not have the trees and structures that murrelets require for nesting. Inventory is required to verify if these forests have capability as murrelet habitat. In the meantime, high-elevation old growth should not be excluded from the inventory of suitable murrelet habitat.

Characteristics of nest stands, in part, reflect the availability of habitat within the study area. These data are presented to show the range of forest characteristics that murrelets nest in on the Sunshine Coast and should not be interpreted as preferred habitats. Several stand characteristics of my nest sample have not been included in

definitions of suitable habitat used in recent management plans (e.g., Identified Wildlife Management Strategy draft). For example, suitable habitat is defined as height class 5 in CWH and height class 4 in MH (IWMS draft). These characteristics are used to help identify stands with larger trees but if applied to my sample would exclude 49 of 52 nest trees. Recommendations that are phrased to highlight particular features should be careful not to exclude potential habitats. Murrelets use and nest in a wide variety of old-growth habitats that meet their structural requirements throughout their range. This variation is likely to increase as more areas on the B.C. coast are inventoried.

Most alcid species nest at high densities in offshore colonies (DeSanto and Nelson 1995), but exceptions occur in 4 species. Pigeon Guillemots (*Cepphus columba*) nest in associations ranging from isolated pairs to small-medium sized colonies (Ewins 1993). Craveri's Murrelet (*Synthliboramphus craveri*) is thought to nest in loose aggregations (DeSanto and Nelson 1995). Kittlitz's Murrelet (*Brachyramphus brevirostris*) is closely related to Marbled Murrelets and is thought to be a true solitary nester (Freisen *et al.* 1996, Naslund *et al.* 1994). Marbled Murrelets have been considered solitary nesters or loosely colonial, however there is little evidence of the degree of nest aggregation. Concurrently active nests have been found within 30 and 100 m of each other (Hamer and Cummins 1991, DeSanto and Nelson 1995). Marbled Murrelet nest sites in my study showed a high degree of aggregation. Fifty-two percent of the nest sites in my study were associated with at least one other nest tree within 100 m. The degree of clustering may be much higher if plots of 50 to 100 m radius were searched around nests systematically. For the majority of nest clusters, I did not have direct evidence that nests were active at the same time. Nest clusters may also represent multiple nesting attempts within the same stand by a breeding pair and indicate fidelity to a nest patch instead of a nest tree or platform. Two pairs of nests within 38 and 50 m of each other were active at the same time and could indicate nest aggregation. Long term observations of these nest clusters would provide evidence to distinguish stand fidelity from semi-colonial nesting.

There are few published estimates of Marbled Murrelet nesting density. Nests in my study area appear to be at higher densities based on the numbers of nests located, but there is little data available for comparison. Rodway and Regehr (1998c) estimated that

93

the best valley bottom habitat in the Ursus Valley (Clayoquot Sound) had a nesting density of less than 0.3 nests /ha. Maximum nest densities of 4.2 nests/ ha were documented in my study.

High nest density, clustering of nests and re-use of nest sites/stands (Chapter 1) are all possible indicators that habitat and specifically nest sites are limiting in the Bunster Range. Marbled Murrelets selected for specific features of nest microhabitat, nest trees and nest patches. Nest sites with these specific combinations of features may be limited even in a relatively large forested area. Habitat loss would increase the rarity of suitable nest sites, increase the density of birds in remaining habitat, and increase the competition for remaining nest sites. At this time there is insufficient information on the density of murrelet nests, how density changes with habitat availability, and how this affects population viability to conclude that habitat is limiting. On the other hand, I can not reject this hypothesis either. Nesting density of murrelets should be investigated at different amounts of habitat availability to understand how availability of habitat influences murrelet populations and habitat selection.

Conclusion

Marbled Murrelets selected for structural characteristics of their nesting habitat at each spatial scale. Murrelets selected large diameter limbs with epiphytes and cover above the branch at a microsite scale. Nest trees used by murrelets were larger in diameter and had more potential nesting platforms than did available trees. Murrelets selected nest trees adjacent to canopy gaps, and they used these gaps to approach their nests from below. Nest patches used by murrelets had higher densities of large diameter trees, higher densities of platforms, and a higher proportion of platforms with moss pads. Nest patches had lower densities of small diameter (10-39 cm) trees than available patches. At all scales, selectivity was expressed most strongly for the availability of platforms, which are a basic structural requirement of nesting murrelets.

Most studies of habitat selection by Marbled Murrelets have focused on landscape and stand scales using inland activity data. By examining selectivity at smaller scales, which are congruent with structural nesting requirements, the biological basis of selectivity

94

at larger scales is revealed. For example, selectivity for features strongly linked to the nest site, such as overhead cover, were most strongly expressed at the micro-site and element levels. A multi-scale approach also shows how animals resolve conflicting requirements such as the murrelets' need for both cover and access at nests.

Habitat managers need to know the habitat requirements of Marbled Murrelets to develop forest management strategies. For these strategies, information on both coarse and fine levels of habitat selection identifies nesting habitat requirements which should be satisfied at all scales and those which can be satisfied at specific scales.

Chapter 3. Use and Suitability of Forests for Marbled Murrelets

Introduction

Most studies of nesting Marbled Murrelets attempt to identify habitat characteristics that distinguish nesting habitat from non-nesting habitat or that are related to activity of murrelets. Researchers and managers hope to apply this information: 1) to identify important habitats; 2) to decrease the number of habitat variables needed to evaluate habitat suitability; or 3) to find habitat variables that can be easily assessed. Most research on habitat of murrelets has focused on surveys of murrelet activity because nest sites are difficult to locate. If habitat analyses based on activity produce similar results similar to those based on nest sites, then conclusions about habitat use could be inferred from activity.

In B.C., many studies of murrelet habitat have occurred in old-growth landscapes on Vancouver Island and the Queen Charlotte Islands that have not been modified greatly by logging (Rodway *et al.* 1991, 1993a, 1993b, Savard and Lemon 1994, Burger 1995b). Activity of murrelets was greatest in low elevation spruce hemlock forests on the Queen Charlotte Islands (Rodway *et al.* 1993b). These results may not apply to the Sunshine Coast, where murrelet habitat is mostly at high elevation and consists of forests with shorter and smaller diameter trees (Chapter 2). Other studies report that high activity is positively associated with the number of large diameter trees, potential platforms and mossy platforms, but have been unable to discriminate differences in murrelet activity among forest types at the variant or site association level (Burger 1995b).

The goal of this chapter is to identify habitat characteristics associated with habitat use and activity by murrelets at inland locations. I expect murrelet activity at the stand level will reflect the strong selectivity for platforms that was expressed by murrelets at the microsite, element and patch levels (Chapter 2). Habitat selection can be seen as a bottom up process whereby many features selected at the finest scales are also selected at coarser scales (Weir and Harestad 1997). However, other features selected at coarse scales are not necessarily expressed at finer scales. I use platform density as a measure of habitat suitability for Marbled Murrelets. I then describe differences in habitat suitability that occur among Biogeoclimatic Ecosystem Classification units (variants and

site associations), elevations, and tree species. If the availability of nesting structures varies consistently among these basic criteria then they could be used to predict habitat suitability. Variants and site associations could be identified and used to manage forests for habitat of Marbled Murrelets.

Methods

Study Area

Activity of Marbled Murrelets was surveyed at 144 sites in the Sunshine Coast Forest District between 1995-1997. Data in this chapter come from 3 years of surveys conducted by the SFU Marbled Murrelet Research Project (1995, 1996) and B.C.Ministry of Environment/ B.C.C.F. Marbled Murrelet Inventory Program (1997). Survey methods were the same during the 3 years, but each year, locations were chosen to address different objectives. The choice of study locations for each year is explained below.

1997

Murrelet surveys were conducted in 6 landscape units on the Sunshine Coast that were high priority for management purposes. Landscape units (LUs) are geographic regions that have been delineated as management units under the Forest Practices Code (B.C. Ministry of Forests and B.C. Ministry of Environment 1995). The objectives of these surveys were to document distribution of murrelets at inland sites within the Sunshine Coast Forest District, measure activity of murrelets and assess habitat characteristics. The data could then be used to assess the location's potential as a Wildlife Habitat Area (WHA) for Marbled Murrelets. A cursory analysis of habitat in each landscape unit was used to prioritise survey sites (Crocker and McKeown 1997). All survey sites were located in potential WHAs, areas with >150 ha of age class 9 forest (>250 yr), and a height class greater than 9.5-19.4 m. Designation of WHAs is the primary management strategy for Marbled Murrelets recommended in the draft Identified Wildlife Management Strategy (IWMS draft 1998). Areas with these habitat characteristics have been delineated using forest cover maps for most landscape units on the Sunshine Coast. Survey sites were selected and surveyed in pairs with one site located at a forest edge and its paired site located in the stand 250 m from the edge. A total of 44

pairs of sites were surveyed in 1997 at locations on the Sunshine Coast between Sechelt and Desolation Sound. Vegetation plots were completed at all sites.

1996

In 1996, 36 sites were surveyed in accessible forests within the Bunster Landscape Unit to provide detailed information on murrelet distribution and habitat use within this management area (Drever *et al.* 1998). Sites were selected using 1:20 000 forest cover maps and included second growth forest (age class 4-5, 60-100 yr, $n = 6$), mature forest (age class 8, 140-250 yr, $n = 2$) and old growth (age class 9, >250 yr, $n = 1$) at low elevation. Twenty-seven sites were located in high elevation old-growth forests. Vegetation plots were completed at 26 sites and transects were completed at 22 of these 26 sites (see habitat sampling).

1995

Sites were surveyed in forested stands around Desolation Sound, a foraging area of Marbled Murrelets, from May 16 to August 26, 1995. Sites were chosen over a wide geographic area (1750 km^2) to investigate the inland distribution and types of habitat used by murrelets. The study area included sites as far west as Cortez, West Redonda and East Redonda Islands, and extended north to Forbes Creek on Homfray Channel and east to MacMillan Creek on Powell Lake (see Lougheed *et al.* 1998a for details).

I chose 21 stands of late successional forests (>250 yr) using 1:20 000 forest cover maps. Eleven stands were in high elevation forests (>600 m) and 10 were located in low elevation forests (<400 m). Vegetation plots were completed at all sites.

Surveys of Marbled Murrelets

Use of inland habitats by Murrelets was determined with dawn activity surveys following a standard protocol (Ralph *et al.* 1994, RIC 1995). These surveys recorded murrelet activity during a 2-h period centered at sunrise. Activity was recorded in "detections" of murrelets seen or heard. A "detection" is defined as the sighting or hearing of a single bird or group of birds acting in a similar manner (Ralph *et al.* 1994).

The following data were recorded for each murrelet detection; time, number of birds, direction and distance of detection, closest distance of detection to observer, height of detection, behaviour, type of flight path, and vocalization type. Each site was surveyed 3-4 times during the breeding season. Surveys were conducted between May 19-July 26, 1995, May 13-July 28, 1996, and May 22-July 27, 1997.

Measures of total and occupied activity (maximum, mean and standard error) were calculated to evaluate use of sites by murrelets. Occupied detections were visual detections of birds flying below canopy, circling over forested areas or calling from a stationary point (Ralph *et al.* 1994). Also, I classified sites as one of three status categories; occupied (murrelets exhibiting nesting or below canopy behaviours), present (murrelets detected but occupied activity not observed), or not detected (murrelets not detected) (Ralph *et al.* 1994).

Habitat Sampling

Although vegetation plots varied in location and size, data collected at each plot were generally the same among years. Distance from salt water and elevation were measured using 1:50 000 topographic maps. Forest cover characteristics (age class, height class and canopy closure) were obtained from 1:20 000 forest cover maps. Slope, aspect, and slope position were measured at the plot center using a clinometer and compass. In each plot, all plant species were recorded following the methods of Luttmerding *et al.* (1990). Vegetation at each plot was classified to biogeoclimatic variant and site association (BGSA) using ecological maps and indicator plant species (Green and Klinka 1994).

Diameter at breast height (dbh) was measured for all trees >10 cm in diameter within the plot. Tree height was measured using a clinometer for one or two dominant trees in the plot and then estimated for all others using these trees as a reference. Tree canopies were scanned with binoculars to estimate the number of potential nesting platforms. Platforms are branches or structures at least 15 cm in diameter that provide a level surface (Burger 1995b). In addition to recording numbers of platforms, the following characteristics were also recorded for each platform: epiphyte cover (None= no epiphytes, Lichen/litter, Moss1 = patchy thin moss < 2 cm thick, and Moss2 = moss pads

>2 cm); and cover above (exposed = < 1/3 covered above, partly covered = 1/3-2/3 covered, and covered = >2/3 covered). Platforms that could not be classified were recorded as unknown. We recorded signs or presence of potential predators, searched for eggshells beneath trees with platforms, and collected any signs of murrelet presence (feathers, eggshells, prey items).

Habitat data from plots were summarized into the following variables; tree density (trees/ha); platform tree density (trees/ha); total platforms/ha; Moss2 platforms/ha; and total platforms/ha for each tree species. Variables specific to only one year or one type of plots are described below.

Placement of plots

Methods used to evaluate habitat at survey sites varied among the 3 study years. In 1997, paired stations were established at survey sites, one centered at the forest edge and one 250 m into the forest interior. A vegetation plot was placed 25 m into the forested portion of the edge station. Another vegetation plot was placed at the center of the interior station (see Manley 1998 for details). At the vegetation plots, I measured all trees >10 cm in dbh within a 15-m radius and all trees >50 cm dbh within a 25-m radius. In 1997, gap area was estimated for each plot by identifying all canopy gaps >9 m^2 within the 25-m radius plot. Each gap was mapped, its length and width measured, and an ellipsoid formula was used to calculate gap area. Irregular gaps were divided into sections to facilitate measurements. Canopy gaps were not assessed in 1995 and 1996.

