Geographic distribution,
habitat selection,
and population dynamics
with respect to nesting habitat characteristics,
of Marbled Murrelets *Brachyramphus marmoratus*

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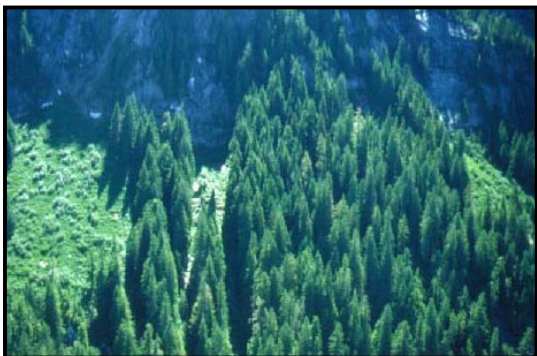Simon Fraser University
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Table of Contents

List of Tables

Geographic distribution, habitat selection, and population dynamics with respect to nesting habitat characteristics of Marbled Murrelets *Brachyramphus marmoratus*

1   Summary

Marbled Murrelets occur during the breeding season in near-shore waters along the north Pacific coastline from Bristol Bay in Alaska to central California. Unlike most auks, Marbled Murrelets nest solitarily on mossy platforms of large side branches of old-forest trees. This has allowed them to exploit the abundant and continuous forest habitat along the coast rather than being restricted to colonies on offshore islands. This review summarizes recent knowledge about factors influencing the species' distribution, breeding habitat selection and population biology, emphasizing the relationship to nesting habitat characteristics, based on scientific literature and reports produced since 1992.

Marbled Murrelets are believed to be continuously distributed from Alaska into southern British Columbia, but the species is rare or absent off stretches of coastlines further south, where suitable nest sites are no longer available within commuting distances of marine feeding sites. Murrelets are sparsely distributed along parts of southeast Vancouver Island, near Vancouver B.C., and in parts of southern Oregon and northern California. The largest gap in their distribution occurs between Humboldt and San Mateo Counties, California.

The distribution of marine resources may preclude nesting along some stretches of the coastline with suitable nesting habitat; a possible example of this is in southern Oregon. However, marine resource distributions appear to shift location with annual or El Niño-related changes in water temperatures, and two studies suggest changes in local breeding propensity or nesting success with unusually warm water temperatures in nearby marine areas. Studies relating murrelet breeding abundances to both terrestrial and marine attributes should be done at a scale of ca. >2000 km^2.

Murrelets breeding on the Aleutian Islands are somewhat genetically distinct from mainland birds. Mainland populations studied thus far are more homogeneous, and there is some evidence of asymmetric gene flow between different sites in Alaska and British Columbia, suggesting consistently asymmetrical dispersal of individuals in some areas. Few data have been analyzed to assess potential differentiation among murrelets nesting in California, Oregon and Washington, but DNA samples should now be available for analysis.

Marine census data suggests that all Marbled Murrelet populations are declining in numbers. However, the data from British Columbia, Washington, and California are limited to relatively small survey areas and have not been consistently sampled over the years. Monitoring programs such as that under the Northwest Forest Plan will allow for better tracking of future population trends. Progress has been made parameterizing and quantifying demographic components for use in modeling future population dynamics. Demographic models suggest that populations in California are not self-sustaining, although a population breeding in a harvested landscape on mainland British Columbia appears stable.

Marbled Murrelets are known to commute distances over 100 km between nesting sites and marine foraging areas. However, commuting distances vary across their range and are shortest in the California and longest in Alaska. For example in Oregon, birds did not nest more than 40 km from the sea. One study of radio-tagged birds in British Columbia found that commuting distances did not influence nesting success. However, it is unknown if greater nest distances reduce survivorship of the fledglings leaving the nest and reaching the sea.

In the past, the Marbled Murrelet's cryptic nesting sites have made precise description of suitable nesting habitat difficult, beyond broadly specifying old-forest as necessary. Recent radio-tracking and ground- based studies have doubled or tripled the number of known nest sites, refining our understanding of both what type of forest nest sites Marbled Murrelets use and what rates of nesting success occur. Throughout their range, murrelets require nest platforms covered with an epiphyte layer. Thus, moist microclimatic conditions, and large side branches, are necessary to provide appropriate sites. Ground nesting occurs with reasonable frequency in some parts of Alaska, but this strategy is extremely rare elsewhere, perhaps due to ground predator communities.

Potential effects of forest attributes at forest stand and landscape scales on nesting probability and nesting success are less universal and less well documented. We know that sites with nests are more likely to be found in stands with greater numbers of trees with platforms, but we do not know how whether there is a threshold or linear relationship between platform density and nesting probability. Future research assessing suitable habitat should attempt to move beyond dichotomous or categorized classifications of environmental variables and probability of usage or success. Several habitat suitability models have been generated, and one tested in British Columbia.

Usage and nesting success may vary in critical ways depending on the community ecology. For example, early studies showed negative effects on nesting success from forest fragmentation and concomitant increased use of "edge" habitat, but recent work in a different landscape failed to detect such an effect; these situations may reflect different predator communities at the sites. Human-occupied edges that enhance corvid populations are most likely to be most deleterious to nesting success.

At a landscape scale (e.g. watersheds) within a region, the numbers of murrelets commuting between marine and terrestrial areas is consistently related to the area of old forest. However, the mathematical slopes of those relationships differ among regions, reflecting the overall abundances of murrelets in these areas. The configuration of forest patches also appears to be important, since several studies show that murrelet numbers are reduced in fragmented landscapes. Further multiscale and multivariate research may help resolve these relationships as more at-sea survey, radar, and nest site data become available.

The three demographic components most likely to be affected by forest structure are: adult breeding propensity, if safe nest sites are limited in availability; nesting success; and adult

surviviorship while commuting or incubating eggs. Limited data are available with respect to nesting success, and potential influences on the other two variables are undocumented.

Prospects for continuing progress in relating habitat characteristics to Marbled Murrelet distributions and breeding performance are good. Ongoing population monitoring efforts in California, Oregon and Washington should provide useful data, and British Columbia is initiating a monitoring process along its coastline. Continued analysis of data on actual nest site locations relative to GIS-based habitat descriptions, and studies of nest predator communities, will allow for more precise descriptions of habitat suitability for nesting Marbled Murrelets.

2   Introduction

This review summarizes current knowledge about the geographical distribution, population differentiation, factors affecting nesting habitat suitability, and factors influences the population dynamics of the Marbled Murrelet *Brachyramphus marmoratus*, a small auk found in the northeastern Pacific Ocean (Nelson 1997). Most members of the family Alcidae nest in colonies, typically at sites protected from mammalian predators, such as offshore islands or on cliff faces (De Santo & Nelson 1995). In contrast, this small seabird seeks safe and solitary nest sites on vegetated platforms, typically found on large side branches of old-growth forest trees (Hamer & Nelson 1995a). Many of the forests along the Pacific coast used by Marbled Murrelets have substantial economic value for the wood products industry. Since the minimum time needed to regenerate trees with suitable nest platforms is on the order of 100–200 years, the maintenance of old-growth forests is a necessary part of a strategy to maintain local breeding populations of Marbled Murrelets (Kaiser et al. 1994; USFWS 1997). A recent review of Marbled Murrelet biology, with an emphasis on British Columbia, was produced by Burger (2002a), in consultation with the Canadian Marbled Murrelet Recovery Team (http://www.sfu.ca/biology/wildberg/bertram/mamurt/team.htm).

Concern for the persistence of Marbled Murrelet populations led to the listing of the species in Canada in 1990, by the Committee on the Status of Endangered Wildlife in Canada, and in the US in 1992, under the US Endangered species act. Murrelets in California, Oregon and Washington were classified as "threatened" by the U.S. Fish and Wildlife Service (USFWS 1992), as "threatened" by state agencies in Washington and Oregon, and as "endangered" in California. The species is classified as "threatened" in Canada, and is an "identified wildlife species" in British Columbia, the only relevant province. Each of these designations influences land-use decisions that may affect its nesting habitat in each jurisdiction.

Unfortunately, clearly identifying suitable, productive or preferred nesting habitat for this seabird has been difficult, complicating management decisions. The species was the last North American bird to have its nest site found and described by scientists, with the first nest described in 1974 (Binford et al. 1975) in the U.S., and in 1993 in Canada (Jones 1993). Traditionally, additional nests have been located by climbing trees in suspected nesting

habitat, a process that has proved time consuming and expensive. Singer et al. (1997) estimated that over 2150 person hours were needed to locate a single nest in Redwoods State Park in California. Summaries of information available as of 1994 included only 61–65 nests (Naslund et al. 1995; Nelson & Hamer 1995a, b). Thirty-seven nests were located during a five-year study by climbing 1890 trees and searching 3,778 platforms in western Oregon (Nelson & Wilson 2002a).   A total of 102 sites are now known in Oregon and Washington from tree climbing and dawn surveys (Nelson et al. 2003).

Due to innovative and collaborative efforts by researchers, government and industry, the number of nests found has increased dramatically in the past four years by radio-tracking birds marked on the water (Quinlan & Hughes 1992).   Successful studies have been carried out at four locations in British Columbia (Bradley 2002; Kaiser & Keddie 1999; Manley et al. 2001; Zharikov et al. submitted), and two in California (Acord et al. 2003, unpublished; Peery et al. 2003c unpublished report; R. Golightly, pers. comm.). These six studies now account for ca. 2/3 of all nest locations, including at least 174 from British Columbia (Nelson 1997; Manley 1999; Hooper 2001; Bradley 2002; Nelson et al. 2003; Zharikov et al. submitted). A radio-tracking study is planned for Washington in 2004 (M. Raphael, pers. comm). Thus, the database available to directly analyze nesting habitat preferences, nesting success, demography and breeding biology, has grown substantially in the past four years, and will continue to grow as the number of radio telemetry studies increase.

The earlier difficulty in locating nests led to the development of three indirect methods to help identify suitable Marbled Murrelet nesting habitat, at three geographic scales. (1) At-sea surveys of murrelet numbers during the breeding season have been used to identify adjacent terrestrial areas of potential interest at a watershed or larger landscape scale (Burger 1995b; Marks et al. 1995; Becker et al. 1997; 2002). One limitation of such studies is that they do not provide direct evidence of breeding versus non-breeding populations, although identifying juveniles towards the end of the breeding season takes a step in this direction (Beissinger 1995; Beissinger & Nur 1997; but see Raphael & Evans Mack 1997).

(2) At a smaller, but still "landscape-level" scale, modified marine radar units have been used to assess the "traffic rates" of murrelets flying between terrestrial and aquatic habitat (Burger 2001, 2002b; Burger et al. 1997 unpublished report; Cooper & Blaha 1999 unpublished report; 2002; Cooper et al. 1999 unpublished report; Cooper et al. 2001; Cullen 2002; Drever & Kaiser 1999; Drever et al. 1998; Lougheed et al. 1998). Although the exact marine origins, the terrestrial destinations and the breeding status of commuting murrelets are not identified, such studies at least demonstrate a linkage between terrestrial and aquatic usage, providing a more direct link to terrestrial nesting habitat than is available from marine survey data alone. They may therefore be useful in narrowing the terrestrial geographic areas of greatest interest. Researchers are also now attempting to track birds directly to nesting areas with inland radar studies (Hamer et al. 1995; Meekins & Hamer 1998 unpublished report; Bigger et al. 2003), but backscatter from vegetation will probably limit the utility of this technique at this scale at most sites. Nonetheless, analyses of patterns of variation in murrelet radar traffic rates among watersheds with respect to terrestrial habitat characteristics should help further define habitat use (see Section 4.2.1.4)

(3) At a local or "forest stand" scale, ground-based audio-visual surveys utilizing standardized protocols (Rodway et al. 1991; Evans Mack et al. 2003) have been used throughout the 1980s and 1990s as the principal operational tool to evaluate the likelihood of usage by nesting murrelets. These surveys have the virtue of following standard protocols, and a great deal of effort has gone into examining their statistical properties with respect to the probability of missing birds when they are in fact present (Jodice & Collopy 2000; Jodice et al. 2001; Smith & Harke 2001). A distinction based on the birds' in flight behavior is made between "detections" and "occupied detections", with the latter being taken as an indication of local nesting activity, as opposed to commuter activity (Paton 1995). These criteria evolved from ground observations of the behavior of birds at known nest sites, but may generate "false positives", or miss such behaviors with some unknown frequency (Rodway & Regehr 2000). However, since the behaviors in question appear to increase the risk of predation on adults, it is reasonable to assume that when observed, they are meaningful indicators of nest prospecting, if not nest presence.

Audio-visual surveys have provided useful information for the purpose they were originally designed to serve, namely the absence, presence, and possible breeding status of murrelets at a stand level (e.g. Kuletz et al. 1995). The sheer magnitude of the data base also makes them useful for broad scale studies of murrelet distributions (e.g. >17,000 surveys (Meyer et al. 2002). However, these data have substantial limitations. Even at the stand level, detections themselves and detections of "occupied behavior" may vary with station location or canopy closure (Rodway & Regehr 2000; Schroeder & Henderson 2000, unpublished report). They clearly underestimate absolute numbers of birds using local areas, as opposed to relative indices for local areas. Three of three studies found that audio-visual surveys detected a quarter or fewer murrelet movements compared with simultaneous radar observations (Bigger et al. 2003; Burger 1997; Cooper & Blaha 2002). Finally, in severe landscapes, the locations that audio-visual surveys are conducted may themselves be biased by the accessibility of sites to ground-based observers. At Desolation Sound, B.C. about 20% of the nests located were at sites inaccessible to human observers, even with helicopter support (Bradley 2002; Huettmann et al. *manuscript*; Zharikov et al. *submitted*). While this may not a major bias in southerly areas, it may be along mountainous portions of the B.C and southeast Alaskan coastline.