Habitat characteristics at survey sites in 1996 were evaluated using a combination of vegetation plots and transects. Plots were 25-m in radius (0.20 ha) and randomly located within 200 m of the site where murrelet activity had been surveyed (Drever *et al.* 1998). All trees >10 cm in dbh were measured in the 25-m radius plot. The average dbh and height of platform trees were summarized for each plot. One 0.6-ha belt transect, 200 m long and 30 m wide, was established on a random bearing from the centre of each survey site. Within the belt transect, I measured the height and dbh of all trees that had platforms and assessed characteristics of each platform. The following summary variables were calculated for transects: average dbh and height of trees with platforms;

tree density (trees/ha); platform tree density (trees/ha); total platforms/ha; mossy platforms /ha; and total platforms/ha for each tree species.

In 1995, forest characteristics were sampled using a 40 x 40 m plot (0.16 ha) at each stand (RIC 1995). If murrelets were detected in the stand, the plot was located at the fixed station with the highest activity of murrelets. In stands at which murrelets were not detected, plots were located in the area with the highest numbers of potential nesting platforms. This ensured that in stands without murrelet activity, the best potential habitat was sampled and analyses would be conservative. All trees >10 cm dbh were measured within the plot and platforms were recorded as described previously. Average diameter was calculated for all trees >10 cm in dbh within the plot. I used the data from the plots to estimate tree and platform density. These estimates were 5 times higher than those for plots surveyed in 1996 and 1997 when stratified by habitat type. I believe the estimates of density were higher in 1995 because plots were not randomly located but were placed in areas with high numbers of platform trees. Because of this difference, the 1995 habitat data were not included in my evaluation of habitat suitability. Data from 1995 should be considered maximum densities instead of typical densities for habitat types.

Data Analyses

Relationships between status, activity and habitat variables

I used two methods to model habitat variables that may influence murrelet use and activity at inland sites. I compared all summarized habitat variables among occupied, present and not detected sites using a MANOVA procedure to test for an overall difference in habitat characteristics with site status. If the MANOVA was significant, I identified which variables differed between occupied, present, and not detected sites with univariate tests and contrasts. I also used stepwise multiple regression to identify habitat variables that accounted for variation in murrelet activity. The regression was used only for descriptive purposes and not intended for predictive purposes. A correlation matrix of all habitat and activity variables was produced to identify correlated habitat variables. For pairs of habitat variables with a correlation coefficient >0.8, only the variable most correlated with activity was used in the regression procedure. Categorical variables were tested for their significance on maximum activity using a Kruskal Wallis Anova.

101

Significant categorical variables were added as dummy variables to the model (Freund and Ramon 1991). A forward stepwise regression procedure was used with P $_{enter}$ =0.05 and P $_{remove}$ =0.10. In the modeling procedure, a Durbin Watson statistic was used to evaluate auto-correlation. Variance Interference Factors were produced to evaluate multicollinearity, and outliers were identified (>2 SD) (Freund and Ramon 1991). Residuals were plotted against predicted values to assess the fit of the model.

For 1997 data, maximum total activity (maximum number of detections recorded during three surveys) was used as a dependent variable and was ln+1 transformed for the model. Mean total detections and mean occupied detections were used as dependent variables for 1996 and 1995 data (also ln+1 transformed). Percentage data were square root transformed. Mean total detections and percentage occupied behaviour were summarized over 100-m elevation categories for 1997 survey data.

Suitability of habitat types for Marbled Murrelets

The availability of potential nesting structures has been identified as a key feature of nesting habitat throughout the range of Marbled Murrelets. Selection for platforms was expressed at microsite, element and patch levels (Chapter 2). Platforms are the most basic structural requirement of nesting murrelets and their density can be considered a measure of the habitat suitability, or the current ability of the habitat to support murrelets. I examined platform density in relation to biogeoclimatic ecosystem classification units, which are commonly used as a system to categorise and manage habitats. I summarized densities of platforms and mossy platforms by 4 criteria; biogeoclimatic (BEC) variants, 100-m elevation categories, site associations, and tree species. I calculated mean density of platforms and mossy platforms for each of 4 BEC variants in the study area. Densities were summarized for zonal site association and for all site associations. Zonal site associations occur at average or moderate nutrient and moisture regimes and are the most common and representative site association for a variant. I calculated platform densities for zonal sites in 2 variants for 4 landscape units distributed throughout the Sunshine Coast. I used this information to determine if suitability differed for the same habitat type among different geographic locations. I used a Kruskal Wallis non-parametric Anova to test for differences in platform density among landscape units.

To examine the relationship between elevation and platform density, I summarized platform density for 100-m intervals of elevation in the study area. Platform densities were summarized for all site associations documented in the CWHvm2 and MHmm1 variants to examine the effects of nutrient regimes and moisture regimes on platform density. I tested for differences between 4 site associations with moisture regimes ranging from moderately dry to very moist using 1997 habitat data from the Bunster Landscape Unit. A non-parametric Anova was used to test for differences in total and mossy platform densities among site associations.

Suitability of tree species

The average structural characteristics for 6 species of trees found within the study area were summarized using data from all vegetation plots (1995-1997). Douglas-fir, western redcedar, western hemlock, Pacific silver fir, yellow-cedar and mountain hemlock trees with platforms were included in analyses. I calculated the range and average for dbh and height of trees. I calculated total number of platforms and number of mistletoe, Lichen/litter, mossy, exposed and covered platforms to compare the suitability of tree species. For each tree species, I calculated the frequency distribution of all trees >10 cm dbh, and of all trees with platforms to determine the sizes of trees that supply platforms. Average number of platforms and proportion of trees with platforms were calculated for each diameter category and tree species.

Results

Multivariate Habitat Analysis

Results of the MANOVA indicate that habitat characteristics differed among murrelet status categories for sites surveyed in 1997 ($F_{0.05, 22} = 2.23$, $P<0.001$, Power $=0.993$). Four habitat variables differed significantly among status levels in multiple contrasts (Table 32). Sites classified as "not detected" had steeper slopes, larger area of total gap, and lower elevations than present and occupied sites. 'Occupied' sites had higher densities of mossy platforms and yellow-cedar platforms than 'present' and 'not detected' sites (Table 32).

103

Table 32. Habitat characteristics of sites classified by murrelet status. Summaries are from a MANOVA for 1997 data. Different letters indicate habitat variables with significantly different values by status level (multiple contrast P<0.05).

Variable	MANOVA P value	Not detected (n=18) Mean (SE)	Present (n=25) Mean (SE)	Occupied (n=31) Mean (SE)
Slope (%)	0.03	50.1 (5.7)[a]	31.7 (4.8)[b]	34.1 (4.4)[b]
Aspect (°)	0.98	159.4 (24.0)	163.9 (20.3)	159.5 (18.4)
Total tree density (trees/ha)	0.77	182.1 (23.5)	176.9 (19.9)	158.6 (17.9)
Gap area (m^2/ha)	0.03	3494.5 (439.6)[a]	1993.1 (371.8)[b]	2936.1 (336.1)[ab]
Trees >90 cm dbh/ha	0.60	11.2 (3.9)	14.0 (3.3)	17.1 (3.0)
Platform trees/ha	0.19	17.4 (4.2)	21.4 (3.6)	28.2 (3.2)
Platforms/ha	0.28	60.9 (17.9)	63.2 (14.8)	95.5 (13.8)
Moss2 platforms/ha	0.05	20.1 (15.4)[a]	25.7 (12.9)[a]	65.2 (11.7)[b]
Yellow-cedar platforms/ha	0.12	22.9 (14.3)[a]	25.2 (12.0)[a]	55.0 (10.7)[b]
Douglas-fir platforms/ha	0.29	8.5 (4.4)	9.8 (3.8)	2.3 (3.4)
Elevation (m)	0.02	695.2 (62.9)[a]	910.8 (53.2)[b]	887.8 (48.2)[b]

Of 22 locations surveyed in 1996, murrelets were not detected at 4 sites, murrelets were present at 3 sites and 15 sites were occupied. All locations surveyed in 1996 were within the Bunster Landscape Unit. Habitat characteristics did not differ significantly with murrelet status categories (vegetation plot variables, $F_{0.05, 24} = 1.7$, $P=0.10$, Power=0.81; transect variables, $F_{0.05, 22} = 0.84$, $P=0.65$, Power=0.41; Table 33). Although, occupied sites appear to have higher densities of platform trees, mossy platforms and yellow-cedar platforms than not detected and present sites, these differences were not significant.

Of 21 locations surveyed in 1995, murrelets were not detected at 5 sites, they were present at 8 sites and 8 sites were 'occupied'. Habitat variables differed significantly amongst sites with different murrelet status ($F_{0.05, 14} = 6.3$, $P=0.02$, Power=0.89). Marginally significant differences ($P<0.10$) were found for average diameter and elevation in subsequent univariate tests (Table 34). Sites at which murrelets were not detected sites appear to have lower average tree diameter than did present and occupied sites, however these differences were not significant.

Multiple Regression

1997

Murrelet activity differed by landscape unit with the highest activity occurring in the Brittain and Bunster Landscape Units (Table 35). Categorical forest cover variables did not have a significant influence on murrelet activity. Correlation coefficients between habitat characteristics and murrelet activity ranged from -0.22 to 0.44 (Table 36a). The only significant correlation was between Moss2 platforms (platforms with thick moss pads) and activity. The multiple regression models included two variables, number of mossy platforms and slope, which together explained 37% of the variation in total activity (Table 37).

105

Table 33. Habitat characteristics for sites classified by murrelet status. Summaries are from a MANOVA for 1996 data.

Plot variable	Not detected (n=4) Mean (SE)	Present (n=3) Mean (SE)	Occupied (n=15) Mean (SE)
Slope (%)	27.0 (12.2)	16.2 (3.9)	22.9 (4.9)
Aspect (°)	264.0 (28.9)	52.3 (24.9)	215.6 (21.6)
Total trees /ha	268.0 (53.4)	242.4 (64.1)	158.7 (13.4)
Mean dbh (cm)	31.2 (19.9)	69.6 (14.8)	78.2 (8.4)
Mean height (m)	9.7 (6.3)	22.6 (4.1)	24.5 (2.0)
Platform trees/ha	5.1 (1.3)	13.2 (3.6)	23.4 (3.6)
Platforms/ha	3.6 (2.5)	23.4 (7.6)	59.1 (12.7)
Mossy platforms/ha	0.0	5.1 (3.6)	30.6 (6.6)
Yellow-cedar platforms/ha	0.0	8.1 (3.6)	38.7 (9.7)
Mountain hemlock platforms/ha	0.0	1.5 (1.5)	1.5 (1.5)
Western hemlock platforms/ha	0.0	3.1 (2.0)	9.7 (3.6)
Douglas-fir platforms/ha	3.6 (2.5)	10.7 (7.6)	7.6 (4.1)
Transect variable			
Mean dbh (cm)	63.0 (23.5)	84.3 (4.1)	74 (3.2)
Mean height (m)	24.8 (9.1)	27.5 (3.9)	25.3 (0.9)
Platform trees/ha	3.7 (1.3)	12.5 (4.0)	24.7 (3.8)
Platforms/ha	5.3 (3.0)	31.3 (11.0)	60.1 (9.5)
Mossy platforms/ha	0.0	5.5 (5.5)	27.6 (7.0)
Yellow-cedar platforms/ha	0.0	10.0 (6.7)	38.4 (8.4)
Mountain hemlock platforms/ha	0.0	0.0	3.3 (1.7)
Western hemlock platforms/ha	0.0	6.7 (0)	8.4 (1.7)
Douglas-fir platforms/ha	5.3 (3.0)	13.4 (8.7)	7.2 (4.0)

Table 34. Habitat characteristics for sites classified by murrelet status. Summaries are from a MANOVA for 1995 data.

Variable	MANOVA P value	Not detected (n=5) Mean (SE)	Present (n=8) Mean (SE)	Occupied (n=8) Mean (SE)
Slope (%)	0.14	31.8 (5.1)	21.8 (3.9)	19.4 (3.6)
Aspect (°)	0.94	161.8 (48.5)	177.9 (123.6)	161.5 (43.3)
Total trees/ha	0.40	462.5 (35.6)	558.1 (101.9)	415.0 (55.6)
Mean dbh (cm)	0.05	27.4 (1.5)	37 (3.6)	39.9 (3.2)
Trees >60cm dbh/ha	0.27	50.0 (18.1)	88.1 (18.8)	75.6 (14.4)
Platform trees/ha	0.33	22.5 (5.4)	48.7 (15.0)	46.3 (8.8)
Platforms/ha	0.57	96.3 (41.9)	190.6 (74.3)	150.0 (38.8)
Mossy platforms/ha	0.64	6.5 (6.5)	74.4 (60.3)	60.0 (17.5)
Yellow-cedar platforms/ha	0.46	16.3 (16.3)	49.4 (28.1)	64.3 (23.1)
Douglas-fir platforms/ha	0.14	80.0 (46.3)	43.8 (22.5)	5.0 (5.0)
Elevation (m)	0.07	258.0 (155.6)	394.8 (139.7)	764.6 (111.9)

Table 35. Average activity for categorical variables considered for inclusion in a multiple regression model. Significance values are for a Kruskal Wallis non-parametric Anova. a) 1997 survey data, only edge sites are included. b) 1996 survey data.

a) 1997

Variable	Classes (n)	Maximum detections		χ^2	df	P value
		Mean	(SE)			
Landscape unit	Brittain (9)	29.7	12.4	13.3	5	0.02
	Bunster (19)	22.2	6.1			
	Cortes (3)	0.0	-			
	Nelson (1)	0.0	-			
	Salmon (3)	3.7	3.2			
	Sechelt (9)	8.1	3.5			
BEC variant	CWHxm (1)	0.0	-	6.2	3	0.10
	CWHdm (1)	0.0	-			
	CWHvm2 (33)	19.7	4.4			
	MHmm1 (9)	13.7	10.1			
Canopy closure	2 16-25 (1)	0.0	-	5.7	8	0.46
% closed	3 26-35 (2)	0.5	0.5			
	4 36-45 (7)	29.6	14.9			
	5 46-55 (17)	16.7	5.2			
	6 56-65 (7)	10.9	4.4			
	7 66-75 (5)	10.4	4.2			
	8 76-85 (3)	39.7	32.9			
Canopy height class	3 19.5-28.4 (11)	19.5	8.2	2.4	2	0.30
Range (m)	4 28.5-37.4 (26)	19.7	5.6			
	5 37.5-46.4 (5)	5.6	3.4			

b) 1996

Variable	Classes (n)	Detections		χ^2	df	P value
		Mean	(SE)			
Age class	4 61-80 yr (2)	0.0	-	18.2	3	<0.001
	5 81-100 yr (4)	0.1	0.1			
	8 141-250 yr (2)	0.0	-			
	9 > 250 yr (28)	13.5	2.3			
Canopy closure						
% closed	3 26-35 (1)	12	-	4.95	4	0.29
	4 36-45 (7)	9.3	2.3			
	5 46-55 (22)	11.7	2.7			
	6 56-65 (5)	8.9	7.8			
	7 66-75 (1)	0.0	-			
Canopy height class	3 19.5-28.4 (14)	10.6	3.1	3.65	2	0.16
range (m)	4 28.5-37.4 (17)	12.5	3.3			
	5 37.5-46.4 (5)	3.5	1.6			

Table 36. Pearson correlation coefficients between continuous habitat variables considered for inclusion in a multiple regression model and murrelet activity: a) 1997, b) 1996, c) 1995.

a) 1997

Variable	Pearson's r	
	Total detections	Occupied detections
Slope	-0.01	-0.04
Aspect	-0.22	-0.09
Elevation	-0.02	0.10
Gap area	0.04	-0.05
Tree density >10 cm dbh	-0.21	-0.18
Number of mossy platforms	0.41***	0.02
Number of covered platforms	-0.08	-0.04
Tree density >90 cm dbh	0.15	0.11
Number of Douglas-fir platforms	-0.16	-0.11

b) 1996

Variable	Plots Pearson's r		Transects Pearson's r	
	Total detections	Occupied detections	Total detections	Occupied detections
Slope	-0.14	-0.10		
Tree density >10 cm dbh	-0.29	-0.15		
Mean dbh	-0.01	-0.11	-0.03	-0.01
Mean height [1]	-0.04	-0.19	-0.08	-0.10
Number of trees with platforms[1]	0.40*	0.26	0.58**	0.64***
Total platforms[1]	0.35*	0.23	0.54**	0.59**
Number of mossy platforms	0.45**	0.27	0.47**	0.51**
Number of western hemlock platforms	0.29	0.22	0.46*	0.46*
Number of Douglas-fir platforms	-0.19	-0.12	-0.13	-0.08
Number of yellow-cedar platforms[1]	0.44*	0.28	0.55**	0.57**

c) 1995

Variable	Pearson's r	
	Total detections	Occupied detections
Slope	-0.42	-0.33
Aspect	0.23	0.11
Elevation	0.54*	0.49*
Tree density >10 cm dbh	0.12	-0.16
Average dbh	0.26	0.31
Number of trees with platforms	0.29	0.26
Total platforms	0.14	0.18
Number of mossy platforms	0.12	0.07
Number of western hemlock platforms	0.15	0.24
Number of Douglas-fir platforms	-0.37	-0.33
Number of yellow-cedar platforms	0.46*	0.30

*** significant $P<0.001$

**$P<0.01$

* $P<0.05$

[1] variables correlated with other habitat variables and not included in multiple regression

Table 37. Multiple regression models relating activity of Marbled Murrelets to landscape and vegetation variables.

1997

	Dependent variable	Predictors	Estimate mean (SE)	T	P value	Standardized estimate
	Mean total detections	Constant	3.08 (0.46)	6.67	< 0.001	
	$r^2=0.37$, $F_{0.05, 1, 39} = 12.2$, $P<0.001$	Moss2 platforms	0.06 (0.01)	4.21	0.002	0.55
		Slope	-0.27 (0.08)	-3.24	< 0.001	-0.43

1996

	Dependent variable	Predictors	Estimate mean (SE)	T	P value	Standardized estimate
Transect	Mean total detections	Constant	1.20 (0.42)	2.89	0.01	
	$r^2=0.26$, $F_{0.05, 1, 22} = 7.56$, $P=0.013$	Platform trees	0.07 (0.03)	2.75	0.013	0.54
Transect	Mean occupied detections	Constant	0.19(0.22)	0.87	0.39	
	$r^2=0.39$, $F_{0.05, 1, 22} = 15.8$, $P=0.001$	Platform trees	0.06 (0.02)	3.97	0.001	0.65
Plot	Mean total detections	Constant	-2.08 (0.65)	-3.21	< 0.01	
	$r^2=0.71$, $F_{0.05, 1, 23} = 20.4$, $P<0.001$	Age[1]	0.53 (0.09)	5.86	< 0.001	0.78
		Moss2 platforms	0.10 (0.03)	3.91	0.001	0.49
		Mean height	-0.04 (0.01)	-2.83	0.01	-0.40
Plot	Mean occupied detections	Constant	0.44 (0.17)	2.7	0.01	
	$r^2=0.24$, $F_{0.05, 1, 23} = 8.9$, $P=0.01$	Mossy platforms	0.07 (0.02)	2.9	0.01	0.52

1995

	Dependent variable	Predictors	Estimate mean (SE)	T	P value	Standardized estimate
	Mean total detections	Constant	1.99 (0.58)	3.5	0.003	
	$r^2=0.49$, $F_{0.05, 1, 20} = 10.7$, $P=0.001$	Elevation	0.002 (0.00)	3.01	0.007	0.49
		Slope	-0.047 (0.02)	-2.57	0.019	-0.42
	Mean occupied detections	Constant	0.15 (0.23)	0.64	0.95	
	$r^2=0.23$, $F_{0.05, 1, 20} = 6.97$, $P=0.02$	Elevation	0.0001 (0.0)	2.64	0.02	0.52

[1]age was coded as a binary variable: old or not

Murrelet activity varied significantly with forest age class (Table 35). No or very low activity was recorded for stands aged <250-years-old, although sample sizes were small. Other forest cover variables (canopy closure, height class) did not affect amount of activity.

Number of platform trees, total platforms, mossy platforms and yellow-cedar platforms were all significantly correlated with activity (Table 36b). Because these variables were correlated with each other, only mossy platforms was used in the regression model. None of the plot habitat variables were significantly correlated with occupied activity. Five transect habitat variables were significantly correlated with both total and occupied activity. Transect habitat variables were correlated more strongly with activity than were plot variables, and had higher correlation coefficients with occupied activity than with total activity. The five variables describe the availability of platforms and were correlated with each other. I used only number of platform trees in the regression model because it was most strongly correlated with total and occupied activity.

I used mean number of total and occupied detections in the multiple regression models, because these variables had stronger correlations with habitat variables than did maximum number of total and occupied detections. Multiple regression models using transect habitat data selected number of platform trees as significant predictors of variation in total and occupied activity. Number of platform trees explained 26% of the variation in total activity and 39% of the variation in occupied activity (Table 37). The model for plot habitat variables selected age class, mossy platforms and average tree height as significant predictors of total activity. Mossy platforms were the only variable selected for occupied detections.

1995

Murrelet activity recorded in 1995 was correlated significantly and positively with elevation and yellow-cedar platforms. Occupied activity was correlated significantly and positively with elevation only. Both total and occupied activity were negatively correlated with slope and number of Douglas-fir platforms (Table 36c).

Multiple regression models using transect habitat data selected elevation and slope significant predictors of variation in total and occupied activity (Table 37), Elevation and slope explained 49% of the variation in total activity and elevation explained 23% of the variation in occupied activity (Table 37).

Effect of elevation

Occupied stands in my study area occurred between 600 and 1200 m in elevation. Activity and the proportion of occupied stands were greatest in sites between 701-900 m and decreased with increasing elevation above these elevations (Fig. 13).

Suitability of Habitat Types for Marbled Murrelets

Average platform density ranged from 27.5 platforms/ha in the CWHxm to 91.7 platforms/ha in the CWHdm (Table 38). Mossy platforms were not found in the CWHxm sites. These 2 low-elevation variants were not sampled enough to characterise their suitability. Platform and mossy platform densities were higher on average in the MHmm1 than in the CWHvm2, both for all sites combined and zonal sites only (Table 38). However, there was substantial variation in the density estimates for these subzones which ranged from 0-310 platforms /ha in the CWHvm2 and from 10-361 platforms/ha in the MHmm1. Given these ranges of platform density, BEC variant classification is not a useful predictor of habitat suitability for the sites that I sampled.

Measures of platform density for representative habitat types vary among different geographical locations that I surveyed. Zonal sites in the CWHvm2 variant differed in total platform density and mossy platform density among landscape units (Kruskal Wallis Anova; P=0.009 and P=0.001, respectively). Sites in the Brittain Landscape Unit had significantly higher densities of platforms than in any of the other landscape units (Table 39).

In the MHmm1-01 site association there were no significant differences in in total platform density and mossy platform density between the Sechelt and Brittain landscape units (Mann-Whitney U-test; P=0.08 and P=0.46, respectively), but both densities were higher in the Brittain Landscape Unit (Table 39).
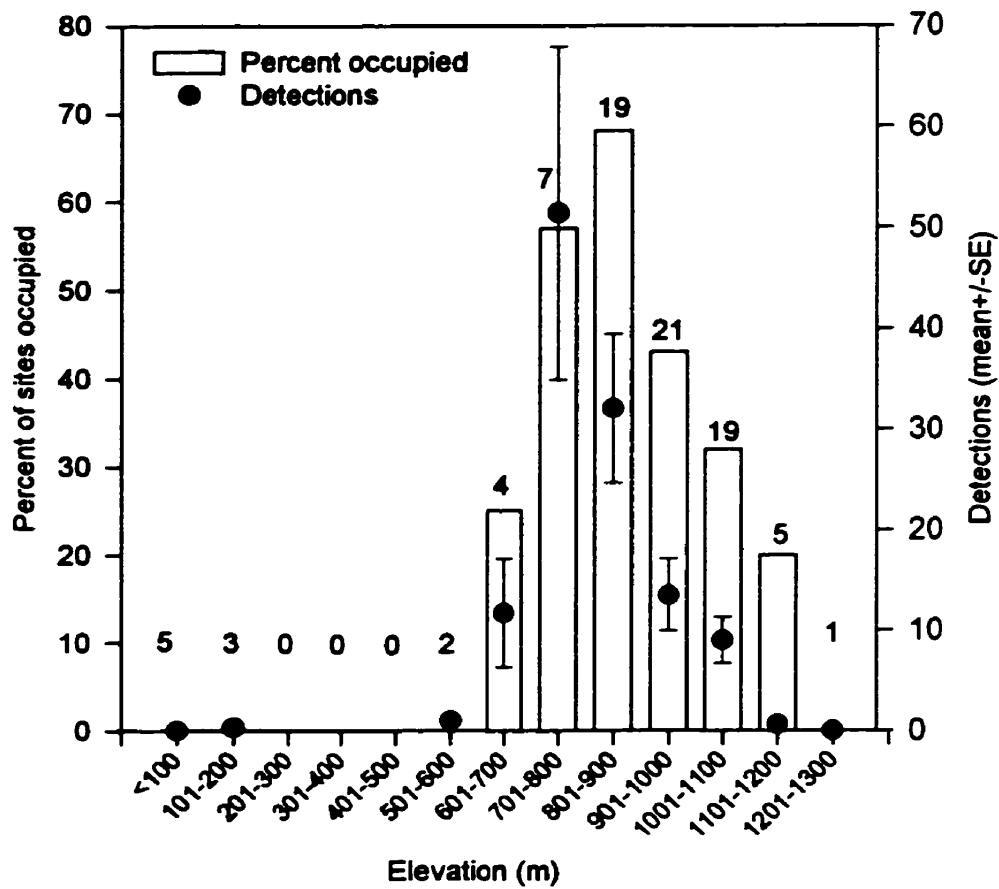
Figure 13. The percentage of occupied sites and murrelet activity summarized for 100-m intervals in elevation. Sample size is given above each bar. Data are from 86 sites surveyed in 1997.

Table 38. Platform and mossy platform density in 4 biogeoclimatic variants. Data are from 1996 and 1997. Mean and range presented for vegetation plots.

	Variant			
	CWHxm	CWHdm	CWHvm2	MHmm1
All sites				
n	5	2	89	20
Total platforms/ha	27.5 (0-66)	91.7 (61-122	62.5 (0-310)	86.6 (10-361)
Moss2 platforms/ha	0.0	15.3 (15.3)	34.6 (0-280)	46.6 (0-213)
Zonal sites				
n	4		36	15
Total platforms/ha	21.6 (0-66)		67.3 (0-310)	100.5 (25-361)
Moss2 platforms/ha	0.0		39.8 (0-280)	55.7 (0-213)

Table 39. The availability of nesting structures in CWHvm2-01 and MHmm1-01 site associations within 4 landscape units on the Sunshine Coast, 1997.

| Site association | Bunster | Landscape Unit | | Salmon |
| | | Brittain | Sechelt | |
		Mean ± (SE)		
CWHvm2-01				
Total platforms/ha	36.9 (6.6)	144.2 (42.8)	59.6 (17.8)	45.9 (25.5)
Moss2 platforms/ha	14.8 (3.6)	123.8 (38.2)	7.1 (3.1)	29.1 (29.1)
n	12	6	7	3
MHmm1-01				
Total platforms/ha		163.1 (51.9)	73.9 (15.8)	35.6
Moss2 platforms/ha		89.7 (36.7)	43.3 (17.3)	20.4
n		5	8	1

There were no consistent differences in suitability between the CWHvm2-01 and MHmm1-01 site associations within landscape units. I did not find greater densities of platforms or mossy platforms in the CWHvm2-01 (Table 39). In the Brittain Landscape Unit, total platforms were higher in the MHmm1-01 and mossy platforms were higher in the CWHvm2-01 but neither of these results were significant (Mann-Whitney U-test; P=0.5 and P=0.67, respectively). In the Sechelt Landscape Unit Moss2 platforms were more abundant in the MHmm1-01 (Mann-Whitney U-test, P=0.04).