The difficulty in locating nests of Marbled Murrelets, and the economic consequences of protecting potential sites, has made management decisions controversial, with respect to both protecting habitat and allowing its harvest (e.g. in British Columbia: (Forest Practices Board 2003, van Drimmelen 2003)). Lawsuits have been brought against government agencies in both the U.S. and Canada by advocates of more aggressive conservation measures and those favoring increased harvest. While we will always wish for greater certainty in decision making, we do not have the luxury of postponing action indefinitely. A major goal of this review is to contribute to scientifically based management by outlining our current state of knowledge and providing a context for interpretation that will support those charged with making policy and land-use decisions.

3   Geographical Distribution and Population Differentiation

The geographic range of a species is determined by the environmental conditions under which it can survive and breed. Different environmental factors may become limiting in different places. At the broadest scale, species are often limited in their distribution by physical factors such as temperature and moisture. Species distributions are further restricted by ecological attributes, such as availability of suitable habitat, social interactions and dispersal, and interactions with prey and predators, which limit an individual's opportunity to find and exploit suitable habitats (Krebs 2002).

3.1   Breeding range

Marbled Murrelets have a broad geographical coastal range extending from central California north to the Aleutian Islands in Alaska (Nelson 1997), and for the most part, a relatively continuous distribution within that range. Both the range and distribution reflect nesting solitarily in mature forests. This adaptation has allowed them to exploit abundant and continuous coastal forest habitat, rather than restricting the species to highly patchily distributions at offshore or cliff-related colony sites, as occurs in most other alcids (De Santo & Nelson 1995; Divoky & Horton 1995). Tree-nesting is shared with the congeneric Long-billed Murrelet *Brachyramphus perdix*, a morphologically and genetically distinct species that occupies a similar nesting niche along the northeast Pacific coast of Asia (Friesen et al. 1996; Nelson 1997).

The breeding range of Marbled Murrelets extends from Bristol Bay, Alaska, south to the Aleutian Islands, northeast to Cook Inlet, Kodiak Island, the Kenai Peninsula and Prince William Sound; and south through the Alexander peninsula in south-eastern Alaska and along the coasts of British Columbia, including the Queen Charlotte Islands, to Washington, Oregon and northern and central California. A large break in their current distribution occurs between Humboldt County and San Mateo County, California where suitable nesting habitat is largely absent (Nelson 1997; Strong et al. 1997 unpublished report; USFWS 1997; see Strong 2003 unpublished report, for recent survey results in Central California). The following papers summarize the most recent information on the distribution and abundance of Marbled Murrelets across their range: Alaska – Piatt & Naslund 1995; Agler et al. 1998; B. C. – Savard and Lemon 1994; Burger 2002a; Manley & Cullen 2002, unpublished report; Washington – Bentivoglio et al. 2002, unpublished report; Raphael et al. 2002a; Oregon – Bentivoglio et al. 2002, unpublished report; Raphael et al. 2002a; Strong 2002a, unpublished report; California – Ralph et al. 1996, unpublished report; Schmidt et al. 2000 unpublished report; Strong 2003a, unpublished report).

The U.S. Marbled Murrelet Recovery Plan has divided Washington, Oregon and California into six 'conservation zones' based on specialist knowledge of habitat types (USFW 1997; see Figure 1 in Bentivolgio et al. 2002 for a map). In each of these zones, systematic marine surveys of murrelet distributions in the breeding season have been conducted under the auspices of the Northwest Forest Plan (Bentivoglio et al. 2002) and through work commissioned by the USFWS in collaboration with state agencies (Strong 2002a; b; 2003a; b; see Bentivoglio et al. 2002 for details of the sampling structure and calculation of

estimates). Table 1 summarizes the most recent estimates of the density and population of Marbled Murrelets within each of these zones. The species is distributed more or less continuously from zone 1 to 5, albeit at low densities in zone 5. In general, murrelet numbers increase from south to north. Murrelets within zone 6 are restricted to two sites in San Mateo and Santa Cruz counties, where small pockets of suitable nesting habitat remain (Miller & Ralph 1995; Peery et al. 2002; Peery et al. 2003a).

The distribution of Marbled Murrelets in British Columbia is incompletely known, but is assumed to be continuous down the coastal fringe. Although historically abundant, relatively few birds are now found along the southeastern coast of Vancouver Island and the southernmost mainland coast, near and north of Vancouver. Figure 1 in Yen et al. (*in press*) plots murrelet density across B.C. based on marine survey work (data from 1972–1993).

Marbled Murrelets appear to be distributed continuously throughout the waters of southeastern Alaska, and patchily through the Aleutian Islands, although their fine scale distribution is incompletely known (Piatt & Ford 1993; Piatt & Naslund 1995). In the breeding season, murrelets are concentrated in three main areas: Kodiak Archipelago, Prince William Sound and the Alexander Archipelago (Piatt & Ford 1993, Piatt & Naslund 1995). Figures 1 and 2 in Piatt & Naslund (1995) provide a summary of their distribution.

Table 1. Estimated densities of Marbled Murrelets (Birds / km^2 $\pm$ SE if cited) and population sizes (95% confidence interval, where applicable) based on systematic marine surveys during the 2000, 2001 and 2002 breeding seasons in conservation zones 1 - 5, as designated in the Marbled Murrelet Recovery Plan. See Bentivolglio et al. (2002) for details on methodology, sampling structure and

Recovery Zone	2000 Northwest Forest Plan[1]		2001 Northwest Forest Plan[2]		2003 Crescent Coastal Research[3,4]	
	May to July 2000		May to July 2001		*May - July 1999-2002 **June-July 2002	
	Density	Population Size	Density	Population Size	Density	Population Size
Zone 1	0.613 $\pm$ 0.389	5,635 (3,198-8,453)	2.408	8421 (5,506-11,882)	No data	No data
Zone 2	0.455 $\pm$ 0.088	769 (500-1,100)	1.136	1,918 (957-3,173)	No data	No data
Zone 3	4.268 $\pm$ 1.236	6,738 (3,943-11,007)	4.358	6,879 (5,389-9,243)	3.574 $\pm$ 0.573**	5,641 (3,794-7,488)**
Zone 4	4.185 $\pm$ 0.904	4,876 (4,135-8,100)	3.335	3,888 (2,901-6,567)	3.626 $\pm$ 0.720**	1,916 (1,094-2,738)**
Zone 5	0.089 $\pm$ 0.048	78 (9-173)	0.132	117 (30-276)	0.0714*	117 (38-214)*
Zone 6	No data	No data	No data	No data	No data	No data

statistical approach.

[1]Bentivoglio et al. 2002
[2]Jodice et al. 2002
[3]Strong 2003a
[4]Strong 2003b

3.2   Marine influences on breeding distribution

The distribution of Marbled Murrelets between April-August is clearly related to the availability of suitable breeding resources, including both nesting and aquatic components. Nesting habitat associations are considered in detail in Section 4. Here we concentrate on what is known about distributions relative to marine resources, including their influence on terrestrial distributions.

The breeding distribution of Marbled Murrelets may be restricted by the distribution of suitable marine resources. During the breeding season, the species feeds predominantly on small fish in the near shore habitats (Nelson 1997). Although primarily a marine bird, a small number of murrelets in British Columbia feed on freshwater lakes (Carter & Sealy 1986; Hobson 1990). In British Columbia, Marbled Murrelets occur at higher at-sea densities in areas with lower sea surface temperatures, less glacial run-off, estuarine habitat and sandy substrates (Yen et al. *in press*). Sandy substrates, bays, and river mouths also correlated positively with murrelet distributions in Oregon (Meyer & Miller 2002; see also Strong 1995; Varoujean & Williams 1995). These factors may correlate with fish densities in these areas, but no data are currently available.

Marine productivity also appears to influence the distribution and abundance of Marbled Murrelets in terrestrial surveys. Meyer & Miller (2002) found that at the broadest landscape scale (3200 ha) marine productivity (spring and summer chlorophyll concentrations) was related to the abundance of Marbled Murrelets in Oregon and northern California. For example, sites in southern Oregon with low murrelet abundances were situated near apparently suitable habitat, but areas of relatively low marine productivity. In addition, two studies suggest that annual changes in marine conditions affect annual abundances of Marbled Murrelets in adjacent forests. Although sample sizes were small, data collected from SW Vancouver Island between 1979 and 1998 suggest negative relationships between sea-surface temperatures and both radar and audio-visual measures of inland occupancy (Burger 1999). In the central California population, demographic work suggests that large differences in annual breeding propensity occurred in an El Niño versus a non-El Niño year, and that nestlings starved when the sea was warmer (Peery et al. 2003c unpublished report; Becker et al., 2002, cited in Peery et al. 2003c). These are the first illustrations of the potential effects of sea changes on Marbled Murrelet breeding distribution and reproductive performance.

Studies of radio-tagged individuals have greatly increased our understanding of the linkages between marine and terrestrial habitat. Breeding Marbled Murrelets have marine "home ranges", used more or less consistently while breeding (Yen et al. *in press*; Bradley 2002; Krebs et al., unpublished data). Although breeding adults typically forage less than 2 km from shore (CWE unpublished data; Strachan et al. 1995; Golightly et al. 2002), they will fly long distances to travel between nesting to foraging grounds. Whitworth et al. (2000) and Hull et al. (2001a) report radio-tagged birds commuting over 100 km from apparent nesting sites to marine foraging areas (B.C. mean = 39.2 ± 23.2, range = 12–102 km, Hull et al. 2001a; Alaska mean = 78 ± 28 km, maximum = 124 km, Whitworth et al. 2000). In western Washington, Hamer (1995) found the highest detection rates of murrelets between

16 and 64 km inland, but reported one occupied stand 84 km inland (Hamer 1995). These probably represent maximum values for Marbled Murrelets, since birds in California and Oregon are not thought to travel so far inland. Marbled Murrelets in Northern California and Southern Oregon did not occupy sites more than 40 km inland (Meyer et al. 2002). In California, murrelets in Santa Cruz and San Mateo counties are thought to commute shorter distances (Golightly, pers. comm.). These studies suggest that appropriate scale for relating terrestrial and marine attributes is very large, extending at least 50 km inland. To date, only two studies have examined marine and terrestrial locations on a >2000 km^2 scale (Huettmann et al. 2003; Huettmann et al. *manuscript*; Miller et al. 2002; see section 4.2.4).

Commuting long distances between breeding sites and marine foraging grounds must be energetically costly for adults, and may decrease survivorship or fecundity. However, commuting distance was independent of mid-chick nesting success for 23 radio-tagged birds in Desolation Sound B.C. (Hull et al. 2001a), and successful nests were located further from the sea than unsuccessful nests in a univariate analysis of a larger samples at that site (Bradley 2002; Zharikov et al. *submitted*). However, the probability that a fledgling survives its initial flight from the nest to the sea is presumably reduced in nests located far inland. Data on the post-fledging survival of chicks from differing nest sites is needed in order to fully understand the costs, in terms of breeding success, of nest site location relative to the sea.

The influence of marine resources on breeding murrelet distributions has important implications for conservation strategies. Firstly, it reminds us that factors other than nesting habitat will have strong effects on murrelet populations. Demographic models (section 5.3) show that adult mortality has the strongest effect on murrelet population growth rate, and much of this mortality must occur during the non-breeding season when their distributions may differ. Secondly, if the distribution of marine resources shifts with sea temperatures, terrestrial locations that support successful breeding in one year may not do so in other years. Conversely, areas with nest sites but no adjacent feeding areas, not used at present, could become "suitable" if prey populations shift towards such sites. The most valuable areas for nesting may be those where local heterogeneity buffers prey populations from large variations.

3.3   Population Differentiation

We review evidence for population structure throughout the range based on documented movements, seasonal mixing, morphometric variation, and genetic evidence.

3.3.1   Movements

Most alcids are restricted to patchy breeding sites and considered to be highly philopatric, factors that should lead to limited gene flow and differentiation of populations (Moum et al. 1994; DeSanto and Nelson 1995; but see Moum et al. 1991). In contrast Marbled Murrelets are widely dispersed among breeding sites, although currently there are no data on the level of philopatry by juveniles or adults (Divoky & Horton 1995). It is clear that most Marbled Murrelets are not sedentary and undertake seasonal movements away from nesting areas,

(Klosiewski & Laing 1994; Burger 1995b; Divoky & Horton 1995; Strong 1995; Beauchamp et al. 1999; Peery et al. 2003b, unpublished report; Burger et al. *in press*). Peery et al. (2003b, unpublished report) monitored the post-breeding movements of 20 radio-tagged murrelets in central California. Birds either remained in the local molting area, or moved > 160 km south to winter foraging grounds. Radio-tagged juveniles from Clayoquot Sound, B.C. (n = 26) moved at least 200 km north after the breeding season, but their final destination was not determined (Parker et al. unpublished data). Seabird surveys of the southwest coast of Vancouver Island also showed strong seasonal patterns in numbers of Marbled Murrelets, consistent with post-breeding movements (Burger et al. *in press*).