Elevation

Total platform density and Moss2 platform density were highest in sites in the 701-800 m elevation range (Fig. 14). Lower elevation sites had small sample sizes but had low densities of Moss2 platforms. Sites between 801-1200 m had similar densities of mossy and total platforms.

Site associations

Sites surveyed in 1997 included samples from all 10 site associations in the CWHvm2 variant (Table 40). Zonal sites (CWHvm2-01) were the most common making up 41% of 87 sites. The majority of sites (91%) had very poor-medium nutrient regimes. Moisture regimes included moderately dry (6.3%), slightly dry (20.3%), fresh (42.2%), moist (6.3%), very moist (10.9%), and wet (4.7%). Four sites in the driest site association, 02 HwPl-Cladina, had the lowest densities of total platforms. The highest densities of total platforms and Moss2 platforms recorded were in site associations 06 and 07/08 (Table 40). Platform densities were highest in fresh and moist sites, and lower in sites with drier or wetter moisture regimes. Sites with rich-very rich nutrient regimes had similar or higher densities than poor-medium sites with the same moisture regime (Table 40). Mossy platform density was highest at sites with fresh to very moist moisture regimes (Table 40).
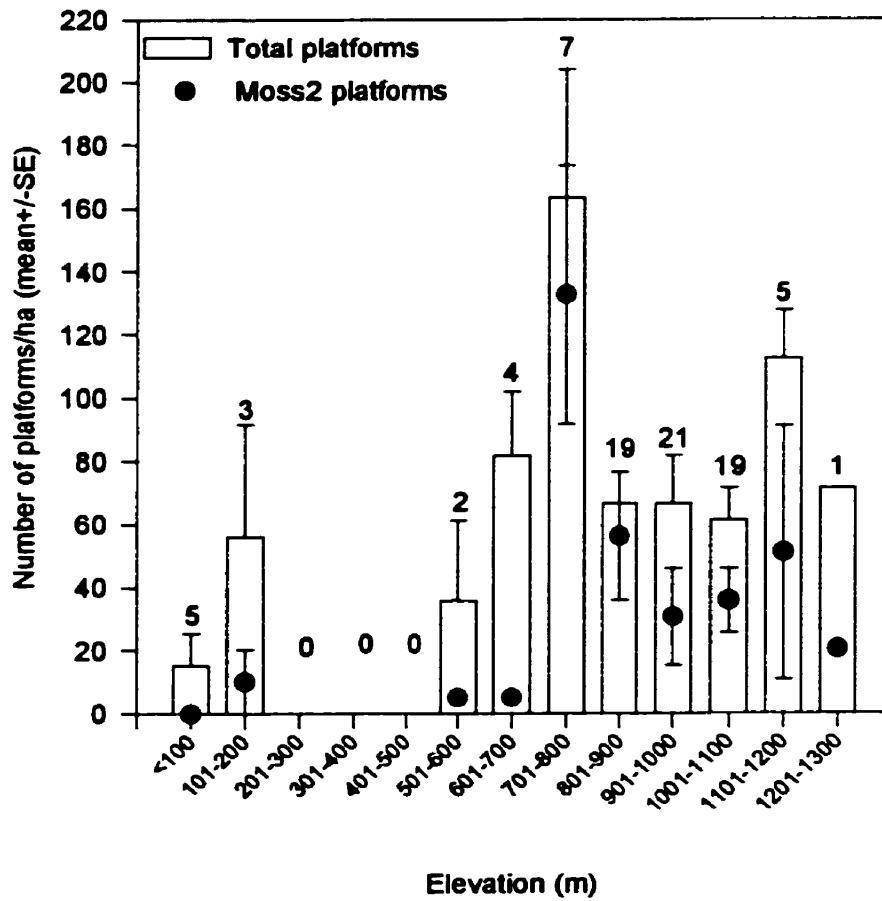
Figure 14. Platform and mossy platform density (platforms/ha) in relation to elevation. Mean and standard error are plotted for each 100-m elevation category. Sample size is shown above the bar. Data are from sites surveyed in 1997.

Table 40. Platform density and mossy platform density for site associations in CWHvm2 and MHmm1. Sites are arranged with very poor-medium nutrient level on the left and rich-very rich sites on the right.

CWHvm2

Soil moisture regime	Soil nutrient regime					
	Very poor-medium			Rich-very rich		
	Site series	Platforms/ha Total mean (SE) Moss2 mean (SE)	n	Site series	Platforms/ha Total mean (SE) Moss2 mean (SE)	n
Moderately dry	02 HwPl Cladina	6.4 (3.8) 0.0	4	-		
Slightly dry	03 HwCw Salal	49.8 (11.0) 6.8 (2.7)	18	04 CwHw Swordfern	106 36	1
Fresh	01 HwBa Blueberry	67.3 (11.2) 39.8 (9.6)	36	05 BaCw Foamflower	66 31	1
Moist	06 HwBa Deerfern	142.6 (48.5) 112.1 (51.1)	4	07 BaCw Salmonberry	150.2 (44.5) 100.3 (50.4)	4
Very moist	09 CwYc Goldthread	30.2 (8.8) 16.6 (6.9)	15	08 BaSs Devil's club	86.6 (50.9) 58.6 (48.4)	2
Wet	10 Pl Sphagnum	10.2 (10.2) 10.2 (10.2)	2	11 CwSs Skunk cabbage	10 0	1

119

MHmm1

	Soil nutrient regime					
	Very poor-medium			Rich-very rich		
Soil moisture regime	Site series	Platforms/ha Total mean (SE) Moss2 mean (SE)	n	Site series	Platforms/ha Total mean (SE) Moss2 mean (SE)	n
Moderately dry	-			-		
Slightly dry	02 HmBa Mountain-heather	71.3 20.4	1	-		
Fresh	01 HmBa Blueberry	100.5 (21.7) 55.7 (15.9)	15	03 BaHm Oak fern		0
Moist	04 HmBa Bramble	40.7 15.3	1	05 BaHm Twisted-stalk	30.6 (20.4) 5.1 (5.1)	2
Very moist	06 HmYc Deer-cabbage		0	07 YcHm Hellebore		0
Wet	08 HmYc Sphagnum		0	09 YcHm Skunk cabbage	50.9 50.9	1

120

I had enough samples from the Bunster Landscape Unit to examine differences in suitability among site associations in the CWHvm2 variant. The 4 site associations that I examined all had poor-medium soil nutrient regimes but varied in soil moisture (Table 41). Total number of platforms did not vary significantly with moisture regime but numbers of mossy platforms did vary significantly with moisture regime (Table 41). The driest sites (03) had similar numbers of total platforms but very few mossy platforms. The highest numbers of mossy platforms occurred at moist and very moist sites (Table 41). Numbers of total and occupied detections followed a similar trend and were highest in the site association with the highest density of total and mossy platforms (CWHvm2-06).

Suitability of Tree Species

Douglas-fir, yellow-cedar and western redcedar had the highest number of platforms with an average of 3.6-4.1 platforms/tree (Table 42). Although Douglas-fir had the highest number of platforms/tree, most platforms were covered with Lichen/litter and mossy platforms were infrequent on this species. Both western redcedar and yellow-cedar had predominantly mossy platforms and a high total number of platforms, making them highly suitable nest trees for Marbled Murrelets. Western hemlock ranked fourth in number of platforms followed by Pacific silver fir and mountain hemlock. Mistletoe platforms were infrequent for all tree species in my study area. Platforms covered with Lichen/litter predominated for Douglas-fir and mountain hemlock trees.

Trees <51 cm in diameter rarely have platforms. Only 4% of all trees with platforms fall within this diameter range (Fig. 15). The minimum and typical diameters at which platforms occur varies among tree species. No Douglas-fir trees <51 cm in diameter had platforms and 70% of Douglas-fir trees with platforms were between 76-125 cm dbh (Fig. 16). Thirty-five percent of Douglas-fir trees in the 51-75 cm dbh class had platforms, which is a high proportion compared to other species (Fig. 16). All Douglas-fir >100 cm in dbh had platforms, but trees this size were uncommon in the study area (5% of all Douglas-fir). Western redcedar trees with platforms ranged in dbh from 28-200 cm with 77% of platform trees >75 cm in dbh (Fig. 15). After redcedar

Table 41. Platform density and murrelet use for 4 BEC site associations in the CWHvm2 variant within the Bunster Landscape Unit. Data are mean (SE) for each site association.

	03 HwCw-Salal	01 HwBa-Blueberry	06 HwBa-Deer fern	09 CwYc-Goldthread	Kruskal Wallis Anova F, P
Soil moisture	Slightly dry	Fresh	Moist	Very moist	
Platforms /ha	10.8 (2.8)	7.3 (1.3)	18.7 (2.6)	7.4 (3.0)	2.2, P=0.10
M2 platforms/ha	0.7 (0.3)	2.9 (0.8)	12.3 (3.8)	5.6 (2.8)	7.6, P<0.001
Total detections	4.7 (1.7)	12.8 (3.9)	38.4 (8.2)	16.5 (5.5)	17.7, P=0.001
Occupied detections	0.6 (0.3)	0.9 (0.4)	5.3 (3.7)	1.4 (0.6)	8.8, P=0.032
n	12	11	3	7	

Table 42. Mean characteristics of 6 tree species. Only trees with platforms were included from vegetation and climbing plots.

	Douglas-fir n=82	Western redcedar n=67	Western hemlock n=155	Yellow-cedar n=611	Pacific silver fir n=40	Mountain hemlock n=83
Diameter (cm)	94.9	115.7	80.3	87.5	75.4	71.8
range	50-160	50-200	30-155	22-192	43-130	33-117
Height (m)	31.5	34.3	25.6	24.8	30.5	24.5
range	16-52	15-60	14-60	9-40	12-52	12-40
Platforms/tree	4.1	3.6	2.6	3.9	2.1	2.1
range	1-9	1-13	1-13	1-20	1-7	1-7
Mistletoe platforms/tree	0.2	0.2	0.2	0.2	0.2	0.1
range	0-2	0-2	0-4	0-6	0-3	0-1
Lichen platforms/tree	2.4	0.1	0.8	0.1	0.4	1.2
range	0-9	0-4	0-7	0-5	0-4	0.2
Mossy platforms/tree	0.1	2.3	0.6	3.2	1.2	0.4
range	0-3	0-13	0-7	0-9	0-6	0.1
Exposed platforms/tree	1.3	0.6	0.6	1.1	0.7	0.7
range	0-5	0-4	0-4	0-8	0-4	0.1
Covered platforms/tree	0.7	1.1	0.5	0.7	0.3	0.2
range	0-4	0-5	0-4	0-9	0-4	0-3
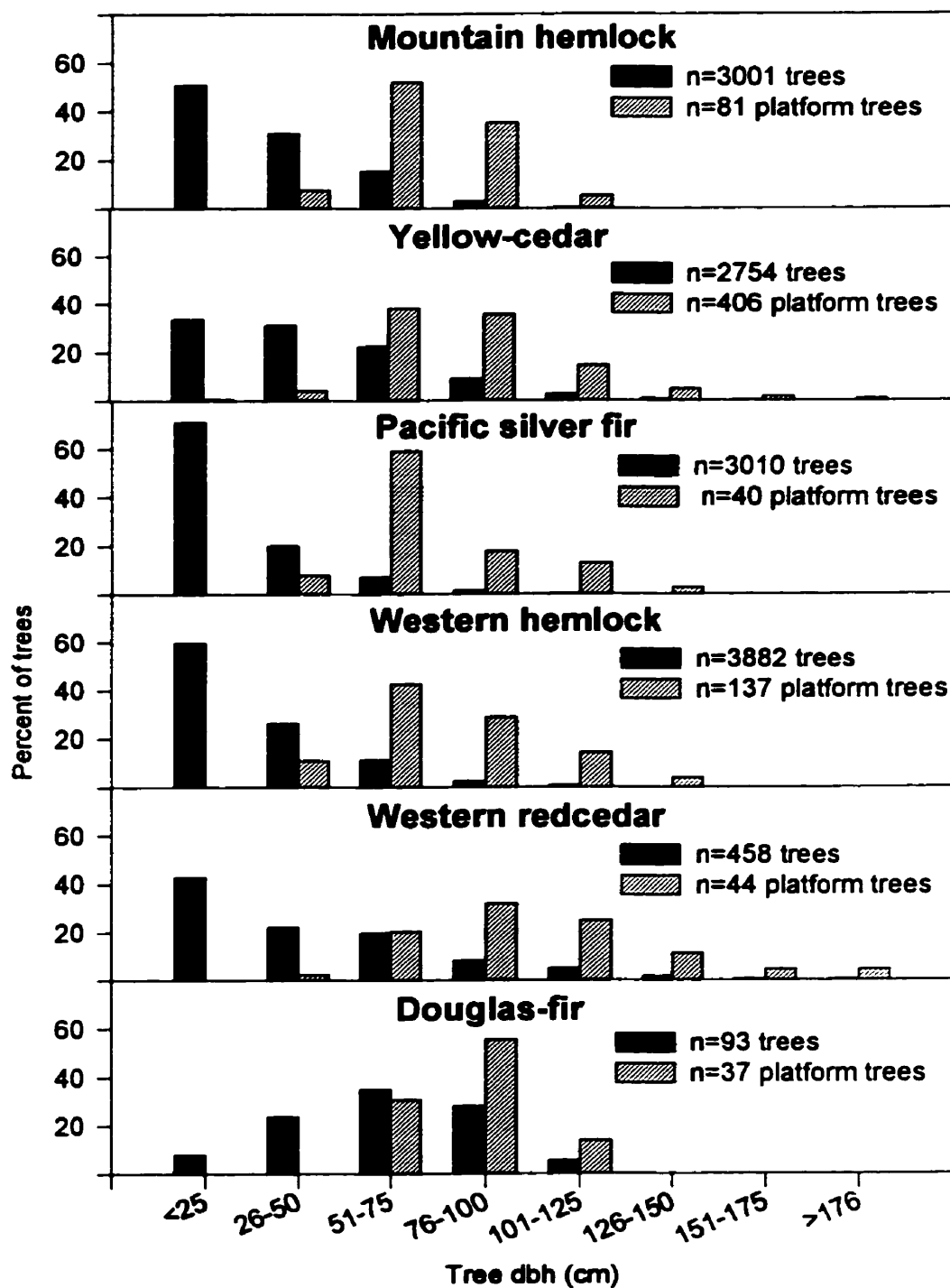
Figure 15. Frequency distributions for trees and platform trees by dbh size class. Data are for 6 tree species from vegetation plots sampled between 1995-1997 in the Sunshine Coast Forest District. Dark bars are all trees >10 cm dbh. Platform trees are trees with at least one estimated platform.
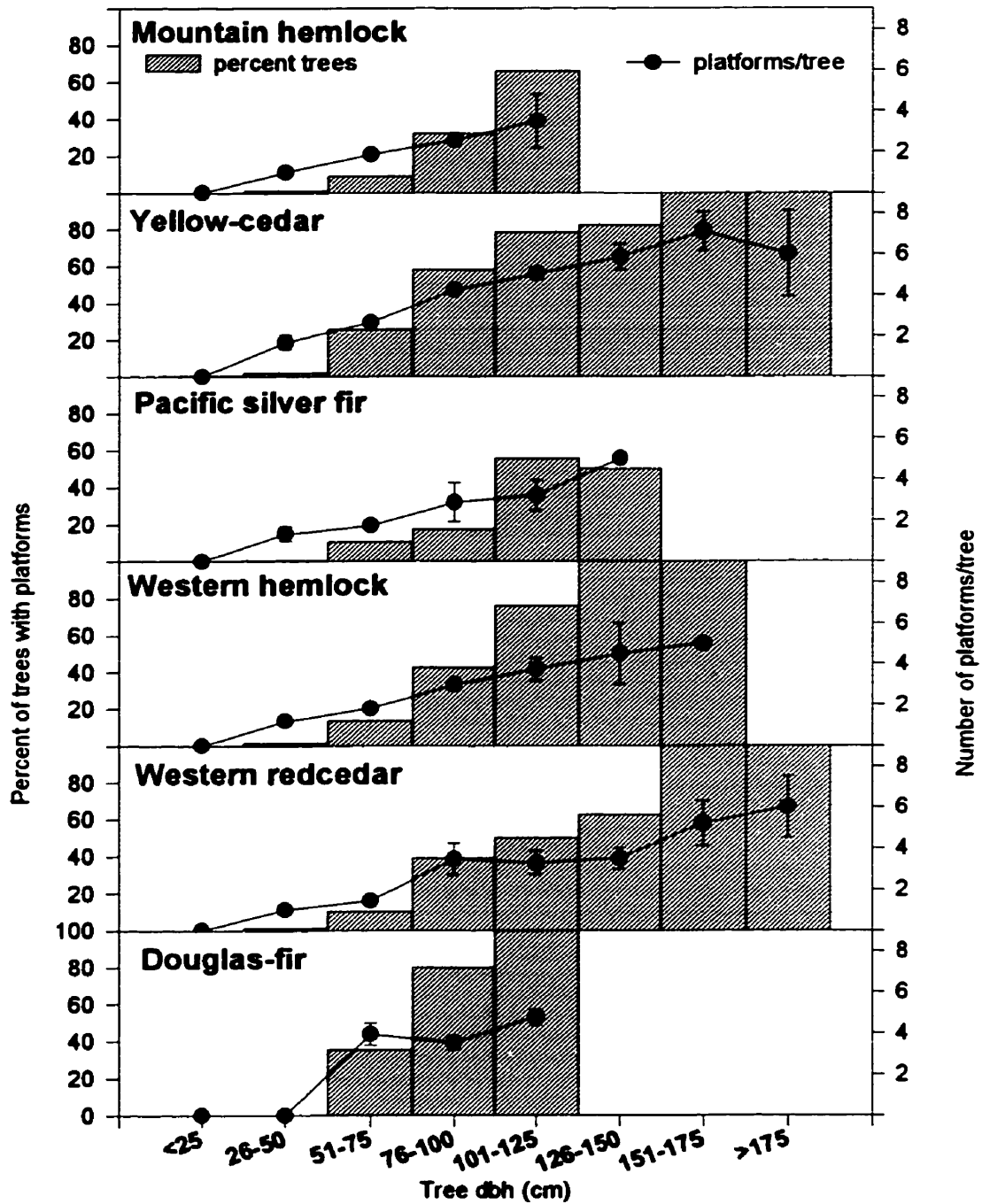
Figure 16. Percentage of trees with platforms (bars) and average number of platforms per tree (points) for tree diameter classes of 6 tree species. Platform trees are trees with at least one estimated platform.

trees reach 101 cm in dbh, more than 50% have platforms and 100% of those >150 cm in dbh have platforms. Both Douglas-fir and redcedar were the least common conifer species in plots sampled because these species are more typical of low elevations. For both of these low elevation species, most platform trees occur between 76-100 cm dbh, whereas for high elevation tree species a greater proportion of platform trees occur in the smaller 51-75 cm dbh class (Fig. 15). Most platform trees for all species are between 50-100 cm in diameter (Fig. 15).

Larger diameter trees, although uncommon, are an important source of platform structures because both the proportion of trees with platforms and the number of platforms per tree increase with diameter (Fig. 16). This trend is similar for all species. Yellow-cedar, western redcedar and western hemlock in the larger diameter classes all had more than 5 platforms per tree. Mountain hemlock and Pacific silver fir trees had the lowest proportions of trees with platforms and lower numbers of platforms per tree compared to other species. Even at their largest diameters, these species never reached more than 60% with platforms whereas all the other species had 100% with platforms at the largest diameter categories (Fig. 16).

Discussion

Several habitat variables were associated consistently with murrelet status. Sites where murrelets were 'not detected' had steeper slopes, greater gap area and were at lower elevations. Sites where murrelets were 'occupied' had more mossy platforms. Numbers of total, mossy, and yellow-cedar platforms appeared to be greater at occupied sites than at present or not detected sites but these were not significant in 1995 and 1996 (Tables 32, 33, 34). Not detected sites were lower in elevation and had greater densities of Douglas-fir platforms than present or occupied sites. Data from 1996 had small samples of sites with not detected or present status and there was no significant difference in habitat variables with status.

Habitat variables that were important for differentiating status were also important predictors of the amounts of total activity and occupied activity. These included mossy platforms, elevation and slope in 1997; number of platform trees and number of mossy

platforms in 1996; and mean tree diameter, elevation, and slope in 1995. Stepwise multiple regression models explained 23-71 % of the variation in amounts of total and occupied activity. A portion of the unexplained variation is probably due the effects of cloud cover and date that were not accounted for in the models that I used (Beasley *et al.* 1997, Rodway and Regehr 1998b). Murrelet activity varies seasonally (Chapter 1) and the duration and number of detections increases with cloud cover (Rodway et al. 1993a, Naslund and O'Donnell 1995). I did not include these factors in models because I used mean or maximum activity recorded over 4 surveys that were distributed throughout the breeding season.

Platform density, and in particular mossy platform density, are key features of murrelet nesting habitat in Alaska (Kuletz *et al.* 1995), British Columbia (this study, Burger 1995b), and Washington (Hamer 1995). Platforms are important in the southern part of the murrelet's range, but there they may be litter covered instead of moss covered. In contrast to my study area, occupied sites in Oregon had greater densities of large diameter Douglas-fir trees than unoccupied sites (Grenier and Nelson 1995). The importance of platforms is consistent throughout the Marbled Murrelets' range but the tree species providing these platforms vary among regions.

My finding that occupied sites are higher in elevation than not detected sites likely reflects the rarity of potential habitat at low elevation in the highly modified landscape of my study area. Other studies that found greater activity of murrelets at low elevation were conducted in areas with substantial amounts of low elevation old-growth forest (Rodway *et al.* 1993a,b). In my study area, distributions of occupancy and activity by murrelets where late-successional forests are more intact (600-1200 m) indicate that the lowest elevations of this range have the highest occupancy and activity (Fig. 13).

Sites surveyed in 1997 where murrelets were not detected had a greater gap area than sites where murrelets were present or exhibited occupied behaviour. Analysis of gap area was not done for 1995 and 1996 because in these years, I used a canopy densiometer to measure canopy closure and this method is biased (Cook *et al.* 1995). My results are consistent with other studies that found greater canopy closure at occupied sites in forests from Alaska to California (Grenier and Nelson 1995, Hamer 1995, Kuletz *et al.* 1995, and Ralph *et al.* 1995). In Chapter 2, I show that element level selectivity for gaps near

murrelet nest trees did not result in significantly less forest cover at nest patches. This is further evidence that murrelets do not prefer more open forests although they require an opening to access their nest sites. This result occurs in spite of the bias that murrelet detections and especially occupied detections are more frequent at sites with less canopy cover due to increased visibility of the birds (O'Donnell 1995, Rodway and Regehr 1998a). In my study, murrelet activity is higher in closed canopy forest in spite of the fact that it is more difficult to detect murrelets in these locations. There is probably an even greater difference in canopy closure between used and unused sites due to this bias.

Habitat variables assessed from transects in 1996 were more strongly correlated with activity than similar measurements from plots (Table 34b). Transects sample habitat variables over an area similar to that recorded by activity surveys. Rodway *et al.* (1993b) pointed out that activity is measured over an area several hundred metres wide and forest characteristics vary within that distance. Habitat plots (25-m radius) are not large enough to encounter this variation. In areas where densities of platforms are lower or more variable, plots are likely to be less precise. Future habitat assessments for inland activity of Marbled Murrelets at the stand level should use transects or several random plots.

Suitability of Biogeoclimatic Variants and Site Associations

The two low elevation coastal BEC variants, CWHxm and CWHdm, were poorly represented in habitat samples from the Desolation Sound area during the 3 years of my study. I found no reference to these habitats being used by murrelets in other studies in B.C., but they are being evaluated on southern Vancouver Island (A. Burger pers. comm.). Both variants had platform densities within the range of densities at sites occupied by murrelets in the CWHvm2 and MHmm1 (Table 38), however very little or no murrelet activity was recorded at these sites. Hypotheses to account for the low use of these habitats include the following: insufficient samples, difficulty detecting low densities of birds, platform types are not suitable, and habitat patches are too small and fragmented (see Lougheed *et al.* 1998a). Sites in the CWHxm had the lowest density of platforms, and high proportions of Douglas-fir trees providing platforms. Douglas-fir trees in my study had very low occurrence of moss cover on platform limbs and I did not

find mossy platforms in the CWHxm subzone (Table 38). Murrelets nest on Douglas-fir limbs without moss in the southern part of their range, but most nest sites in B.C. are associated with mossy branches (Hamer and Nelson 1995b, Chapter 2).

Late successional stands in the CWHxm and CWHdm are very rare in my study area because most low elevation late-successional coastal forests have been logged on the Sunshine Coast. The late successional stands that remain at this elevation are small and patchily distributed which may diminish use of these habitats by murrelets. Forest stands sampled in the CWHdm had high densities of platforms (61-122/ha) and mossy platforms were present although less frequently than in the higher elevation variants. Because most remaining late successional stands at low elevation are small, they do not meet the minimum requirements for Wildlife Habitat Areas and have not been investigated by inventory crews. Either tree climbing, activity surveys or telemetry research could determine if these low elevation habitats are used by murrelets. This information is needed to determine if murrelets continue to use these habitats.

At the present, most of the remaining habitat and nesting murrelets occur within the CWHvm2 and MHmm1 BEC variants. It is within these habitats that immediate conservation efforts for murrelets on the Sunshine Coast should be focused. Based on the data in this chapter, I cannot conclude that one of these variants is more suitable than the other for murrelet nesting. The average platform density is higher in the MHmm1 although both variants have wide, overlapping ranges of platform densities. It may have been difficult to detect differences between these habitats because most sites were located between 900-1100 m in elevation where the transition between these two variants occurs. Variants like the CWHvm2 and MHmm1 are represented on maps as zones that occur in distinct elevation bands. In practice however, there is a gradual transition between these variants, and the gradation between habitats depends on many factors including slope, aspect and local environmental conditions. Perhaps habitat suitability was not distinctly different between these two variants because most samples came from the transitional habitats in the upper CWHvm2 and lower MHmm1.