Juvenile Marbled Murrelets may disperse from their natal breeding areas. In Desolation Sound, B.C. only two of 106 juvenile birds banded at this site have been recaptured in subsequent years, suggesting that most juveniles are dispersing to new areas to breed (Centre for Wildlife Ecology, unpubl. data).   However, once paired, adult murrelets appear to show some level of fidelity to their breeding sites since several studies have reported re-use of nest sites (Nelson & Peck 1995; Singer et al. 1997). In addition there is a single record of an adult bird banded in Desolation Sound B.C. that was recaptured 220 km south in the San Juan Islands, Washington in the autumn and subsequently recaptured back in Desolation Sound the following breeding season (Beauchamp et al. 1999).

Although nest site fidelity will act to restrict gene flow between populations, the chronology of pairing can increase mixing between populations. In waterfowl, many species pair on the wintering grounds, prior to the breeding season (Anderson et al. 1992). If individuals from more than one breeding area mix during the non-breeding season, this will increase gene flow between nesting "populations", which become part of much more widespread breeding populations. Murrelets are estimated to breed when 2–4 years old (De Santo & Nelson 1995), but currently nothing is known about the timing of pairing. If murrelets are pairing during the non-breeding season, information on relationships between their nesting and winter distributions will be necessary for interpreting patterns of genetic population differentiation.

The winter distributions of Marbled Murrelets are poorly described, however, the available data suggests that movement patterns are complex and differ between areas. To date, two studies have systematically examined post-breeding movements of individual birds using radio telemetry (Peery 2003b, unpublished report; Parker et al. *submitted*). In California, most of the adult Marbled Murrelets that spend the breeding season in Año Nuevo Bay move southward during their post-breeding molt, ca. 20–40 km. However, ca. 10% of the marked birds moved 200–300 km further south later in the season, presumably after completing their post-breeding molt, while others remained more local (Peery et al. 2003b, unpublished report). Parker et al. (unpublished data) found that radio-tagged juveniles marked at Clayoquot Sound, on the west coast of Vancouver Island, moved northward to the tip of Vancouver Island in later summer, and then disappeared. Almost immediately after breeding, marked adults disappeared completely, despite searches both northward along the Alaska panhandle and southward to the San Juan Islands. The birds may have moved offshore.

In the absence of more precise data, movements are inferred by comparing seasonal abundances from marine surveys, however this does not allow short distance movement by local birds to be differentiated from an influx of birds from other areas. On the outer Washington coast and the west coast of Vancouver Island, numbers of birds drop dramatically after the breeding season, although it is unknown where they over-winter (Burger 2002a; Thompson 1997, unpublished report). It is likely that some birds move to overwinter in the more sheltered waters of the San Juan Islands, where murrelet numbers increase four-fold in late summer (Collins 2000). The single bird that moved from Desolation to Puget Sound may have followed this pattern, but 7 other marked birds were resighted as residents remaining at Desolation Sound during the winter (Beauchamp et al. 1999). In southeastern Alaska, Marbled Murrelet numbers drop dramatically between summer and winter, again indicative of post-breeding movements (Agler et al. 1998).

3.3.2   Morphometrics

Ornithologists often use morphological and plumage variation to identify population differentiation, or sub-species and variants. If Marbled Murrelets were strongly differentiated across their range, consistent differences in their measurements might be observed due to adaptation to local conditions, reflecting differing ecological conditions combined with restricted gene flow. Differentiation to the point of speciation has occurred between Marbled and Long-billed Murrelets, with concomitant morphological differention. Measurements of Marbled Murrelets show some differences between sites, but no consistent patterns or clines across their range (e.g. latitudinal variation). However, there are limited morphometric data available making it difficult to evaluate variation across whole the range. Hull et al. (2001b) compared morphometric data from four sites from Alaska and British Columbia and detected some between site differences in culmen width and tarsus lengths. However interpretation of these data is difficult because of the associated high level of inter-observer error she found and because these samples were collected in many different years, and could reflect cohort effects rather than consistent regional differences. In Alaska, Marbled Murrelets nest both in trees and on the ground, suggesting that birds may form two distinct groups based on nesting preference (Piatt & Ford 1993; Marks & Kuletz 2001). Ground-nesting birds are estimated to make up around 3% of the Alaskan nesting population (Piatt & Ford 1993), but may include more substantial fractions of some local populations. Using a principal component analyses, and combining the body measurements from ground and tree nesting murrelets, Pitocchelli et al. (1995) detected no overall differences in size between the two groups.

3.3.3   Genetic variation

Ultimately, we would like to understand the extent of genetic substructure among ecological nesting populations. Several studies have examined genetic variation across much of the Marbled Murrelet's range (Pitocchelli et al. 1995; Friesen et al. 1996; Congdon et al. 2000). However to the best of our knowledge, genetic samples from California have not been analyzed, and populations in Washington and Oregon were characterized based on very small sample sizes (Friesen et al. 1996). In addition, characterizing the level of gene flow between populations and therefore the level of genetic divergence within a species, requires molecular markers of sufficient spatial resolution (see Manel et al. 2003 for a good review).

Thus, failure to find genetic divergence between populations can arise because of high levels of gene flow, small sample sizes, or because the molecular markers were of low resolution for that species.

Friesen et al. (1996) examined the genetic structure of a sample of 43 Marbled Murrelets collected across Alaska, Washington and Oregon. They detected no genetic divergence in the sample using mitochondrial cytochrome-b sequences, but found small but significant differences in allele frequencies using allozymes (Friesen et al. 1996). This variation apparently occurred across the range and could not be attributed to particular sites. There is no evidence that variation between sites could be attributed to nesting habits. Pitocchelli et al. (1995) found no significant mitochondrial variation between ground and tree nesting Marbled Murrelets and estimated their population divergence as 0.03%. A more detailed genetic study examined the level of genetic structuring among populations, based on 120 birds sampled from nine sites ranging from the Aleutian Islands, Alaska to Desolation Sound, British Columbia. Congdon et al. (2000) used nine variable nuclear intron SSCPs (single-stranded conformational polymorphisms) to quantify gene flow and population divergence. Pairwise sequence divergence between the two most distant sites (Attu Island, Alaska versus B.C.) was very similar to the within site variation at each of those sites. However, Marbled Murrelets nesting in the Aleutian Islands were found to have diverged genetically from those at mainland sites. Across mainland sites there was no significant variation or isolation by distance effects (Congdon et al. 2000). Thus, gene flow between Marbled Murrelet populations can be restricted by geographical barriers (e.g. island populations), but appears to be maintained where distributions are more continuous.

Although little genetic differentiation was observed among mainland sites, Congdon et al. (2000) documented clear asymmetries in gene flow. These results suggest directional movements of individuals, and/or variation in site productivity. For example, there was net gene flow from B.C. into Alexander Peninsula, Alaska and from the Alexander Peninsula into the Alaskan Peninsula. As expected, the Aleutian Islands had low overall genetic variability and higher gene flow from than to mainland populations.

The most likely place to look for further genetic differentiation is the isolated remnant populations in central California. On the other hand, if they are maintaining their population size in the face of insufficient local reproductive success, as suggested by demographic models (section 5.3), they may be little differentiated from more northerly populations. There is a need for additional genetic study to quantify the level of genetic structuring among more southerly populations. The material needed for such work should now be available. Substantial numbers of blood samples were taken from birds captured for radio-tracking studies at several sites in British Columbia and California, and new studies are planned for Washington (M. Raphael, pers. comm.). Much could be learned from collaborative analysis of this material.

3.4   Summary

Marbled Murrelets are broadly distributed from Alaska to central California. The largest gap in their distribution is between Humboldt and Santa Mateo Counties in California,

where little potential nesting habitat remains. Overall murrelet abundance increases from south to north. Although the abundance of Marbled Murrelets can be predicted by the distribution of marine resources at a scale on the order of e.g. 50 km, over much of their range they are likely most restricted in their distribution by the availability of suitable nesting habitat. Genetic data suggests that there is little population divergence of Marbled Murrelets where populations are continuously distributed. Isolated populations in the Aleutian Island are genetically distinct from mainland populations, and this could be the case for remnant populations in central California. On the other hand, they may remain quite similar due to immigration from more northerly populations. Genetic analyses of Washington, Oregon and Californian populations are necessary to evaluate this question, and samples should be available for such analyses from birds captured in association with radio-tracking studies. Evidence of asymmetric gene flow between continuous populations in Alaska and B.C. suggests that movement patterns and/or productivity may differ between sites, creating source and sink populations. Estimates of the productivity of populations, the extent of seasonal movements, the degree of philopatry by breeding or juvenile birds, and the chronology of pairing are key data to understanding how gene flow is maintained between Marbled Murrelet populations.

4   Terrestrial Habitat Suitability

Marbled Murrelet nesting habitat has considerable economic and aesthetic value. Decisions about where to conserve habitat must be based on the best possible information about relative and absolute habitat suitability. We start by considering the basic assumptions behind analyses of terrestrial habitat suitability, because the inferences to be drawn from different kinds of information are rarely discussed in the literature.

4.1   How do we define "suitable nesting habitat"?

There are major conceptual issues associated with determining what "suitable habitat" is for any species. We consider the implications of three possible bases for defining "suitable habitat" for nesting Marbled Murrelets.

4.1.1   Usage?

The simplest definition of habitat suitability focuses simply on usage versus non-usage of an area or site. This has been the principal working definition of "habitat suitability" for nearly all studies of the Marbled Murrelet. For reasons outlined in the introduction, "usage" or "non-usage" (e.g. occupancy or not) has typically been established based on audio-visual surveys rather than absolute documentation of nesting. This dichotomous variable is used principally to assign values to small areas ("stands" or "patches"), and is an absolute categorization of habitat ("presence-absence") that makes no distinction with respect to ranked or relative "suitability".

A more refined measure of usage examines usage per area (population density), or probability of usage per area. This creates relative measures for stands or larger areas that may then be ranked or prioritized for consideration for preservation or harvest (e.g., Meyer

et al. 2002). Survey data that quantifies numbers of "occupied detections" within a stand approaches this standard, as do comparisons of radar traffic rates per hectare of forest among watersheds (e.g., Burger 2001; Raphael et al. 2002a).

It is worth noting that the common assumption that higher population densities equate with "more suitable" habitat need not be true (Van Horne 1983). Higher densities (or probability of usage) may fail to represent higher quality habitat in cases where social dominance plays a substantial role in determining population density. Although dominance-displacement systems do operate in birds (e.g., Marra & Holmes 2001), we know of no clear examples where negative relationships between population density and other measures of quality such as reproductive performance persist at equilibrium population levels. Marbled Murrelets probably are not "territorial" beyond perhaps their nest sites, however they may use social information in determining their forest distribution. The vocalizations given by the birds when moving above or through the forest, used by researchers during occupancy surveys, likely influence nest-placement decisions in some way.

4.1.2   Population growth rate?

A more refined definition of "suitable habitat" refers to sites or areas at which a population can sustain itself or increase its numbers over time. "Unsuitable habitat" would then be locations incapable of sustaining populations. If the habitat is used for only part of an animal's annual cycle, we would restrict our assessment to survivorship and reproductive success during that stage, assuming that birds could move elsewhere when less constrained by association with nesting areas. For Marbled Murrelet nesting habitat, we might measure the relative suitability of forest types primarily with respect to the breeding season survivorship of adults and fledging success of young (Section 5.4), rather than the annual survivorship of breeding birds, which will also include a non-forest habitat component for most of the year.

Under this definition, some habitat "used" by a species (as in Section 4.1.1) would be considered "unsuitable". If animals behave adaptively in an evolutionary sense, they should not continue to use "unsuitable" habitat indefinitely. However, we might observe persistent usage of "unsuitable" habitat under this definition due to at least three mechanisms or situations: (1) non-adaptive behavior due to historical time lag, (2) density-dependence and/or behavioral dominance within populations, and (3) "sink" populations maintained through immigration.

(1) Animals might continue to use "unsuitable habitat" if the habitat has changed in ways that they are not adapted to respond to. An "ecological trap" might be created due to rapid habitat change, as might result from human activity. For Marbled Murrelets, it has been hypothesized that a proliferation of easy landing access to nest sites along edges of roads or clearcuts could result in usage of more dangerous sites, if higher predation rates occur along edges. In this situation, the "selected" or "preferred" habitat, as defined below in Section 4.1.3, might in fact be less productive than "avoided" habitat.

One generalized behavioral mechanism that operates in many species of birds to mitigate against such a possibility is a tendency to follow a "succeed-stay"–"fail-move" rule for

returning or not returning to a nesting site from year to year (Haas 1998), or even for renesting attempts following failures within a season, which occur in Marbled Murrelets (McFarlane Tranquilla et al. *submitted*). Such "fitness-dependent dispersal" rules can stabilize population densities among sites (Ruxton & Rohanni 1998). Despite a real potential for the generation of "ecological traps" for naïve individuals, longer-lived species, in particular, may have mechanisms that partially offset such effects. The only data set with even indirect information potentially relevant to the operation of such a mechanism in Marbled Murrelets is consistent with the existence of such a rule in this species (Section 5).

(2) When habitats approach saturation in terms of their ability to support a species, the population itself may decrease the "suitability" of the habitat it uses, if defined in terms of population growth rate. In theory, birds will move to other sites, if available, and local equilibrium populations will stabilize due to negative-density dependence within and among sites (Fretwell 1972; Fretwell & Lucas 1970; Ruxton & Rohanni 1998; Watkinson & Sutherland 1995). When populations become too dense, habitat suitability drops, while when population levels are low, habitat suitability increases. These equilibrium populations could be thought of as reflecting the demographic "carrying capacity" of sites. A similar, but slightly different situation occurs if dominant individuals or pairs monopolize the "most suitable" habitat, and subdominant individuals disproportionately utilize "unsuitable" habitat to their fitness detriment relative to dominant individuals birds (Marra & Holmes 2001; Sutherland & Parker 1985). Note that under both these definitions, habitat suitability is a dynamic function of population densities. For Marbled Murrelets, density-dependence in nesting success will occur if the birds compete for some limited resource, such as the safest nest sites, and/or simply change the probability of nest predation, e.g. by attracting predators to murrelet nest sites when at higher densities.

Whether density-dependent mechanisms determine murrelet breeding productivity is an unknown but crucial area for future research. When nesting habitat is removed due to forestry, Marbled Murrelets may or may not pay a reproductive or survivorship price by "packing into" remaining stands. Finding a linear relationship between population growth rate and the area of habitat used would suggest that packing would likely be detrimental. Alternatively, if population growth can be maintained within smaller areas (e.g. an asymptotic relationship between productivity and area), negative-density dependence is not operating. We have in fact no hard data on density-dependent productivity among nesting Marbled Murrelets, but discuss some ideas and make inferences about indirect evidence in this regard below.

(3) Although a definition equating suitable habitat with a sufficient level of population growth rate might seem reasonable, under it, one could conclude that an entire local population was nesting in "unsuitable habitat", even though the habitat was "used" or even locally "selected" or "preferred" (see below 4.1.3). Local populations that are non-self sustaining are sometimes referred to as population "sinks" (Pulliam 1998). Sink populations can persist due to consistent immigration from productive "source populations" elsewhere. Demographic modeling, albeit based on assumptions about age of first breeding, strongly suggests that populations of Marbled Murrelets in California are not self-sustaining, primarily due to poor nesting success. This failure appears to be due to aspects of the forest

habitat itself and associated marine conditions (Beissinger 1995; Beissinger and Nur 1997; Peery et al. 2002, unpublished report; Peery, 2003a, unpublished report, c, unpublished report; Section 3.2). In contrast, a population along the central coast of British Columbia was deemed to be at or near to demographic stability (Cam et al. 2003).

4.1.3   Preference?

Finally, one could theoretically rank habitats by preference, under the assumption that birds exhibit adaptive choices when such choices are available to them. The most common approach used to infer such preferences is to quantify the usage of habitat types relative to their availability (Jones 2001). We define habitat "selectivity" as what is used relative to what is available (Manly et al. 1993; Manly et al. 2002). "Selected" habitat ('preferred', *sensu* Manly et al. 1993; Manly et al. 2002), is used disproportionately relative to its abundance. We assume that selectivity reflects in part intrinsic habitat preferences of organisms that evolved due to fitness differences attributable to habitat choice (Jones 2001). One difficulty in applying this approach is determining the appropriate geographic area within which to calculate "availability" (e.g., Porter & Church 1987). This approach has been applied to Marbled Murrelet distributions at several landscape scales (e.g. Nelson & Wilson 2002b; Huettmann et al. *manuscript*; Zharikov et al. *submitted*), and the specific preferences inferred will be detailed below.

In a stable environment, we expect to observe better breeding performance in preferred habitat, by definition, barring a tradeoff against other components of fitness. As discussed in section 4.1.2 (2), if there is limited habitat availability, some individuals will be unable to occupy the most preferred sites or breeding areas. Thus, the sites used by a population reflect the product of both intrinsic behavioral preferences and habitat availability (Fretwell 1972; Fretwell & Lucas 1970). Without controlled studies of preference where "all else is equal", calculating habitat selectivity could provide our best insight into real habitat suitability. This approach allows us to make inferences about the relative value of habitat types to population growth rate without having to measure growth rate directly.

This approach must be used cautiously since it could produce misleading results if rapid change produces "non-adaptive" patterns of selectivity, as considered above in 4.1.2 (1). It is therefore important, at least initially, to test for associations between selectivity and performance, as done for murrelets by Zharikov et al. (*submitted*) and Huettmann et al. (*manuscript*); see section 5.4. If birds perform better in habitat they prefer, we can make as strong a case as possible that we have correctly identified attributes of the "most suitable" breeding habitat for Marbled Murrelets. Inconsistencies could suggest that rapid habitat alterations may not be tracked in an adaptive way by the birds.

4.1.4   Habitat suitability: conclusion:

Most of the information available on Marbled Murrelet habitat suitability is based simply on usage/non-usage, or presence/absence as a criterion, but we will point out where components of reproductive fitness affecting population growth rates, and selectivity have been demonstrated to strengthen the potential importance of particular characteristics.

4.2   Attributes of suitable terrestrial habitat

Ultimately, suitable nesting sites for Marbled Murrelets are safe and productive nesting sites. We typically recognize or define suitable habitat with respect to botanical structural elements. However, a site possessing appropriate vegetation and microclimate should be classed as unsuitable, under a population growth rate definition, if the chance of depredation of the egg or nestling, or the commuting or feeding costs by adults, are too high.

We structure this section at four scales: nest site within tree, nest tree itself and nest plot surrounding the tree; forest stand; landscape; and regional. Within each section, we consider what is known about usage, nesting success, as and/or habitat preference.

4.2.1   Site, tree and nest plot scale

The "site" or "platform" scale is the location of the nest in the tree, and the tree scale the nest tree itself (Manley 1999, 2003, unpublished report). The "nest plot" scale is the habitat in the immediately surrounding the tree (e.g., within a 25-40 m radius around the nest tree, Resource Information Standards Committee 2001; Nelson & Wilson 2002a).

4.2.1.1 Nest site

The greatest consensus about Marbled Murrelet habitat requirements is at the site scale. The basic structural elements for nesting Marbled Murrelets are "platforms" of a sufficient-size with epiphytes, and with cover above and over the nest. These have been documented for nests throughout the species range, and appear unequivocal (summaries and reviews in (Hamer & Nelson 1995a ; Burger 2002b;); Alaska – (Naslund et al. 1995; DeGange 1996; Quinlan & Hughes 1990); British Columbia – (Jones 1993; Burger et al. 1996; Dechesne & Smith 1997, unpublished report; Manley 1999; Conroy et al. 2002); Washington – (Meekins & Hamer 1998); Oregon – (Witt 1998; Nelson & Wilson 2002a, unpublished report); and California – (Singer et al. 1995; 1997)). The majority of nests are found on large moss covered limbs, in large (primarily old-growth and mature) tall, conifer trees (Nelson & Wilson 2002a unpublished report). However, non-tree nests also occur in certain locations and habitat (see 4.2.1.4). Bradley & Cooke (2001) report an unusual nest in a deciduous red alder (*Alnus rubra*). A survey of available nesting sites at the plot and adjacent stand level for this nest indicated most potential nesting trees were deciduous and that deciduous trees had a higher density of potential nesting sites. Elsewhere, a few red alders and broad-leafed maple have been climbed and found to offer few potential nest sites (Rodway & Regehr 1999, in Burger 2002).

Murrelets typically nest on the larger limbs within nest trees (Manley 1999), with a range in diameter of nest limbs (at the nest) from 7-74 cm (Burger 2002). The substrate available on the limb appears to influence the size of the limb required, where small limbs supporting heavy moss growth (typical of nests in Alaska) can provide a large enough surface for nesting (Naslund et al. 1995). While the most common nest substrate is thick moss (Manley 1999, Nelson & Wilson 2002a, unpublished report), nests have been found in lichen/litter (Manley 1999) or accumulations of tree debris and needle duff (Singer et al. 1995; Burger et

al. 2000, unpublished report), and are also associated with mistletoe deformities (Meekins & Hamer 1998, unpublished report, Burger et al. 2000, unpublished report, Nelson & Wilson 2002a unpublished report). Moss cover in drier areas is typically less (Burger et al. 2000), and in these areas of lower epiphyte abundance murrelets tend to nest in these alternative substrates, such as fallen needles and other loose debris (Hamer and Nelson 1995). Singer et al. (1997, unpublished report) report a nest found in an old grey squirrel nest. Overhead cover at the site level has been noted in most nest descriptions and thus appears important (Singer et al. 1995; Dechesne & Smith 1997, unpublished report; Manley 1999; Burger et al. 2000, unpublished report; Nelson & Wilson 2002a, unpublished report). Cover may serve to hide nests from predators, and provide protection from the sun and inclement weather (Manley 1999).

4.2.1.2 Nest tree

Nests have been recorded in Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menzieii*), western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), yellow cedar (*Chamaecyparis nootkatensis*), coastal redwood (*Sequoia sempervirens*), and mountain hemlock (*Tsuga mertensiana*) trees (Hamer & Nelson 1995a; Hull 1999). See Burger (2002) for a more detailed summary of heights, diameter at breast height (DBH) of nest trees, and the height of nest limbs. Clear regional differences occur, with nests from Vancouver Island, Oregon and Washington in larger trees than those from the Sunshine Coast, Queen Charlotte Islands and Alaska. Manley (2003, unpublished report) found nest trees in Desolation Sound, on the Sunshine Coast of BC, were taller, had more potential nest platforms, and higher moss cover than those in Clayoquot Sound, but the Desolation Sound sample did not include nests at inaccessible sites, which may have been smaller.

Several studies have evaluated tree level selectivity by comparing the characteristics of nest trees to those of available trees within the nest plot (25-40m radius around the nests). Nest trees tend to be significantly larger in diameter, and taller, than non-nest trees. They provide more platforms (Meekins and Hamer 1998, unpublished report, Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002a, unpublished report) of a larger diameter, and more moss or mistletoe infestation, than surrounding trees (Nelson and Wilson 2002a, unpublished report). Nest limbs are also associated with canopy gaps, and with murrelets selecting trees located next to larger than average canopy gaps (Manley 1999). thus likely facilitating access to the nest.

Marbled Murrelet researchers concur that murrelets do not select specific tree species, but rather are simply more likely to use those species that provide suitable platforms (Burger 2002, Manley 2003). To the best of our knowledge, no study has tried to measure selectivity for species as a relative to the number of platforms provided per species.

Finally, species that produce suitable side branches may not be growing at sites where the microclimate supports epiphyte growth or accumulation of duff. The simple existence of trees of appropriate age, height, or species provides no guarantee that suitable platforms will in fact be available for use by murrelets.

4.2.1.3 Nest plot

Manley (2003, unpublished report) compared the nest plot characteristics (25 m radius) of accessible tree nests from Desolation and Clayoquot Sounds, and found nest plots in Desolation Sound had taller canopy trees, greater variation in canopy tree height and higher rates of mistletoe infestation than nest plots in Clayoquot Sound.

One study has related nesting success (as measured by the proportion of nests that fledged a chick, as determined by tree climbing), to nest tree and plot characteristics (Manley 2003, unpublished report). In this multivariate analysis of accessible tree nests from two study sites (Desolation and Clayoquot Sounds), overall there were no significant differences in the nest tree and patch characteristics of successful and unsuccessful nests. However, location was a significant covariate, and the study sites were also investigated separately. At Desolation Sound, trees with successful nests occurred on steeper slopes (a variable that also appears significant at the landscape level, see section 4.1.2.3), had more platforms and higher nest limbs. At Clayoquot Sound, successful nests had a higher percentage of moss cover.

4.2.1.4 Ground nests

One confirmed and two probable cliff nests have been documented in British Columbia (Bradley and Cooke 2001). The "structure" of these nests was similar to those of coniferous tree nests: heavy epiphyte cover, a large platform, and vegetative cover. This exception thus confirms these basic attributes of suitable nest sites.

In Alaska, over a dozen nests have been found on the ground in a variety of locations including in the open, under vegetation, in cavities, on rock scree slopes, or on cliffs (DeGange 1996; Nelson 1997). On the basis of marine distribution during the breeding season, (Piatt & Ford 1993) estimated that approximately three percent of the Alaskan population may nest on the ground. DeGange (1996) reviews 33 nests reported for Alaska, of which 17 were ground nests. these proportions probably reflect the higher probability of finding ground nests (DeGange 1996), as opposed representing to the actual percentage of ground nesting murrelets in Alaska. Ground nesting may account for substantial fractions of nests in certain local areas. On the Kenai Peninsula, murrelet audio-visual activity was about a third as common in scrubby areas as those with well-developed forest (Marks & Kuletz 2001). One cannot estimate from these observations the relative proportions of ground nests, but they raise the possibility of larger fractions (e.g. 20–30%) of ground nesting pairs at some sites.