I expect for several reasons that a broader sample of these variants would indicate that the lower elevation CWHvm2 has greater suitability for Marbled Murrelets. First, platform and mossy density was greatest for sites that occurred between 701-800 m

elevation which is in the middle elevation range of CWHvm2 (Fig. 14). This suggests that if more habitat samples came from this elevation it would increase the overall suitability of the CWHvm2. Second, at higher elevations in the MHmm1, the habitat grades into more open parkland (Green and Klinka 1994). From the 1997 data, I found that sites where murrelets were not detected had more gap area than sites where murrelets were present. Hence, I expect less use by murrelets of higher elevation habitats in the MHmm1, as sites become more open and less forested (Fig. 14). Third, analyses of tree species showed that mountain hemlock trees were the lowest ranked species in terms of number of platforms and mossy platforms. The MHmm1 zone by definition has more than 50% of hemlock as mountain hemlock (Green and Klinka 1994). This species increases in abundance at higher elevations while other species more suitable to murrelets become less common. Given this transition, I expect platform density to decrease at higher elevation sites in the MHmm1. Increased sampling over a wider range of elevations (including more sites between 600-800 m and above 1100 m) is needed to test these hypotheses.

Assignment of a suitability ranking to BEC variants has been attempted as a management tool to prioritise options for conservation of murrelet habitat. However little data exist that demonstrate higher use or greater suitability of particular variants for murrelets. Results in this chapter show that platform density is highly variable within zonal site associations of a variant (Table 38). Furthermore, the suitability of variants differed among landscape units within the Sunshine Coast Forest District (Table 39). Setting aside a particular habitat type in one location may not confer the same benefits to nesting murrelets as the same amount of this habitat in a different location. Given the available evidence, I conclude that BEC variants should not be used as an index of suitability. Site specific information is required to determine if habitats provide nesting structures and if these sites are used by murrelets. Several variants that occur in the Sunshine Coast District have not been sampled including the CWHms1, CWHvm1, and MHmm2. When more information becomes available ranking of BEC variants may be possible for specific regions.

Within a BEC variant, platform density varies among site associations with different moisture regimes. The lowest densities of platforms were in the driest and

wettest site associations. The highest densities of mossy platforms were in sites with intermediate moisture regimes. These differences probably result from differences in the productivity and tree species composition of these site associations. In drier site associations, Douglas-fir trees provide most of the platforms, but few mossy platforms. In wetter site associations yellow-cedar and western hemlock provide most of the platforms. Most of the variation in platform density and mossy platform density results from the density of trees with platforms and the species of trees. For future habitat assessments, these variables, which are simpler to obtain than platform counts for each tree, could be used to rank the suitability of site associations and stands.

Murrelet activity and occupied activity reflect differences in suitability of site associations (Table 41). Based on activity, murrelets appear to prefer site associations with high densities of mossy platforms (CWHvm2-06, CWHvm2-09). This is consistent with patch level selection that I observed for nest sites (Chapter 2). Activity of Marbled Murrelets appears to reflect habitat quality among site associations within a watershed or landscape unit. However, the suitability and use of a site association differs among landscape units and likely depends on the amount and type of available habitat and the landscape context of different areas.

Suitability of Tree Species

Marbled Murrelets nest in 5 of the 6 species of conifer trees that occurred in my study plots (Chapter 1, C. Conroy pers. comm.). Both western redcedar and yellow-cedar ranked the highest in characteristics suitable for nest sites (number of platforms and number of mossy platforms). In part, because of extensive logging at low elevation, yellow-cedar was the most frequent platform tree encountered in the areas that I sampled and was 10 times more abundant than redcedar. Given the high suitability and abundance of yellow-cedar it is not suprising that over 90% of the murrelet nests found in the study area were in this species (Chapter 1). Although yellow-cedar is the most common nest tree in my study area, use or suitability of this species by murrelets has not been documented outside of the Sunshine Coast. In southern B.C. yellow-cedar is extremely long lived and is the oldest tree species in Canada (Alaback 1991). More information on

the characteristics of yellow-cedar elsewhere in their range is needed to determine the potential of this species to provide nest sites for murrelets beyond south coastal B.C.

Characteristics of redcedar indicate that it has high potential as nest trees for murrelets. This species should not be overlooked as a potential nest tree, especially where it is more abundant. Recent nests (n=8) located by telemetry in Desolation Sound included 3 redcedar trees at low elevation sites (C. Conroy pers. comm.). Both yellow-cedar and redcedar reach large diameters, are long lived and persist through many disturbances (Alaback 1991). These characteristics may be favoured by murrelets, which may return to the same nest site or nest tree throughout their reproductive lifetime (Chapter 1).

Western hemlock is the most abundant tree species and second most abundant platform tree at the sites that I studied. This species ranked fourth out of the 6 species in platform and mossy platform abundance. In Washington and Oregon, western hemlock is considered one of the most important tree species for murrelets because it has high numbers of mistletoe created platforms (Hamer 1995). Mistletoe platforms were uncommon on all tree species in my study area (Table 42).

Douglas-fir trees were ranked highest in platform abundance but lowest in abundance of mossy platforms. Two nests on the Sunshine Coast have been found in Douglas-fir and in both cases they were located on limbs with thick moss pads. Douglas-fir trees with or without moss are an important nest tree species for murrelets in the southern part of their range (Hamer and Nelson 1995b).

Mountain hemlock and Pacific silver fir ranked lowest in suitability for murrelets in my study area and in Washington (Hamer 1995). One nest site in Desolation Sound was located in a mountain hemlock tree, but nests have not been found in Pacific silver fir here or elsewhere. Both of these species never reached more than 60% of trees with platforms even in the largest diameters. These species do not develop branches as large in diameter as other conifers at high elevation. As well, Pacific silver fir branches often slope downward at a steep angle. I have observed large diameter Pacific silver fir with large mossy limbs at low elevation sites in Desolation Sound, but at higher elevations it rarely has characteristics suitable for murrelet nests.

My data on the suitability of tree species are based on estimates of platform numbers from the ground and their interpretation is affected by any bias in these estimates (Appendix 2). A comparison of ground estimates with measurements from climbed trees shows that the number of platforms is over-estimated for small diameter trees and under-estimated for large diameter trees. Ground estimates reach a maximum of about 10 platforms/tree whereas actual counts of platforms increase with diameter up to as many as 45-50 platforms/tree (Appendix 2). Given this bias, I expect that the actual number of platforms is lower for small diameter trees and higher for large diameter trees than the estimates shown in Figure 16. Large diameter trees contribute more platforms and smaller diameter trees contribute fewer platforms than shown by Figure 16.

Conclusion

Density of platforms is associated with habitat use (activity and status) by Marbled Murrelets. Elevation was an important variable for describing murrelet use and platform availability, but the availability of habitat in relation to elevation in my study area affects this interpretation. Murrelets use higher elevations where late successional forests are available, but within the range of available habitat the lower elevation stands have higher activity and availability of platforms. In my study, I did not find differences in murrelet activity among BEC variants. BEC variants in my study were not consistent predictors of platform availability and their use and characteristics varied among landscape units. Selectivity across the full range of variants in my study area could not be expressed by murrelets because of the limited types of variants available for nesting murrelets. The structural characteristics of forests vary within a variant and at the site association level. This variation is due largely to variation in species and density of trees. Murrelet activity is highest in site associations with the highest density of Moss2 platforms. As with variants, use and characteristics of these site associations vary amongst landscape units. Tree species within my study area vary in their ability to provide suitable nesting structures for murrelets. Structural characteristics of these trees likely vary among regions and therefore my results may only apply to the Sunshine Coast region. However, within my study area, species and density of trees are surrogate

variables of microsite and element level selection for nest sites and could be used to evaluate nesting habitat for Marbled Murrelets.

Throughout their range Marbled Murrelets are flexible in the forest types and tree species that they use for nesting. Forest types and features of stands and landscapes that are related to murrelet use are important for identifying habitat at coarse scales. However, it is unlikely that such co-associated variables can be applied over large areas of the province. The use and suitability of habitats for Marbled Murrelets varies regionally and depends on local forest and marine conditions. Management of murrelet habitat requires local information on patterns of habitat use and availability. This information has not been collected over most of the range of Marbled Murrelets within B.C.

Chapter 4. Recommendations for Managing Nesting Habitat of Marbled Murrelets in South-coastal British Columbia

Introduction

Marbled Murrelet populations are listed as endangered or threatened in the southern portion of their range due to the loss of nesting habitat (Rodway 1990, Ralph *et al.* 1995). Forest harvesting decreases the availability and quality of nesting habitat and alters its distribution within landscapes. Each of these factors has consequences for populations of Marbled Murrelets. Habitat loss could have several effects on murrelets and many of these are difficult to document. Loss of nesting habitat could displace breeding birds resulting in increased numbers of non-breeding birds or crowding in remaining suitable habitat (Ralph *et al.* 1995). Crowding or supersaturation of remaining habitats can alter intra- and inter-specific competition for resources (Saunders *et al.* 1991). Logging of nesting habitat during the breeding season has killed adult birds, chicks and eggs (Carter and Sealy 1987). Indirect mortality may result from disturbance of nesting birds and from increased predation in fragmented habitat (Nelson and Hamer 1995a, Hamer and Nelson 1998). As the distribution of available habitat is altered, energetic costs may increase if birds must nest further inland or at higher elevations. Opportunities for breeding and natal dispersal are constrained by the distribution of available habitat (Divoky and Horton 1995). All of the above hypothesized or documented effects could influence the number of Marbled Murrelets and the dynamics of their populations.

In Chapter 1, I described the activity and behaviour of murrelets at nests and in stands where nesting occurs. Murrelets in my study area have low nesting success and a large proportion of nests failed because of predation. In addition to incubation and chick rearing, murrelets visited nest sites before nesting began, after nests failed, and in years when nests were not used. This behaviour suggests that nest sites are important resources. Attendance at nest sites may function to defend nests, maintain familiarity with nests, or to secure their use in future years. In Chapter 2, murrelets selected for the structural characteristics of nesting habitat at the microsite, element and patch scales. Selection for platforms, or potential nesting structures, was expressed at all scales. Murrelets selected

for the juxtaposition of cover and openings in their nesting habitat. Nests had cover above the nest, and were located in large diameter trees next to canopy gaps. Murrelet activity and habitat use at coarse scales reflected the strong selectivity for platforms at fine scales (Chapter 3).

In this chapter, I discuss the present management of habitat occurring in the Bunster Range and its effects on Marbled Murrelets. I propose recommendations for managing and conserving the nesting habitat of Marbled Murrelets at the landscape scale and for dealing with nest trees within areas planned for forest harvesting. Management of habitat should be approached with both a short term and long term perspective. In the short term, it is important to retain critical habitats for the present population. In the long term, management should plan for the recruitment of habitat and to enhance the suitability of second rotation forests.

Current Management of Nesting Habitat in the Bunster Range

During my study, nest trees of Marbled Murrelets were found in stands with approved or proposed cutting plans. Currently, there are no requirements to manage or conserve the nesting habitat of Marbled Murrelets when it is in conflict with proposed logging. The B.C. Ministry of Forests voluntarily established interim strategies for murrelet nests in the Bunster Range, in recognition of the research value of these sites. The interim strategies consisted of: 1) a freeze on approvals of new cutblocks within the Bunster Range until a management plan for the area is developed; and 2) retention of nest trees as wildlife trees or wildlife tree patches where nest trees occur in previously approved cutblocks.

Since the start of my study, logging has removed or altered the habitat near 10 nest trees of Marbled Murrelets (Table 43). These nests were monitored to determine if murrelets would re-use these nest trees in the same or following seasons. Although based on a small, short-term sample, they are the only available data and offer preliminary insight into the effects of logging near murrelet nests.

Three nest trees were left as single trees (Nests 16, 17) or in a small group of trees (Nest 49) within cut blocks (Table 43). Murrelets landed in Nest 16 during May 1997 as

Table 43. Modifications to habitat at 10 nest trees of Marbled Murrelets in the Bunster Range.

Nest tree	Pre-modification distance to edge (m)	Date and type of modification	Post-modification distance to edge (m)	1997	1998
16	107	May 1997; single tree retained	0	Not used	Not used
17	15	May 1997; single tree retained	0	Not used	N/A tree blew down
18	70	Winter 96/97; retained on block edge	6.5	Not used	Not used
19	27	Winter 96/97; cut down	N/A	N/A	N/A
28	503	August 1998; wildlife tree patch 24.1 ha	~30		
29	500	August 1998; wildlife tree patch 24.1 ha	~30		
30	471	August 1998; wildlife tree patch 24.1 ha	~30		
38	166	May 1998; retained in riparian reserve	5		Not used
39	151	May 1998; retained in riparian reserve	7		Not used
49	269	September 1997; wildlife tree patch <0.2 ha	0		Not used

the surrounding forest was being cut. Nest 17 was located on a hill and when I visited the nest in January 1998, the tree was exposed to high winds. All of the large moss pads on the tree limbs had blown off. On a return visit in May 1998, the tree had blown over. In 1998, Nests 16 and 49 remained standing but were not re-used. Three nest trees (Nests 18, 38, 39) were left <10 m from new clearcuts between 20 and 30 ha in size. Re-use of these nests was not observed in the year of cutting or in the following year. Three nest trees (Nests 28, 29, 30) were left within 30 m of a clearcut in a 24-ha Wildlife Tree Patch. The cutting in this stand did not occur until August 1998, re-use of these nest trees should be evaluated in 1999 and following years.

During my study, 5 nest trees were found on the edges of clearcuts that were 9-10 years old. These nest trees contained active nests and thus indicate that Marbled Murrelets use trees on edges some time after cutting has occurred. The use of trees close to edges is associated with higher rates of nest failure due to predation (Nelson and Hamer 1995a, Manley and Nelson 1999). Nesting on edges of clearcuts occurred mostly in one part of the study area where large diameter yellow cedar trees occurred at edges.

The retention of nest trees as single trees or as small Wildlife Tree Patches does not appear to have immediate utility for nesting Marbled Murrelets. Over the long term these trees may provide nesting opportunities but nesting success at these trees may be diminished because of predation. Thus the provision of nesting habitat for Marbled Murrelets in managed forests must be larger scale and proactive if habitat needs of Marbled Murrelets are to be met within a region.