While ground nesting may be a productive nesting tactic in parts of Alaska, the mammalian ground predator community may preclude its widespread use further south. Although cliff sites with platforms and cover such as those found in B.C. may be rare, these few sites may in fact be safer at least from mammalian predators, than sites in trees.

4.2.2   Stand scale

The 'stand scale' is that which is commonly available to land use planners. Marbled Murrelet biologists have adopted the GIS databases and tools developed by forestry and park planners in their characterization and analysis of habitat for murrelets. This useful development allows biologists, government, and industry land use planners to exchange information using similar language. In addition to the information we present, we refer interested parties to Burger's extensive recent review of this topic (Burger 2002a, his section 4)

4.2.2.1 Stands: nest versus non-nest or random samples

Several studies have compared habitat attributes of forest 'stands' or polygons, as recognized on forest cover maps, in which confirmed nest-trees occur versus those from randomly selected plots within the same stand, or adjacent stands. Nests were found by a number of methods including tree climbing, through observations of birds during audio-visual surveys (opportunistic nest finds) (Meekins and Hamer 1998, unpublished report, Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002a, unpublished report), and through radio-telemetry (Waterhouse et al. 2002). Comparisons with non-nest stands were conducted using two methods: ground-based habitat surveys (Meekins and Hamer 1998, unpublished report, Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002a, unpublished report), or aerial photographs (Waterhouse et al. 2002). These studies compare nest stands with random samples, rather than unoccupied sites (Jones 2001), since it was unknown if the random stands contained nests.

For the sample of nests found by tree climbing, or observations of birds during audio-visual surveys, nest plots had significantly higher densities of large diameter trees (Manley 1999, Nelson and Wilson 2002a, unpublished report), significantly higher densities of trees with platforms, and a higher proportion of platforms with moss pads than non-nest plots (Meekins and Hamer 1998, unpublished report, Manley 1999, Conroy et al. 2002, Nelson and Wilson 2002a, unpublished report). Vertical complexity was an important attribute predicting use of a forest polygon for nesting, and for predicting whether the nest would remain active in the polygon at least until the mid-chick stage (Bradley et al. *submitted*). Nest polygons had >20% height differences between canopy dominants and the average tree canopy layer, and had visible canopy gaps. Vertical complexity may be an important habitat attribute with regard to the canopy gaps selected at the patch level (see section 4.1.2.3, Manley 1999), in that they provide access to nest sites (Waterhouse et al. 2002). Meekins and Hamer (1998, unpublished report) and Nelson and Wilson (2002a, unpublished report) also noted that nest trees were located in areas of forest that included a minimum of two or three canopy layers.

The results of comparisons between used and either unused or random plots allow for statements of selection, but the authors do not usually produce a picture of the *shape* of the relationship between feature and usage, and instead just report the mean difference. This is a critical point, because there is a substantial difference between stating that "plots with nests have e.g. 30% more platforms than random plots", versus *drawing a resource selection function*, which would *show how the probability of usage changes with platform density*.

The difference is important because linear versus non-linear relationships suggest different management approaches. A non-linear 'threshold' effect helps draw a line between more and less suitable habitat. A linear relationship would allow for trading of areas of different sizes and qualities, that is, recognizing that from the Marbled Murrelets' point of view, twice as much area with platforms half as dense would be just as valuable as half as much area with twice as many platforms. One can approximate resource selection functions from these comparisons by doing e.g. logistic or other types of non-linear regression on the data, rather than simply comparing mean values from the two types of samples.

One case approximating the shape of such a resource selection function curve comes from Waterhouse et al. (2002), who used aerial photographs to compare the habitat features of nest polygons versus adjacent random polygons. Models including age and vertical complexity as covariates showed that polygons continued to be more likely to be used as forest age increased between ca. 140 and 200 years of age, but the rate of increase leveled off beyond 200 years of age. Thus, from the point of view of Marbled Murrelet nest suitability, we have some reason to believe that in parts of British Columbia, a 200-year-old stand is as suitable as a 300-year-old stand.

4.2.2.2 Stands: audio-visual surveys

As outlined in the introduction, audio-visual surveys are a standard tool used to assess occupancy, relative abundance, and habitat associations of Marbled Murrelets in inland nesting habitat at the stand level (Burger & Bahn *in press*). Several studies confirm that, as a subset of detections, occupied detections (circling and subcanopy flights) or subcanopy detections alone are more realistic indicators of local activity and habitat association than total detections (Burger & Bahn, *in press*; Burger et al. 2000, unpublished report; Rodway & Regehr 2002). However, while audio-visual surveys provide a relatively fast means of identifying or evaluating potential nesting habitat (e.g., Lindsay & Leigh-Spencer 1999, unpublished report; Burger et al. 2000, unpublished report), and for testing habitat suitability models (e.g., Bahn & Newsom 2002a; b), they do not provide confirmation of nesting, and can only allow for weak inferences about habitat selectivity (Huettmann et al. *manuscript*). Presence or relative abundance in a location does not necessarily match with nest site locations, nor does it provide information on relative nesting success. Differences in sampling methods may also translate into differences in inferred characteristics of breeding habitat among studies (Jodice & Collopy 2000; Jodice et al. 2001). In a comparison of radar and audio-visual surveys conducted at the stand level, Cooper & Blaha (2002) conclude that audio-visual survey data may be an inaccurate measure of use of a particular stand, because as only a small percentage of murrelets detected by radar were also detected by surveys. Further limitations to the technique are outlined in (Burger 1995a, 1997; Burger & Bahn *in press*; Cooper & Blaha 2002; Evans Mack et al. 2003; Hull 1999; Jodice & Collopy 2000; Jodice et al. 2001; O'Donnell 1995; O'Donnell et al. 1995; Paton 1995; Rodway & Regehr 2002; Rodway et al. 1993a; b).

Despite these limitations, the structural characteristics of large-tree old-growth forests (availability of platforms, cover and thickness of epiphytes on tree limbs, variable canopy structure and gaps, tree age and size, timber volume/density of large trees) have been found

to be good predictors of the 'occupancy' of a stand (e.g., Bahn & Newsom 2002a; Burger 1995a; Burger & Bahn, *in press*; Burger et al. 1996; Grenier & Nelson 1995; Hamer 1995; Kuletz et al. 1995; Manley 1999; Ralph et al. 1995; Rodway & Regehr 2002; Rodway et al. 1993a). These results largely concur with those of the habitat studies outlined above based on nests (Section 4.2.2.1), which is reassuring. However, Rodway and Regehr (2002) indicated that in Clayoquot Sound, British Columbia, the relationships were weak with forest stand characteristics explaining no more than 10% of the variation in numbers of occupied or subcanopy detections. Numbers of detections within and between stations are highly variable, lowering the predictive power of the relationships and the effectiveness of the data, as noted in several other studies (Bahn 1998; Burger 1995b; Naslund & O'Donnell 1995; Rodway et al. 1993a). Rodway and Regehr (2002) conclude that comparisons of structural characteristics may be a more useful method for differentiating and prioritizing breeding habitats for Marbled Murrelets at small scales of 10s to 100s of hectares (stand-level) within watersheds than are inland surveys measuring relative activity levels.

Murrelet detections, total and occupied, tend to be negatively associated with elevation, with the highest numbers reported at elevations < 600 m (Rodway et al. 1993a, b; Burger 1995; Hamer 1995; (Burger & Bahn *in press*; Burger et al. 1996; Dechesne & Smith 1997; Kuletz et al. 1995; Miller & Ralph 1995). Hamer (1995) suggests this may be attributed to the changing structural characteristics of old-growth trees with elevation. Rodway and Regehr (2002) reported the highest numbers of detections along stream channels, although this was likely related to the use of stream channels as flight corridors. Increasing numbers of detections have also been correlated with increasing slope (Hamer 1995).

Several studies report higher activity levels in stands of intact old-growth, as opposed to fragmented areas, current or historical (Paton et al. 1992; Rodway et al. 1993a, Burger 1995, Deschesne and Smith 1997, Rodway and Regehr 2002).

Burger et al. (2000, unpublished report) compared activity levels of murrelets between coastal stands (20–250 m from the shoreline edge) with those of interior stands (1.5–21.0 km inland) on southwest Vancouver Island. Total detections, including occupied behaviors, were significantly lower in coastal stands. Similar results have been found elsewhere on Vancouver Island (Rodway & Regehr 1999; Rodway & Regehr 2002), and also in Washington (Hamer 1995). These results suggest that in some situations, there may be a zone immediately adjacent to the ocean that Marbled Murrelets avoid.

4.2.3   Landscape scale

We define landscape as a ca. 50 km radius in which murrelets are likely to feed and nest (section 3.2). Several studies have investigated habitat suitability under this scale, using various methodologies: nests found by radio-telemetry and Geographic Information System (GIS) (Huettmann et al. *manuscript*; Zharikov et al. *submitted*), audio-visual surveys and GIS across various landscape scales (Meyer et al. 2002; Raphael et al. 1995), and radar counts of murrelets in watersheds (Burger 2001, 2002b; Cullen 2002; Raphael et al. 2002a).

4.2.3.1 Landscapes: radio-telemetry

Two studies have investigated habitat selectivity and nesting success at the landscape scale, by comparing a set of defined landscape features for confirmed nests, with those of randomly generated points on the landscape, with GIS (Huettmann et al. *manuscript*; Zharikov et al. *submitted*). Selectivity was defined as what is used relative to what is available, with 'selected' habitat used disproportionately relative to its abundance. In both investigations the same sample of nests, found by radio-telemetry in Desolation and Clayoquot Sounds, British Columbia, were used in the analyses. Results confirmed that murrelets select old-growth forest as nesting habitat. For Desolation Sound most nests fell within small forest polygons (Huettmann et al. *manuscript*), although a slightly bimodal distribution in patch size use at this site, suggests that murrelets selected both smaller (< 10 ha) and somewhat larger patches (200–250 ha) than would be expected at random (Zharikov et al. *submitted*). Overall, however, it was not the size of a patch per se that was important to the birds but the proximity of a nest site to an abrupt transition from old-growth to an unvegetated area, with nests found more frequently within 30m of an edge than would be expected at random (Zharikov et al. *submitted*). Mean patch size was 2–3 times larger at Clayoquot, with no clear patch size selection.   At this site, the distribution of nests to forest edge distances did not differ from random (Zharikov et al. *submitted*).

At Desolation Sound, nests typically occurred on steeply sloped sites (mean 33° $\pm$15 SD, range 0-70°), at a mean elevation of 748 m (350 SD, range 38–1530 m) (Huettmann et al. *manuscript*). Nest site selection models indicate murrelets selected nest sites which had a combination of steeper slopes, lower elevations (but not lowest) (Huettmann et al. *manuscript*; Zharikov et al. *submitted*), and colder aspects (north), even when the topographic distribution of Old Forest habitat was taken into account. Flat aspects were strongly avoided (Huettmann et al. *manuscript*). In addition, nests were found to be located at sites with higher densities of hard-edge clear-cuts, closer to streams, and farther from glaciers than would be expected at random (Zharikov et al. *submitted*).

For Clayoquot Sound, nests (n=36) were also located on steep slopes (mean 30° 12 SD, range 4–49°), at a mean elevation of 569 m (326 SD, range 29–1191 m). Although the sample of nests from Clayoquot Sound was smaller, the slope and aspect patterns of nest distribution were similar to those from Desolation Sound. Maximum elevations were lower than for Desolation, however the profiles of nest locations were similar. Nest models for Clayoquot Sound included only aspect, with flat aspects strongly avoided (Huettmann et al. *manuscript*), with nests found closer to streams and further from rock-faces than would be expected at random (Zharikov et al. *submitted*).

Huettmann et al. (*manuscript*) found no relationship between breeding success and large-scale landscape features at either site. In contrast, for Desolation Sound, Zharikov et al. (*submitted*) reported that, compared to failed nests, nests successful to the mid-chick stage were initiated earlier in the season, were located closer to the edge of an area of subalpine vegetation, in a location with higher hard-edge clear-cut density, and at higher elevation.

Colder aspects may be important at the nest site level where the cooler, damper environment may encourage higher moss coverage. Steeper slopes may provide easier access to nest platforms and might facilitate fledging of nestlings making their first flight to the water.

Alternatively, it may not be steepness per se that underlies habitat selectivity, but rather a co-variate, including elevation or forest edge for example (Huettmann et al. *manuscript*). Clear-cuts may also provide convenient flyways to access potential/nest sites, as might streams and roads (Zharikov et al. *submitted*).

4.2.3.2 Landscapes: audio-visual surveys

In northern California, southern Oregon, and western Washington, landscapes surrounding stands occupied by murrelets during the breeding season tended to contain a greater proportion of older forest, larger patches, more interior habitat, and a more complex arrangement of younger forest types compared with unoccupied sites (Raphael et al. 1995). Similar results are reported by Meyer & Miller (2002) for southern Oregon. Occupied landscapes had less fragmented and isolated old-growth forest, were associated with relatively large core areas, relatively complex old-growth shapes (such as those created by streams), high-contrast old-growth edge, and low edge on the entire landscape (more contiguous matrix) when compared with unoccupied landscapes. A decrease in old-growth core area corresponded to a decrease in use of an area by murrelets, which suggests a potentially adverse effect of fragmentation on the use of a landscape by murrelets. The authors suggest this could be because it reduces core habitat that is potentially more protected from predators than edge habitat, or that edge habitat affects the microclimate. The higher edge contrast index suggests that the birds' abundance was greater in landscapes with numerous abrupt transitions between forest and non-forest land cover types. The largest plot sizes provided the best regressions and may more fully capture the fragmentation characteristics of the landscape important to the murrelet. This is likely related to an increasing ability to calculate old-growth patch isolation with increasing plot size. For the smallest plot, local topography (elevation) was predictive of murrelet use, however this was less apparent in the larger plots.