Management of Habitat at the Landscape Scale

Maintaining sufficient amounts of old-growth or late successional forests at the landscape scale is the most important strategy for recovering and maintaining murrelet populations. If sufficient habitat is not retained at the landscape scale, management initiatives at other scales will fail. Retention of old-growth forest at the landscape scale is also the most difficult and controversial management action to implement. To design effective actions managers must consider the amount, spatial arrangement and type of habitat available for Marbled Murrelets.

Amount of habitat

Recommendations in the Biodiversity Guidebook and Landscape Unit Planning Guidebook of the Forest Practices Code provide guidelines for the retention of between 3-13% old-growth forest within BEC variants in landscape units (B.C. Ministry of Forests and B.C. Ministry of Environment 1995). The draft Identified Wildlife Management Guidebook recommends that a minimum of 10-12% of forested area be reserved as Wildlife Habitat Areas for Marbled Murrelets. The amount of habitat required to maintain and recover murrelet populations has not been determined. The density of nesting murrelets has been estimated recently, but few data are available. On the Sunshine Coast, I estimated that nesting density is on average 0.25-0.42 nests/ha at edge and interior plots, but some individual plots had up to 4.2 nests/ha (Manley 1998). In an unlogged watershed in Clayoquot Sound nesting density was estimated at <0.3 nests/ha (Rodway and Regeher 1998c). Although nest sites may be aggregated in some locations (my study), low nesting density means that large areas of habitat are required to maintain populations of murrelets.

Estimates of nesting density and nesting success in different habitat types are needed to determine the amount of habitat required to maintain or recover murrelet populations. In California Oregon and Washington, about 15% of the historical nesting habitat of Marbled Murrelets remains (Perry 1995, Ralph *et al.* 1995) and populations show evidence that nesting habitat is limiting. Given the situation of murrelet populations in the Pacific Northwest, it is not known if the 10-12% of original habitat recommended for murrelets will maintain current populations in B.C. Management initiatives that extend beyond the proposed strategies may be required in many areas in B.C. Marbled Murrelets in the Bunster Range are using almost all of the 14% of late-successional forests that remain within the landscape unit. Nests of Marbled Murrelets in my study appear to be aggregated, are at higher densities, and are re-used more frequently than in other locations. These data suggest that nest sites may be limiting for murrelets in the Bunster Range, even with less severe habitat loss than under proposed management strategies in the Forest Practices Code Landscape Unit Planning and Biodiversity Guidebooks.

139

The total amount of suitable habitat (i.e., late-successional forests) within a landscape is key to maintaining the ecosystem processes and habitats characteristic of coastal temperate rainforests (Lertzman *et al.* 1996). Loss of forests and the creation of edges can change habitat characteristics in remaining stands through effects on fluxes of radiation, wind, water, and nutrients in a landscape (Saunders *et al.* 1991). The effects of habitat fragmentation and habitat loss are often confounded, and recent studies suggest that habitat loss is more important than fragmentation (Fahrig 1997, Bunnell 1998). The effects of habitat fragmentation on other biological processes may only become apparent once habitat loss exceeds a threshold (Andren 1992).

Spatial arrangement of habitat

Marbled Murrelets in my study and other studies have high rates of nest predation (Nelson and Hamer 1995, Chapter 1). Corvids are more abundant at forest edges and for some species and habitats this can result in higher nest predation (Andren 1992, Marzluff *et al.* 1998). Habitat characteristics at and around nests can influence the density of predators and their ability to locate nests. Successful nests of Marbled Murrelets are significantly farther from edges (mean 141 m vs. 56 m), located in larger stands (491 ha vs. 281 ha), and are concealed in their locations significantly closer to the tree trunk (Nelson and Hamer 1995a, Manley and Nelson 1999). Distance to edge is the most important habitat variable for predicting nest fate (Manley and Nelson 1999). To maintain murrelet populations, large patches of suitable habitat that provide interior forest conditions and minimize edges should be retained on the landscape. Patches, a minimum of 200 ha in size and 600 m in width, have been recommended for Marbled Murrelet Wildlife Habitat Areas (WHAs) under the Identified Wildlife Management Strategy (IWMS draft 1998). There is little information on the effects of patch size on Marbled Murrelet nesting behaviour and habitat use. To ensure that reserved patches support nesting murrelets, WHAs should be aggregated in some areas to create a range of available patch sizes from 200-1000 ha or larger. Research on the effect of patch size and its interaction with landscape habitat availability should be conducted on Marbled Murrelets. Once the threshold of habitat loss and patch size are determined more specific

recommendations can be made. Without this information, only general principles can guide management initiatives.

Type of habitat

Throughout the range of Marbled Murrelets, their nesting habitat consists of old-growth stands with high densities of large diameter trees, high densities of potential nesting platforms, high percent forest cover, and high epiphyte cover on limbs (Ralph *et al.* 1995; Chapters 2 and 3). Although some murrelets nest up to 1250 m in elevation in my study, high levels of murrelet occupancy and activity were associated with forests at mid-elevations (Chapter 3). These results support the idea that high quality murrelet habitat is associated with productive late successional forests (Kuletz *et al.* 1995, Rodway and Regehr 1998b). The suitability of sites for nesting Marbled Murrelets varies greatly. For example density of platforms can differ by tenfold within a stand of trees. High quality habitats should be identified and provided to maximize the benefits of proposed strategies to murrelets.

Recommendations

Habitat management for murrelets should take 3 broad approaches:

1) retain late-successional forests in configurations that minimize edge effects;

2) retain stands of high suitability habitat;

3) accelerate or modify successional processes in second growth stands so that these stands acquire structural characteristics of late-successional stands.

One goal of habitat management at the landscape scale should be to maintain ecosystem processes. Amount and placement of late-seral forest must include forests that provide nesting habitat and the ecological processes that create future habitat. The intent of these approaches is to stabilize and eventually allow the recovery of murrelet populations. To accomplish this nesting habitat must be secure and there must be a continuous supply of habitat through time. The amount of habitat managed for Marbled Murrelets at a landscape scale should be determined based on short and long-term goals

141

for populations size, population recovery, and regional and provincial significance of populations.

Ideally, high suitability habitat for murrelets should be identified based on murrelet activity, nesting density, nesting success, and the densities of platforms and mossy platforms. Biogeoclimatic variants and forest cover characteristics can be used to prioritize inventory efforts or to meet other biodiversity objectives. However, I recommend that BEC variants not be used to indicate habitat suitability unless data become available to confirm their utility. Biogeoclimatic site associations could be used within a landscape unit or habitat patch as an index of habitat suitability. But generally this level of classification will not be available and would be costly to obtain. Instead of site associations, platform or platform tree densities could be obtained to better determine suitability at a similar cost.

Planning at the landscape scale provides stability for forest harvesting by identifying areas available for logging. This increases the security of long term logging plans and avoids reactionary management that can result in costly changes to block placement or road layout when nest sites are discovered.

Retention of late-seral stands for nesting habitat of Marbled Murrelets is a short term goal, but managers should also be planning over the long term. After late-seral habitat reserves have been established, experiments and research should be conducted on the use of alternative silvicultural systems to maintain or increase the recruitment of suitable habitat. Silvicultural systems such as small group selection or selective logging with variable retention could be used in advanced second growth forest and old-growth forest remaining outside of WHAs. The effect of these methods on predator abundance, murrelet use, and reproductive success should be evaluated to determine if these methods could be used to enhance these stands or to log in murrelet habitat with minimal detrimental effects. Selection harvesting could promote successional processes that provide structures for murrelet nests. Group selection that creates small openings could potentially retain habitat characteristics suitable for murrelets. This forest harvesting method is most similar to the natural disturbance regime of wetter coastal forests (Lertzman *et al.* 1996). It would provide canopy gaps used by murrelets (Chapter 2) but maintain the high percent canopy cover characteristic of occupied stands (Kuletz *et al.*

142

1995, Hamer 1995, Ralph *et al.* 1995, Chapters 2, and 3). Openings may also increase limb growth in adjacent trees and stimulate platform development in second growth forests (Maguire *et al.* 1991, Hayes *et al.* 1997).

Responses of corvid predators to the number and size of openings needs to be investigated to ensure that sink habitats are not created for Marbled Murrelets. Steller's Jays on the Oregon coast were most abundant in small group selection logged stands and old-growth stands during winter surveys (Chambers and Macomb 1997). Research in coastal forests on Vancouver Island indicates that Steller's Jays are more abundant along roads and at riparian openings (M. Masselink pers. comm.). Small group selection would probably have to be conducted with minimal roads to avoid increasing corvid use of cutblocks.

Responses of Marbled Murrelets and predators to selection logging methods should be evaluated. Based on the characteristics of murrelet nest patches and occupied stands, current approaches for retention would probably create areas that are too open for Marbled Murrelets. Evidence suggests that trees retained in openings could increase predation by providing hunting perches for raptors and corvids (Hansen *et al.* 1995). However, selection logging could be useful for habitat recruitment once sufficient re-growth has occurred.

Management of Nest Trees

Patch and element scales of habitat management are in general inappropriate for Marbled Murrelets because of the importance of interior forest to nesting success. Scales of habitat management that do not provide these conditions may be detrimental to murrelet populations. Because of these concerns, I recommend element (e.g., retention of single nest trees) or patch scale (e.g., retention of groups of trees around a nest tree) management of murrelet habitat only after landscape level management has occurred. Finer scales of habitat management are risky because they are more vulnerable to stochastic processes. Management of murrelet habitat at these scales should be considered only after management goals have been achieved at the landscape level.

Recommendations

When nest trees occur in stands that are scheduled for logging, I recommend two alternatives depending on the landscape planning in effect.

4a) If landscape planning is in process or has not begun then the nest site and surrounding habitat should be deferred from logging until landscape planning is completed. The Identified Wildlife interim measures recommend a 600-m radius around nest sites and occupied sites.

Deferral is needed to evaluate the importance of the area relative to other areas that are available. Factors such as the size and habitat quality of the stand, the activity or density of murrelets in the stand, and its location relative to important feeding areas should be assessed. Once the area has been considered in the context of other available habitat, an informed decision can be made. The area can then be managed through landscape-scale planning (Recommendation 1 or 4b). If landscape scale planning is implemented, few conflicts should occur because population objectives and the habitat needed for these objectives will be met by these plans.

4b) If landscape scale planning has been completed then less stringent measures are needed at nest sites. Nest sites should be maintained in wildlife tree patches or by using alternative harvesting strategies in the nest stand.

The maintenance of forest structural features and, particularly, potential nesting platforms should have precedence over the preservation a particular nest site and its surrounding habitat. Retaining large diameter trees may decrease the amount of time that logged habitat takes to reach suitability for murrelets. In Oregon, murrelets use second growth stands that contain platforms due to mistletoe infestation or due to the presence remnant trees left behind from fires or past logging. The structures that are retained should include a range of tree sizes because they must persist until the logged habitat has regrown and provide recruitment into large diameter classes. Alternatives to clearcutting could be used to increase the recruitment of future nesting habitat.

Wildlife tree patches and tree retention may have negative impacts on murrelets in the short term. If murrelets use these structures before they are buffered by sufficient

regrowth they may face decreased survivorship and reproductive success from increased predation. Patches and tree retention stands could become population sinks because they are more open and isolated habitats. The potential negative impacts of leaving nest trees in wildlife tree patches on clear-cut edges or in thinned or selectively logged stands need to be evaluated. They are only appropriate if management of habitat at the landscape scale is effective in maintaining murrelet populations. Given the potential negative effects, they may not be appropriate for managing murrelet populations that are vulnerable and at risk.

Conclusion

The best approach for maintaining Marbled Murrelet populations in south-coastal B.C. is to stabilise the current availability of nesting habitat and develop strategies for increasing the recruitment of new habitat. I recommend the retention of sufficient amounts of high quality nesting habitat within landscapes combined with selection logging in second growth stands. The structures and forest stands that murrelets nest in take hundreds of years to develop naturally, especially at high elevation. These structural requirements together with the potential negative effects of forest edges mean that habitat retention at a landscape scale is the best option for maintaining murrelet populations. The amounts of late-seral habitat provided under the Forest Practices Code are likely insufficient to sustain or recover Marbled Murrelet populations in south-coastal B.C. The late-seral stands that are retained should be high suitability nesting habitat to maximise their benefits to murrelet populations. Because there is variation among forest types used for nesting throughout the Marbled Murrelet's range, decisions on habitat retention should be based on local or regional knowledge of habitat use by murrelets and the suitability of tree species and habitat types.

Appendix 1. Histories of Attendance and Re-use of Marbled Murrelet Nest Trees

Nest 1

Nest 1 fledged a chick in 1995 and was surveyed about every 10 days from May 20 to August 8, 1996. Landings and fly-bys were observed during surveys on July 3 and 4. On July 3, 2 birds landed and remained for 13 min at the nest branch used in 1995. On July 4, 2 birds flew past the nest several times and one bird landed at the nest branch briefly. The routes used by these birds to approach the nest and fly past it were the same as those used by murrelets when the nest was active in 1995. In both years, the nest was approached from the south with low flights along the logging road.

Nest 11

Nest 11 was active May 12-13, 1996. The incubating murrelet was flushed from the nest on May 13 when a Common Raven flew over the stand. The nest tree was climbed May 25 and eggshells remaining from the predated egg were collected from the nest. Nest 11 was monitored weekly from May 27 to August 14. No detections in or near the tree were observed on May 22 and 28, or June 5, 11, 18, and 25. On July 3, 2 birds landed briefly at the nest branch. Single landings and multiple fly-bys, all by single birds, were observed at the nest tree during dawn surveys on July 6, 7, 11, 16 and 30. The tree was climbed again August 18, very small eggshell fragments were collected from the nest cup and a pile of feathers plucked from an adult Marbled Murrelet were found on a branch 2 m above the nest.