4.2.3.3 Landscapes: radar

Radar is valuable for estimating numbers of birds entering watersheds, and hence could indicate the relative importance of the inland areas as nesting habitats (Burger 1997). To be effective, the implementation of radar requires suitable topographical features that will funnel birds through a narrow inlet (Burger 1997). As with audio-visual surveys, it is unknown if the birds detected by radar are actually breeding, and in which watershed. Rodway et al. (1993a) documented a few murrelets flying over alpine passes at ~ 1000m in the Queen Charlotte Islands, and this has also been noted in Desolation Sound (R. Bradley pers. comm., 2001). Radar can also underestimate the number of birds entering a drainage, as some low-flying birds are likely missed due to ground clutter, because they fly under the radar beam, or because some radar targets represent >1 bird (Raphael et al. 2002a). However, the technique is becoming the tool of choice in monitoring large areas for changes in murrelet distribution and abundance, and as indicated above (Section 4.2.2.2) is likely a more accurate method for estimating murrelet numbers than audio-visual surveys (see Cooper and Blaha 2002).

Generally, for radar studies to date, murrelet counts are positively correlated with total mature forest (Burger 2001, 2002b; Cullen 2002; Raphael et al. 2002a), are strongly positively associated with the amount of lower elevation forest specifically (Manley 2000 in Burger 2001, Burger 2001, 2002b; Raphael et al. 2002a), and are either negatively correlated with logged and immature areas (Burger 2001, 2002b) or were not associated with these (Raphael et al. 2002a). In contrast, for the Sunshine Coast, Cullen (2002) found counts were more strongly correlated with higher elevation forest area. Cullen (2002) also reports that counts were negatively correlated to the area of alpine tundra.

All radar studies comparing traffic rates among watersheds within a region indicate a linear relationship between murrelet counts and available old-growth forest (Manley 2000 in Burger 2001; Burger 2001, 2002b; Cullen 2002; Raphael et al. 2002a), but the slopes of the lines differ among regions, reflecting the regional abundances of the species. Although they contain unexplained variance, these linear relationships have implications for how murrelets use the forests. Firstly, they imply that when old-growth forest is harvested, murrelets do not pack into the remaining old-growth habitat in higher densities. Secondly, they suggest that habitat suitability per unit area does not change with patch size at the landscape scales being considered. True linearity means that one expects to find twice as many murrelets nesting in e.g. a 2000 ha patch as in a 1000 ha patch, but also that two 1000 ha. patches will produce similar traffic rates as a single 2000 ha patch.

The above notwithstanding, both Burger (Burger et al. 2003, unpublished report; Burger & Tillmanns 2002) and (Raphael et al. 2002a) argue that other aspects of their data suggest negative effects of forest fragmentation. Raphael et al. (2002a) found that numbers of murrelets were positively associated with amount of core area (an indirect measure of edge effect), and with increasing proximity to other late seral patches. Numbers were negatively associated with increasing edge habitat (a direct measure of edge effect) as created by the juxtaposition of late-seral patches with other land cover types. The authors also note a trend towards a higher variability in counts among years for more-fragmented drainages. Burger noted lower than expected numbers for a given area of forest in two drainages that had been extensively harvested.

4.2.4 Multiple scales

One study has investigated habitat suitability (usage), up to and incorporating the regional scale. In this study in northern California, Meyer et al. (2002) aimed to develop statistical relationships between murrelet use (occupancy and abundance as determined with audio-visual surveys) and habitat variables quantified across many spatial scales (patch to landscape and regional) and two time periods in California and Oregon. In general, occupancy was most related to the availability of low elevation, unfragmented old-growth forests within the fog zone that were close to highly productive marine areas. Many of the habitat variables that explained occupancy also explained relative abundance in occupied plots, although abundance was found to be a more precise and accurate measure of habitat quality than occupancy. On a regional scale, occupied plots occurred almost exclusively in the fog zone, and were limited by distance to the ocean. At the landscape scale, low elevation, close proximity to marine areas with high chlorophyll, proximity to other plots

with murrelets, low old-growth forest fragmentation in the mid-1980s, and location within the fog zone were all important predictors of murrelet occupancy. Occupied landscapes contained fewer young and more mature forest than unoccupied landscapes, but were less contiguous, with simple shapes. In contrast to many stand-level studies (see Section 4.2.1.2), characteristics such as mean tree dbh, slope, aspect, and closeness to streams did not improve predictions of murrelet occupancy or abundance.

Interestingly, this same study found that, while fragmentation and isolation of old-growth forest had an adverse effect on both murrelet occupancy and abundance, the effects were not immediately apparent for the former. Areas highly fragmented before the mid-1980s rarely contained murrelets, yet areas highly fragmented after this period often contained murrelets, indicating a time lag in the effect. However, while birds were present, their numbers were lower in recently fragmented areas. These effects were most identifiable at the landscape level.

4.2.5.   Summary

Throughout most of the species' range, nesting habitat requirements of Marbled Murrelets appear consistent, regardless of methodology, at the nest, tree, plot, and stand scales. However, variability occurs in studies examining relationships with predictor variables at the landscape scale. Not all old-growth forest is equally suitable for nesting Marbled Murrelets. While large branches capable of supporting platforms are generally a necessary attribute, large branches alone are not a sufficient criterion on which to classify or rank the relative suitability of habitat. For example, in drier areas, local microclimate differences due to changes in aspect might make a northern slope suitable for epiphyte cover while a southern slope remains unsuitable. As well, the fog-zone effects in southern Oregon are an example of microclimate differences that can alter the relative suitability of habitat. While murrelet biologists have concentrated on mapping out occupied detections, much might be learned by directly studying these microhabitat characteristics, as well as the distribution of platforms and predators.

4.3   Terrestrial habitat suitability modeling

For management purposes, the preservation of areas for nesting murrelets applies most importantly at the landscape scale. However, the micro-habitat characteristics that have been associated with murrelet nests, such as platforms and epiphyte cover, are typically not available on the maps required for this scale of evaluation. Therefore, those forest characteristics that are available on maps must be used as proxies for the micro-habitat characteristics known to be important to murrelet nesting (Bahn & Newsom 2002b, Lindsay and Leigh-Spencer 1999, unpublished report).   The effort to rank the value of different types of old-forest habitat has lead to the development of regional "habitat suitability' algorithms and models, at several different scales (e.g., Meyer et al. 2002). As Jodice et al. (2002) caution, one model will not be suitable for all regions inhabited by murrelets.

In British Columbia, Demarchi (2001, unpublished report) created habitat maps utilizing information from 1:250,000 scale Terrestrial Ecosystem habitat database, the most detailed

available on a province-wide scale. There is widespread agreement that these maps were based on insufficient detail to provide substantial guidance to on-the-ground land use planners charged with delineating Wildlife Habitat Areas for Marbled Murrelets within watersheds. Nonetheless, a second attempt towards generating province-wide maps, using revised recommendations for suitable habitat characteristics generated by the Canadian Marbled Murrelet Recovery Team (Table 2; Burger 2002a; Canadian Marbled Murrelet Recovery Team 2003) is being pursued by the B.C. Ministry of Water, Air, and Land Protection (Louise Blight, pers. comm.).

Bahn & Newsom (2002) created four-class habitat suitability maps of watersheds surrounding Clayoquot Sound, Vancouver Island, B.C. based on detailed forest cover maps. They evaluated the fit between field vegetation data versus the lower resolution database and a map based on 'VRI' (Vegetation Resource Inventory) forest cover data available for that region. In the absence of actual data on nest locations, the models were tested against their ability to predict suitable habitat requirements as derived from the literature. VRI maps seemed more biologically relevant and better reflected the field data at a scale likely to be meaningful for Marbled Murrelet habitat.

In an initial attempt to apply this model to a novel watershed, Conroy et al. (2002) found that habitat rated as 'Excellent' had higher epiphyte thickness on trees, greater tree height, greater variance in tree heights (indicating a more layer canopy), and larger stem diameters than 'Good' or 'Sub-optimal' habitats, and greater epiphyte cover on large trees than 'Sub-optimal' habitat. Thus, the model could predict some important characteristics at the tree and site scales. However, the study was not able to confirm the ability of the model to predict high densities of trees with platforms and densities of platforms.

A second evaluation of the model has recently been carried by examining the distributions of 36 nest locations obtained by radio-tracking at this site (Bahn et al. pers. comm.). Although several nests fell into the lowest-ranked 'Unsuitable' stratum, nest densities were ca. 3 times higher in the highest ranking habitat suitability classes. While further

Table 2. Features of Marbled Murrelet nesting habitat to consider during selection and design of Wildlife Habitat Areas and other maintained habitat patches. The features are grouped by the likelihood that polygons with these features will contain a large proportion of suitable nesting habitat. Additional features are described in the text. Features should not be used in isolation but in combination with other features (from Canadian Marbled Murrelet Recovery Team, 2003).

Feature	Most likely	Moderately likely	Least likely
Distance from saltwater (km): all regions	0.5–30	0–0.5 & 30–50	>50
Elevation (m)			
Central & Northern Mainland Coast	0–600	600–900	>900
Haida Gwaii (QCI)	0–500	500–800	>800
All other regions	0–900	900–1500	>1500
Stand age class: all regions	9 (>250 yr)	8 (140–250 yr)	<8 (<140 yr)
Site index productivity classes: all regions [a]	Class I & II (site index 20+)	Class III (site index 15-19)	Class IV (site index <15)
Tree height class: all regions[b]	4-7 (>28.5 m)	3 (19.5–28.4 m)	<3 (<19.5 m)
Canopy closure class: all regions	Classes 4, 5, & 6	Class 3 & 7	Classes 2 & 8
Vertical canopy complexity: all regions[c]	MU, NU, & VNU	U	VU

[a]Productivity classes as defined in Green and Klinka (1994, p. 197); approximate 50-year site index values also given – application of these indices might vary with different tree species and across regions.

[b]Nests have been found in polygons ranked height class 1 or 2 but the nests were in larger trees than the polygon average.

[c]Vertical complexity ranked from least to highest (see Waterhouse et al. 2002). VU = very uniform (<11% height difference leading trees and average canopy, no evidence of canopy gaps or recent disturbance). U = uniform (11–20% height difference, few canopy gaps visible, little or no evidence of disturbance. MU = moderately uniform (21–30% height difference, some canopy gaps visible, evidence of past disturbance, stocking may be patchy or irregular. NU = non-uniform (31–40% height difference, canopy gaps often visible due to past disturbance, stocking typically patchy or irregular). VNU = very non-uniform (>40% difference, very irregular canopy, stocking very patchy or irregular).

refinements might be made, the model was thus successful in ranking habitat based on map information at the VRI scale.

In British Columbia, the Canadian Marbled Murrelet Recovery Team has recommended a specific stepped approach toward habitat classification of old forest types with respect to Marbled Murrelets. The advisory "Part B" document (Marbled Murrelet Recovery Team 2003), is available at: www.sfu.ca/biology/wildberg/bertram/mamurt/PartB.pdf . Broad guidelines for initial ranking of landscape and forest attributes thought to be favourable or detrimental to Marbled Murrelet nesting and nest platform presence are reproduced above as Table 2. These are consensus recommendations, and there is recognition that the attributes will change somewhat regionally and be refined with additional research. An initial analysis of these characteristics may be made from forest cover maps. A second recommended step involves analysis of air photos by a trained observer. Thirdly, areas may be flown using helicopters or assessed from the ground for direct evidence of platforms and/or murrelet activity. It remains to be seen whether this hierarchical approach proves practicable on the landscape

5   Population Dynamics With Respect to Nesting Habitat

This section focuses on what is known and might be inferred about the population dynamics of Marbled Murrelets with respect to aspects of their terrestrial habitat. Ideally, one would perform a set of habitat-specific "Population Viability Analyses" and institute a program of adaptive management, using the following general process:

(1) create a general population projection model incorporating both demographic information and environmental stochasticity, based on initial knowledge of the species' biology;

(2) gather habitat-specific data on identified demographic and environmental variables;

(3) incorporate habitat-specific parameter values into the models to project habitat-specific population dynamics,

(4) draw initial conclusions about specific demographic stages and ecological variables strongly affecting population dynamics and make initial management recommendations.

Further steps would then be to:

(5) continue to monitor dynamics, gather data, and refine the model and parameter estimates,

(6) manipulate habitat and measurement of population responses, which would provide a strong tool for confirming or refuting causal inferences about hypothesized mechanisms derived from observational and modeling studies.

(7) refine management recommendations based in improved understanding of population dynamics or altered environmental circumstances.

The match between this ideal process and what can be done given the current knowledge of Marbled Murrelet population biology is poor. This complete and direct approach towards quantifying relationships between forest attributes and Marbled Murrelet population dynamics is thus premature. Nonetheless, both the U.S. and Canadian Marbled Murrelet Recovery teams have adopted this research paradigm as part of their recovery strategies (Kaiser et al. 1994; USFWS 1997), and ongoing monitoring and research could enable a closer approximation of such a process to operate in the future. Population monitoring programs in Washington, Oregon and California could provide relevant data, and the Canadian Marbled Murrelet Recovery Team has a goal of putting in place population monitoring at sites with ongoing forestry operations to directly assess the effect of habitat loss (Burger 2002a; Marbled Murrelet Recovery Team 2003).

In the absence of complete information, we summarize here what is known or can be inferred about relationships between breeding habitat characteristics and population dynamics and/or demography by reviewing and evaluating:

(5.1) population size relative to habitat availability

(5.2) population trends,

(5.3) population modeling,

(5.4) estimates of specific parameter values relative to forest attributes, and

(5.5) inferred processes responsible for relationships between parameter values and forest attributes.

It must be stated at the outset that hard data on even the simpler of these questions remains quite limited.

5.1 Population size relative to habitat

As previously discussed (section 4.2.3.3), radar studies suggest that the usage of watersheds within regions is more or less linearly related to a coarse measure of old-forest availability. However the absolute regional abundances, and thus the slopes of the relationships, vary widely. Whether this variation reflects the relative suitability of adjacent marine conditions, or reproductive success in terrestrial habitats, is unclear. One approach is to look for deviations from expected values controlling for each variable. A first step towards this goal has been taken by Yen et al. (*in press*). They generated a model of the B.C. coast predicting murrelet summer densities based entirely on marine attributes. They then showed that the fit between observed and modeled densities was better for areas within ca. 30 km of old forest habitat. More refined models of this kind could further refine our understanding of the interactive roles of marine and terrestrial variables in determining local population (see also Meyer & Miller 2002; Meyer et al. 2002; Miller et al. 2002; and Sections 3.2 and 4.2.4).

5.2 Population dynamics and trends

In theory, the simplest approach towards understanding the population dynamics of Marbled Murrelets would be to relate trends in population sizes to changes in habitat availability and/or suitability. After fledging from a nest, Marbled Murrelets have life expectancies on the order of 10 years (Cam et al. 2003), and low rates of annual productivity (< 1 young/pair/year, McFarlane Tranquilla et al. *submitted*). We thus expect relatively stable populations from year to year, rather than observing large cyclic or erratic variations. This stability should operate in favor of detecting long-term trends in population size, because it should reduce the annual variance in census data. On the other hand, breeding philopatry may lead populations to show time lags in response to habitat change and increase the time required to detect population declines (Section 4.2.4; see Meyer et al. 2002 for an example).

Detecting long-term trends in murrelet populations is also difficult due to limitations of sampling techniques and availability of census data. Most long term census data has been collected using marine surveys, a technique that results in high seasonal and interannual variability (e.g., Becker et al. 1997, Speckman et al. 2000). For example, power analyses indicated that marine surveys in California had only a 24% chance of detecting a population declining by 5% per year over 5 years when surveying five times a year (Becker et al. 1997). Consequently only long time series of census data, or frequently sampled areas, are likely to provide accurate population trends. Despite these limitations, analyses of long term data clearly show population declines in Alaska, B.C. and Oregon (summarized in Table 3). It is difficult to evaluate the long term population trends in Washington and California because the available studies are both local and relatively short term (Table 3). However, there is a widespread consensus that elimination of suitable nest platform trees will result in local disappearance of a breeding population, except perhaps for certain areas in Alaska, where ground-nesting occurs (see section 4.2.1.4). While the birds have been locally extirpated (e.g. Burrard Inlet, near Vancouver, Carter & Morrison 1992; Manley & Cullen 2003), and

Table 3. Summary of Marbled Murrelet population trends from Alaska, British Columbia, Washington, Oregon and California.

Location	Years	Method	Trend	Source
Alaska	1972-1991	Christmas bird counts	50% decline	Piatt and Naslund 1995
	1972-1991	Marine surveys	67-73% decline	Klosiewski and Laing 1995
	1971-1993	Christmas bird counts	No decline detected	Hayward and Iverson 1998
	1989-1998	Marine surveys	No recovery after Exxon Valdez oil spill	Lance et al. 2001
	1972-1993	Marine surveys	Decline	Agler 1999
	1984-1998	Marine surveys	No decline detected	Irons et al. 2000
B. C.		Limited census data	Decline on West coast of Vancouver Island	Burger 1995
	1982-1993	Marine surveys	40% decline in Clayoquot Sound	Kelson et al. 1995
	1982-2002	Compiled studies	22-44% decline	Burger 2002
Washington	1996-1999	Marine surveys	Little change in Strait of Juan de Fuca	Thompson 1997, 1999
	1972-1993	Marine surveys	Possible decline after 1989	Speich & Wahl 1995
Oregon	1992-1999	Marine surveys	> 50% decline	Strong 2003
	2002-2003	Marine surveys	No change detected	Strong 2003b
California	1995-2001	occupied detections	Probable decline in San Mateo/Santa Cruz Counties	Suddjian 2001

patterns of current distribution during the breeding season relate more or less strongly to the existing distribution of forest (e.g. Burger 2002; Meyer & Miller 2002; Meyer et al. 2002), we know of no analysis that directly correlates historical decreases in old-forest habitat to changes in Marbled Murrelet population levels, at any temporal scale. The establishment and continuation of standardized, long-term monitoring programs, whether at sea, inland, or using radar, may provide such data as harvesting continues in the future.

5.3 Demographic modeling

We begin with an overview of murrelet population modeling and present the conclusions as stated by the authors. In subsequent sections, we will examine the strengths, weaknesses and assumptions involved with parameter estimation of these models, and finally examine their potential relationships to variation in forest structure.

5.3.1   Overview of results

A general demographic 3-stage (juvenile, first and second year, adult) Leslie matrix population model for Marbled Murrelets was presented by Beissinger (1995) and Beissinger & Nur (1997). In the absence of annual individual age-specific survivorship data from Marbled Murrelets at the time, the authors extrapolated from a comparative analysis of survivorship among auks, while fecundity data were derived from both nesting success data and age ratios from at-sea surveys. While acknowledging numerous shortcomings of the model, the authors nonetheless concluded that murrelet populations in the US Pacific Northwest were not replacing themselves. Boulanger et al. (1996) examined the sensitivity of a similar model, and showed that population changes would be driven most strongly by variation in adult survivorship, followed by juvenile survivorship, and finally annual productivity. They cautioned that the strong effect of adult survivorship meant that small errors in the value of this parameter could substantially alter population projections for the species.

Refined versions of the Beissinger (1995) model have now been applied specifically to Marbled Murrelet populations nesting in the Santa Cruz Mountains (Peery et al. 2002, 2003a, b, unpublished reports), using estimates of adult survivorship derived from capture-recapture data. Fecundity in these populations is clearly extremely low, and these analyses also reached the conclusion that the local population was not replacing itself. This most recent work, from two separate analyses, also suggests that the local population size is stable, albeit over a short time period (3 years). This conclusion is drawn from at at-sea survey data from the area, and an estimation of total recruitment (including immigrants) to the population (Pradel 1996) based on recently-available mark-recapture data (Peery et al. 2003a, unpublished report; Peery et al. 2003b, unpublished report). One way to reconcile these analyses is if the Santa Cruz Mountains population is a "population sink" being sustained by immigration from elsewhere (Pulliam 1998), which the authors suggest is the case.

Capture-recapture data for Marbled Murrelets marked between 1991 and 2000 have been used to model a population breeding in a heavily harvested area on the central mainland coast of British Columbia (Cam et al. 2003; Kaiser et al. 1995). This study produced two estimates of adult survivorship based on different samples, and estimated population growth rate for the period, including immigration, using Pradel's (1996) method. This statistically rigorous study concluded that the population studied was stable or very slowly decreasing, but did not attempt to partition recruitment into locally produced versus immigrant individuals.

Finally, we know of four "risk assessment" tools that have been developed for Marbled Murrelets, which incorporate both demographic and environmental variables. Akcakaya (1997) modeled population viability for Marbled Murrelet metapopulations in southern Oregon and northern California ("Zone 4") under several assumptions about vital rates and forest harvesting. The "LIMBS" model (Swartzman et al. 1997, unpublished report) was developed to cover northern California. We do not know whether or in what ways these models has been implemented or used since their initial creation.

Beissinger (2002, unpublished report) modeled the effects of a 10% reduction in adult population size for the Central California population, as might result from a major oil spill. Using both a maximal and estimated fecundity based on at-sea juvenile ratios, Marbled Murrelet populations in Northern California are currently declining. After the loss of 10% of the population, numbers continued to decline albeit at a slightly increased rate. Because the population is declining, the greatest impacts were observed in the first 15 years, where even by the most conservative estimate, 3453 "bird years" were lost.

The most recent risk assessment model (Steventon, Sutherland, and Arcese, pers. comm.) has been assembled under the sponsorship of the B.C. Ministries of Forests, in association with the Canadian Marbled Murrelet Recovery Team. "Belief weightings" from this group were used to generate function shapes for parameters where data were not available. This model is not yet spatially explicit, but is meant to be used as tool for simulating the effects of alternative management scenarios on the likelihood of population persistence in regions of British Columbia.

5.3.2   Estimating annual survivorship

The two completely independent approaches taken towards estimating adult annual survivorship have produced estimates of similar general magnitude, albeit issues such as annual variability and precision remain poorly documented.

The estimate of adult survivorship derived from the comparative analysis was based on survivorship estimates for other species of auks, taking into account body mass and maximum potential annual productivity as covariates (Beissinger 1995; Beissinger & Nur 1997). The analysis produced a point estimate of 0.85, with a 2 standard error range of 0.81–0.88, for a population of breeding adults. This value might best be viewed as a baseline theoretical prediction for the species as a whole against which field estimates from particular locations might be interpreted. Note that many of the values for other alcids used

in the comparative analysis were not based on capture-recapture analysis, and thus, unless resighting probabilities are 1.0, the values are lower than true values (Cam et al. 2003), biasing this estimate somewhat low. Subadults and non-breeders would not be included in this estimate. Based on comparative studies, in population models, these categories of birds birds were assigned values of 0.71 and 0.88 times the adult rate over the first two years of life (Beissinger 1995; Beissinger & Nur 1997).

Cam et al. (2003) present two annual survivorship estimates from mark-recapture data on Marbled Murrelets gathered in the Desolation Sound area of British Columbia. An estimate based on 966 birds was derived from data collected consistently in mist nests at dawn and dusk at one site in 1991–2000, was 0.9289 (95% CI 0.8493–0.9901). The second estimate based on the mist netted birds plus an additional 533 birds captured with dip nets ca. 6 km from the netting site between 1997–2000 only, appears to be lower: 0.8289 (95% confidence interval 0.7162–0.9029). Low recapture rates (ranging from 0.03–0.13 annually) account for the large standard errors on the estimates. Both these samples exclude juveniles, but include unknown fractions of 1- and 2-year-old pre-breeders, which might lower their value relative to that of a sample of breeding adults only. Although the confidence intervals for the two estimates overlap, there are biological reasons to believe that the difference in point estimates is real. The mist-netted sample was biased towards birds caught later in the season that were feeding young (Vanderkist et al. 1999), and thus may be older, more successful and/or higher quality individuals. The dip-netting sample encompassed a more heterogeneous sample of birds caught prior to initiating nests, and likely including a higher proportion of younger, poorer quality, and/or transient birds. A higher proportion of dip-netted birds received radios, but an analysis with reasonable power was unable to detect an effect of radio attachment on survivorship (Parker et al. *submitted*).

Peery et al. (2003a, b, unpublished reports) estimated annual survivorship based on 291 individuals captured using dip nests between 1997 and 2002 in central California. The birds were caught principally on Año Nuevo Bay, where most of this small central California population congregates at night, and predominantly following the breeding season, when adults were molting. The estimate was 0.823 (95% CI 0.613–0.931), with a recapture rate on the order of 0.21. It is not entirely clear from current progress reports, but this sample may include a small number of birds marked as juveniles. The best fit model included a difference in recapture rate, but not survivorship, as a function of whether or not the bird was radioed when originally marked.

Juvenile survivorship has remained completely unstudied until now. Parker et al. (*submitted*) followed radio-tagged juveniles marked at Desolation Sound for 6 weeks following fledging. They estimated the survival of 34 radiotagged individuals to be 0.86 (95% CI 0.7250–1.001) during an 80 day period post-fledging. When extrapolated over a year, under the assumption of constant survivorship, this translates into an annual survival rate of 0.51, which will be a minimum if survivorship improves with further juvenile experience.

5.3.3   Estimating annual fecundity

Two types of data have been used to estimate annual fecundity in Marbled Murrelets: fledging success rates from nests ("nest success"), and adult/juvenile ratios from at-sea surveys. Note that to use fledging success rates in demographic models, one also needs to estimate the breeding propensity of adult birds, whereas adult juvenile ratios may be used directly as measures of annual fecundity for a population. Conversely, age ratios alone cannot determine the relative contribution to fecundity of nesting success rates and breeding propensity, which may at times be limited by terrestrial habitat availability. Both sources of information are thus needed to elucidate the processes determining rates of annual fecundity.