Nest 13

Landings and fly-bys were observed at this tree during surveys on June 15 and June 19 1996 but murrelets were not detected during a survey on July 22. Climbers located a nest cup in the tree. Landings were recorded between May 26 and June 12, 1997 and a predated egg was found at the nest when the tree was climbed (Lougheed *et al.* 1998b).

Nest 15

Multiple landings and flybys were observed on surveys May 25, June 11 and June 20, 1996. An adult bird was incubating on July 19, but regular incubation exchanges were not observed during surveys July 20 and July 27. When the tree was climbed on August, 3 nest sites were found in the tree. Two of them had eggshells from 1996 and had failed during incubation (including where the bird was observed incubating). The third nest had faded eggshells from a previous year and had small amounts of chick down in the moss indicating that this site may have been successful in a previous year. Nest 15 supported two nesting attempts in 1996. Landings observed from May 25-June 20 were associated with either the failure of the first attempt or the initiation of the second attempt. Landings on July 20 and 27 occurred after the second attempt failed.

Nest 16

Landing activity was recorded at this tree on June 27, 1996. During the survey, 2 birds did repeated fly-bys past the tree. One bird landed on a branch and made 2 short-alternate type calls from the branch. The area was surveyed July 13 and July 27 but landings or nearby detections were not observed. The tree was climbed July 27 and a predated egg was found at Nest 16a, 27.4 m high in the tree. Another nest cup, with a feather but no eggshell, was located lower (21 m) in the tree at the branch where the birds were seen landing on June 27 (Nest 16b). Birds landed at this tree on May 16, 18 and 20 1997 (Lougheed *et al.* 1998b)

147

Appendix 2. Bias in the Estimation of Platform Numbers from the Ground

Number of nesting platforms is an important variable for describing Marbled Murrelet habitat (Ralph *et al.* 1995, Rodway and Regher 1998b, Chapters 2 and 3). Number of platforms is estimated by scanning the tree canopy using binoculars. Factors such as slope, tree height and view of the canopy can affect the accuracy of these estimates. In this appendix, I use paired data from trees where the actual number of platforms is measured by climbing as well as estimated from the ground to determine the accuracy of tree platform estimates taken from the ground.

A total of 292 trees were climbed as part of a study to estimate nesting density at edge and interior habitats in the Bunster Range (Manley 1998). Tree platform numbers and characteristics (see Chapter 2 methods) were estimated from the ground before the tree was climbed. Following ground estimates, number of total platforms were measured and platform characteristics were assessed in the crown by the tree climber.

Platform estimates were accurate within ± 1 platform of the actual number of platforms for 47.9% of trees (Fig. 17). Platform numbers were over-estimated for 20.9% of trees and under-estimated for 31.2% of trees.

The error in platform estimates was strongly correlated to the actual number of platforms (Fig. 18; r=0.86, P<0.001). Two general trends were apparent. Platforms were underestimated for trees with small numbers of platforms (trees with < 5 platforms, difference <0). As number of platforms increased the difference between actual and estimated platforms increased and platform numbers were under-estimated. The tendency to under-estimate platforms increased for trees with higher actual platform numbers and greater dbh (Table A.2.1). These trends have been reported in a similar study of valley bottom habitat in Clayoquot Sound (Rodway and Regehr 1998c). However, Sitka spruce trees climbed in that study had even higher numbers of platforms and there was a greater difference between estimates and actual numbers in that study.
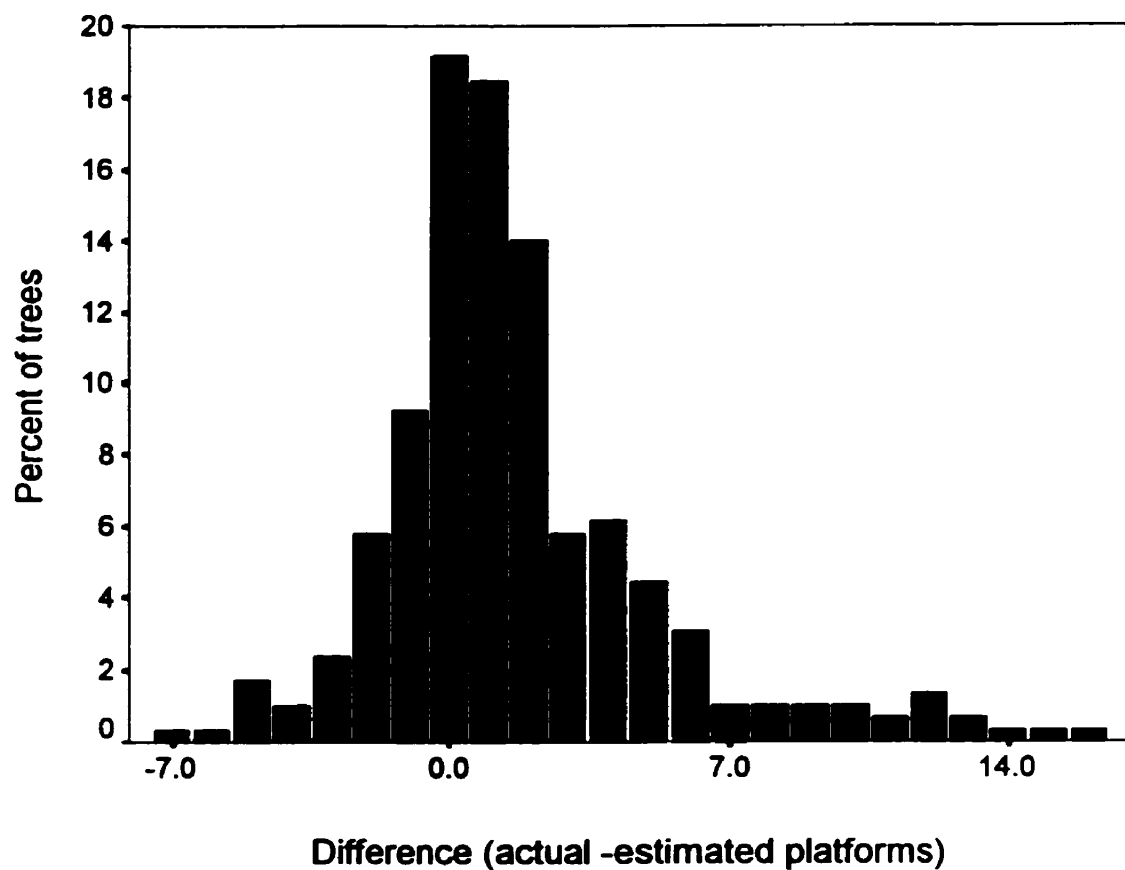
Figure 17. Histogram of platform estimation error for 292 trees climbed in the Bunster Range, 1997.
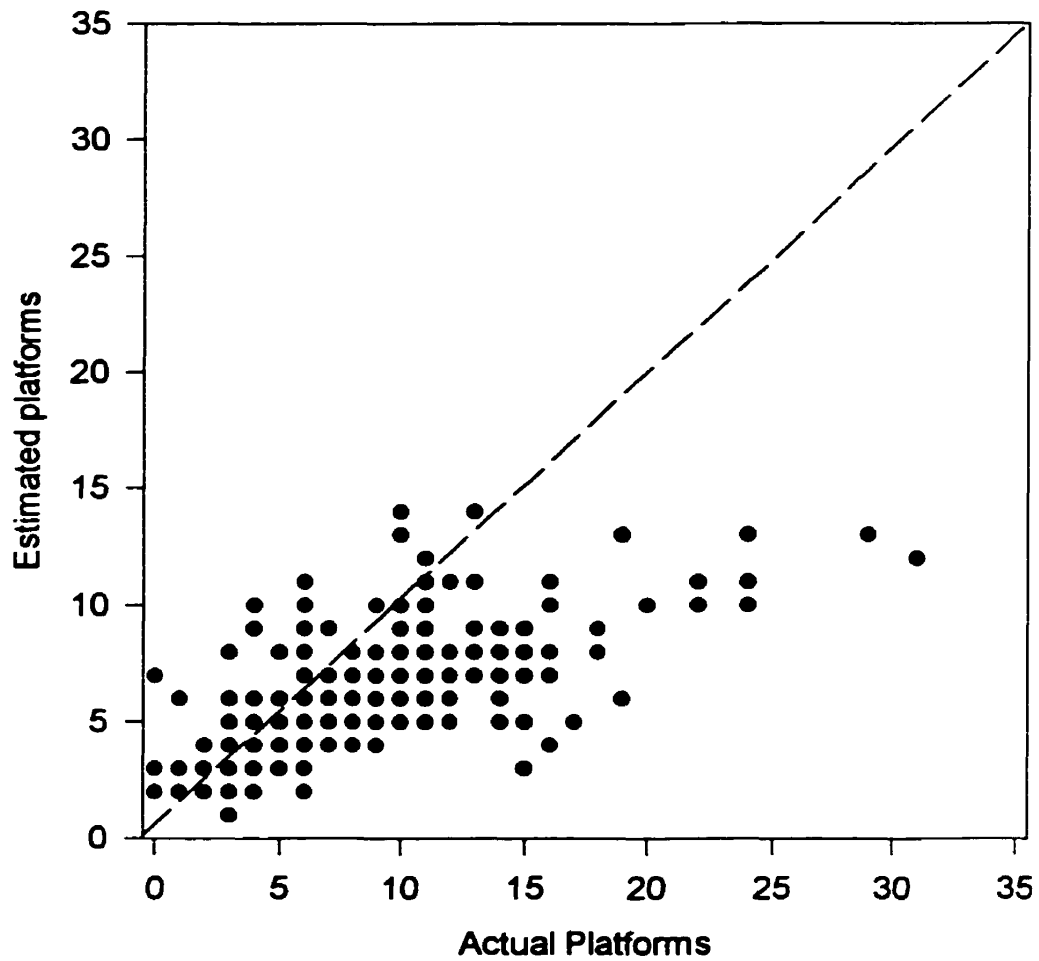
149

Figure 18. Actual and estimated number of platforms for 292 trees climbed in the Bunster Range, 1997. The line is the expected relationship if actual numbers of platforms equaled estimated number of platforms. Estimation error increases with number of platforms.

Table A.2.1. Average number of measured platforms and error of platform estimates for yellow cedar trees within 5 dbh classes.

Tree dbh (cm)	n	Number actual platforms	No. estimated platforms	Difference (actual-estimated)
51-75	33	6.3 ± 0.7	4.9 ± 0.4	1.4 ± 0.5
76-100	99	7.1 ± 0.5	5.6 ● 0.3	1.6 ● 0.3
101-125	54	7.2 ● 0.7	5.9 ± 0.4	1.3 ● 0.5
126-150	10	9.5 ± 2.0	6.1 ± 1.1	3.4 ± 2.0
150-175	3	8.3 ± 1.5	8.0 ± 1.5	0.3 ± 2.2

I tested for differences in the frequency of categories of cover above platforms and platform epiphyte categories between estimated and actual platforms using Chi-square contingency tables. Four tree species, redcedar, western hemlock, Douglas-fir, and yellow-cedar were each tested separately. There were no significant differences in the frequencies of overhead cover categories for estimated or actual platforms ($P>0.10$) for any of the species tested. Platform epiphyte categories had similar frequencies for estimated and actual platforms at yellow-cedar and redcedar trees ($\chi^2 =6.4$, df=3, P=0.10, and $\chi^2=2.5$, df=3, P=0.5, respectively). For Douglas-fir and western hemlock trees epiphyte categories were significantly different between estimated and actual platforms ($\chi^2=13.5$, df=3, P<0.01, and $\chi^2 =21.3$, df=3, P<0.001, respectively). In western hemlock trees Lichen/litter platforms were over-estimated and Moss2 platforms were underestimated. In Douglas-fir trees bare platforms were over-estimated and Moss1 platforms were underestimated (Table A.2.2).

Recommendations for interpreting platform estimates.

1. Estimated number of platforms is higher than actual for trees with <5 platforms.

2. Estimated number of platforms are lower than actual for trees with >10 platforms and increases linearly with increasing platform number.

Table A.2.2. Differences in epiphyte categories for platform estimates and measurements in four tree species.

Tree species		% Bare	% Lichen /litter	% Moss1	% Moss2	Total
Douglas-fir	estimated	20.2	52.7	25.6	1.5	207
	actual	0	51.1	46.3	2.6	231
Western hemlock	estimated	3.4	26.3	51.7	18.6	118
	actual	0	10.8	49.0	40.1	157
Yellow - cedar	estimated	2.3	0.1	13.8	83.8	991
	actual	0	0.4	18.1	81.5	1262
Western redcedar	estimated	0	1.1	14.7	84.2	197
	actual	0	1.6	16.2	82.2	129

3. For detailed assessments of platform density, platforms can be estimated from the ground and adjusted for bias. For cursory assessments, an estimate of density of trees with platforms or of trees with >3 platforms would be a more expedient measure of habitat quality. By assessing trees with >3 platforms problems with over-estimation would be largely eliminated. The use of estimates will obscure differences between sites of high platform density and low platform density. This should be considered in any methodologies used to assess or compare platform densities or suitability of habitat.

4. Estimates of tree species capability are generally under-estimating the true capability of these species but are comparable among species. Data from table A.2.1 are similar to those in Figure 16 for yellow cedar.

5. Platform estimates are fairly consistent for trees with 5-10 platforms. Most trees in my study area fall within this range because it is a high elevation forest with relatively shorter trees. Errors in platform estimates would be expected to be even greater in lower elevation sites where taller trees have greater numbers of platforms.

6. Estimates of platform cover were unbiased for all species.

7. Estimates of epiphyte cover were significantly different for Douglas fir and western hemlock trees. For both species the frequency of platforms with moss cover were underestimated. Given this bias these species are probably more suitable for murrelets than estimates suggest.

8. There were no bare platforms in any trees that were climbed. Platforms classified as bare had lichen or litter substrates.

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