5.3.3.1 Fledging success from nests

Nest success is typically assigned based on assessment of fecal rings following fledging, as per the British Columbia nest site description protocol (Resource Information Standards Committee 2001). For radio-tracking studies, where some nest sites could not be accessed, a "mid-chick success" measure has been calculated (Bradley 2002; Bradley et al. *submitted*).

Nest success rates have been estimated for a sample of nests in the Santa Cruz Mountains (0% in one year, 16% for all nests found (n = 19; Peery et al 2003c, unpublished report). Data will soon be available from Humboldt County in California (Golightly et al. pers. comm.). Nest success rate was 22% for a sample of 22 nests with known fates in California, Washington and Oregon (Nelson & Hamer 1995a). In Western Oregon, nest success was 40% in a sample of 10 nests with known nest fates (Nelson and Wilson 2002a, unpublished report). Higher rates of nest success, up to or exceeding 46% (n = 84), were found at Clayoquot and Desolation Sounds in B.C. (Centre for Wildlife Ecology, unpublished data; Bradley 2002; Bradley et al. *submitted*; Zharikov et al. *submitted*; Manley & Cullen 2003). In Alaska, where both ground and tree nests have been monitored, 0% (n = 9) were successful in one tabulation (Nelson & Hamer 1995a), and 0% (n = 7) in another (Naslund et al. 1995). The scattering of data locations and a host of correlated variables preclude meaningful interpretation of these data with respect to forest characteristics beyond those discussed earlier (Section 4.2; but see discussion of potential "edge effects", Section 5.4.2.1).

5.3.3.2 Age ratios in at-sea surveys

Extensive at-sea survey data are accumulating for Marbled Murrelets in parts of Alaska, in British Columbia (Burger 1995b; Burger et al. 2003, unpublished report; Lougheed 2000; Rodway et al. 1991), and along the Washington, Oregon and northern California Coasts, using various protocols designed by the members of the Pacific Seabird Group (Ralph et al. 1996, unpublished report; Thompson 1997, 1999, unpublished reports; Beissinger & Becker 1999a; b, unpublished reports; Ralph & Long 1995; Strong et al. 1995). Observers during July through late August are able to distinguish juvenile birds from adults using plumage characteristics (Carter & Stein 1995; Kuletz & Kendall 1998). Although such surveys have high variance (Evans Mack et al. 2002; Raphael & Evans Mack 2001)., Beissinger (1995), and Beissinger & Nur (1997) presented techniques for standardizing at-sea counts by date,

to correct for the build up of juveniles as the season progresses, based on the cumulative distribution of fledging dates (Nelson and Hamer 1995), and iteratively adjusting breeding propensity to match the observed juvenile ratios.   Beissinger (1995) and Beissinger & Nur (1997) argued strongly that these surveys, despite their variation, provide the most practicable method for estimating annual fecundity for use in population modeling.

5.3.4   Population models of Marbled Murrelets

Marbled Murrelet local population growth rates have been estimated in two ways, which produce results with somewhat different interpretations.

5.3.4.1 Leslie matrix model

The classic Leslie matrix age-specific demographic model estimates the intrinsic growth rate of populations, usually calculated based on females only, as adapted for demographic "stages" rather than ages (Caswell 1989). The model requires estimates of demographic stage-specific survivorships and fecundities. Survivorships were initially estimated from the comparative study described above (Beissinger 1995, Beissinger & Nur 1997), but the most recent version uses values derived from the capture-recapture study in central California (Peery et al. 2003a, c, unpublished reports).

Fecundity includes the stage-specific probability that an individual female breeds in a given year, multiplied by its expected nesting success. Two approaches have been taken to estimate these parameters: (1) estimates based on the ratios of juveniles to after hatch-year birds estimated during at-sea surveys, and (2) direct observations of nesting success, multiplied by an estimate of the proportion of breeders in the population. The former measure of fecundity summarizes all previous components of recruitment to the juvenile at-sea stage (e.g. adult and sub-adult breeding propensity, clutch size, nesting success, fledging success and initial survivorship on the ocean), but does not allow assessment of the relative contribution of each component to total recruitment. At-sea survey data were adjusted linearly for survey date to compensate for the cumulative hatching distribution (see above) and for the estimated the proportion of sub-adults in the population and those that bred, to ensure that the composite population fecundity matched the observed juvenile-adult distribution as expected under a stable age distribution. The more recent models (Peery et al. 2002; 2003a; c, unpublished reports) also estimate nesting success directly from that observed at nests, and combine this with estimates of population-wide breeding propensity, derived from radio-tracking studies. Age of first breeding is assumed to be 3 years. The sensitivity of the model to this assumption was tested by Beissinger & Nur (1997); in the at-sea survey approach, adjustments made to balance total population fecundity compensate somewhat for variation in this parameter. Regardless of the approaches taken to estimate parameter values, the output from Leslie models representing survivorship and fecundity values for all populations in Washington, Oregon and California (Beissinger & Nur 1997) suggest negative population growth rates. The most detailed study of a small and isolated population in the Santa Cruz Mountains, suggests an intrinsic loss rate up to 29% per year. Peery et al. (2002; 2003a; c, unpublished reports) argue that for the Santa Cruz Mountain population, such losses are not observed at the population level because of immigration from

other populations, an extrinsic source of individuals that are not included in the standard Leslie matrix. This peripheral population would thus be a classic demographic "sink".

No formal Leslie matrix model has been produced for other populations of Marbled Murrelets. We can approximate the outcome for the populations studied at Desolation and Clayoquot Sounds by applying rates of nesting and renesting success (Bradley et al. *submitted*; McFarlane Tranquilla et al. *submitted*; Centre for Wildlife Ecology , unpublished data) combined with estimates of breeding propensity (McFarlane Tranquilla et al. 2003) and juvenile (Parker et al. *submitted*) and adult survivorship (Cam et al. 2003) to population growth rate state-space diagrams (e.g. Fig. 2 in Boulanger 1999; and Fig. 5 in Beissinger & Nur 1997). The fecundity value should be about 0.35. In combination of survivorship values of ca. 0.86 (Section 5.3.2), the two BC populations apparently will fall squarely on a stable or slightly positive intrinsic growth rates.

5.3.4.2 Capture-recapture models

A second class of models derives local population growth rates based entirely on mark-recapture data (Pradel 1996; see also Hines & Nichols 2002; Nichols & Hines 2002). These models produce estimates of adult survivorship (Section 5.3.2) and of total recruitment, which includes, but does not distinguish between, recruits produced through local fecundity and immigrants from elsewhere. For Desolation Sound BC, Cam et al. (2003) estimated population growth rates of 0.9851 (95%CI: 0.8493–1.1426) using the most consistently collected banding sample (see Section 5.3.2). As discussed in the previous section, we believe that a stable population outcome will result from a Leslie matrix analysis of that population. Since the Pradel (1996) estimate includes immigration, however, we would in fact expect this method to produce a higher value, unless permanent emigration rates from Desolation Sound are high.

For central California, Peery et al. (2003a; b, unpublished reports) estimated a population growth rate of 1.090 (95% CL: 0993–1.187). Since local production is extremely low (Section 5.3.3), this rate can only be maintained by substantial immigration from other populations.

5.3.4.3 Population monitoring approach

Peery et al. (2002; 2003a; c, unpublished reports) have estimated population growth rate directly from census data, over a 3-year period. This has proved useful in conjunction with their two other approaches, as outlined above, in helping to partition immigration versus local recruitment. However, as stated previously, no one has yet directly related historical changes in population size directly to changes in terrestrial habitat.

5.4 Variation in life history components with respect to forest attributes

Comparison of the population productivity models between California and British Columbia has little power with respect to relationship to any other variables. It is a two-point comparison and many things differ between sites besides forest attributes. However, some information is available by comparing values of three key components most likely to be

affected by forest structure. The most relevant demographic life history components are: breeding propensity (the probability of attempting to breed), nesting success, and adult survivorship through a nesting attempt.

5.4.1 Breeding propensity and forest structure

Terrestrial habitat could influence the probability of attempting to breed primarily through variation in the availability of what the birds' perceive as safe and accessible nest sites. Studies relating forest usage to platform density suggest that such an effect may be real, and Section 4.2.2 describes specific correlates related to forest structure. However, the only direct information on this topic to date is the suggestion the annual variation in sea-surface temperatures affects breeding propensity (Section 3.2).

It has been suggested that forest fragmentation may increase accessibility for murrelets, but also, as outlined below (Section 5.4.2.1), that doing so might result in birds nesting at sites with higher probabilities of nest predation.

In addition to habitat removal, forestry activity adjacent to nesting habitat may influence the probability of occupancy by Marbled Murrelets in adjacent stands. A carefully designed and executed study of this question in the Santa Cruz mountains was unable to show this to be the case, at the scale addressed, as of 1999 (Suddjian 1999, 2001, unpublished reports; Suddjian et al. manuscript; an updated final report on the project was not available at the time of this review, but should be available shortly). There was no evidence that harvesting activity influenced occupancy rates in adjacent parklands. Nest success was not evaluated, but is already low throughout this region (Peery et al. 2003c, unpublished report). The direct empirical approach taken in this study is a model for future work on such questions

5.4.2 Nesting success and forest structure

Nesting success is primarily influenced by (1) predation rates on eggs or chicks, and (2) by limitations on the parent's ability to provision chicks. Becker (2002, cited in Peery et al. 2003c, unpublished report) provide the first and only data set of apparent nest failures due to chick abandonment or starvation, which they attribute to poor marine resources, as discussed previously. Kuletz, cited in Nelson & Hamer (1995a), suspected starvation of chicks during two years in Alaska. Therefore, we will here revisit forest structural factors likely to affect predation rates at nests. The scanty information relating nest plot level characteristics and fledging success was covered in Section 4.2.1.3. Here we concentrate on what is known about nesting success in relation to edges and forest fragmentation, and to commuting distances.

5.4.2.1 Edges and fragmentation

The original published information, based on 16 nests, found that nesting success of Marbled Murrelets was lower closer to edges of habitat patches than within patches (e.g. > 50 m from an edge; Nelson & Hamer 1995a). Rodway and Regehr (2002) report higher predator frequencies in areas fragmented by logging. However, the data sets gathered

during radio-tracking studies in B.C., analysed in different ways and at different scales, fail to show negative effects of edges on hatching success, and may show positive effects (Bradley 2002; Manley 2003, unpublished report; Waterhouse et al. *in press*; Zharikov et al. *submitted*; Zharikov et al. 2003). This difference in results shows that 'edgey' habitat patches need not dogmatically be assumed to provide poorer or unproductive habitat. At Desolation Sound, many of the edges were in a naturally fragmented landscape of higher altitude patches. Limited predator surveys found lower densities of corvids at higher elevations (Bradley 2002). Thus, the expectation that edge and predator exposure will positively covary may not always be met, and should not be assumed to occur in all situations (Zharikov et al. *submitted*).

Edges can reasonably be assumed to be detrimental when associated with campgrounds, human settlement, or other activities that attract corvids, as shown through artificial nest experiments (Marzluff et al. 1998, unpublished report; Raphael et al. 2002b). Despite some methodological caveats (Luginbuhl et al. 2001), these carefully conducted and analyzed studies make an important contribution. They do help with the difficult task of evaluating the relative probability of predation in the environments tested with respect to the three major factors considered: simple versus complex forest structure, proximity to human activity, and landscape fragmentation. Birds were the major predators on eggs, while mammals were the principle predators on simulated chicks. Predation rates were highest close to edges with ongoing human activity. However, forest fragmentation versus continuous forest per se had no effect on the survivorship curve of eggs, and older clearcut edges showed no negative effects.

5.4.2.2 At-sea juvenile ratios

If juvenile ratios reflect fecundity differences between local populations, correlations between forest characteristics and juvenile ratios might allow better identification of habitats with high breeding success. This has not, to our knowledge, yet been done at the watershed scale (c.f. radar studies, Section 4.2.3). However, juvenile ratios are a highly unreliable measure of local productivity for several reasons, mainly because juveniles are known to make unpredictable post-fledging movement (see Burger 2002, page 16, for summary of the problems of interpreting juvenile ratios). Estimated juvenile ratios vary from 0.02–0.12 (California: 0.022–0.057; Ralph and Long 1995, Strong et al. 1997, unpublished report, Peery et al. 2003, unpublished report; Oregon: 0.027 – 0.065; Strong 1997, unpublished report; Strong 2002; 2003b, unpublished reports, Strong and Carten 2000, unpublished report; Washington: 0.025 – 0.117; Raphael and Mack 1997, Collins 2000; British Columbia: 0.043; Lougheed et al. 2002; Alaska: 0.02 – 0.118; Kuletz & Kendall 1998, not including ratios calculated from the 'nursery', Kuletz & Piatt 1999). There is no strong latitudinal pattern, but the highest rates recorded increase as one goes further north. As with the information on nesting success, there is no obvious method for associating mean or variance in at-sea juvenile ratios with terrestrial forest structure at a meaningful scale.

5.4.2.3 Costs of commuting and forest location

There are no hard data on the marginal economics or risks of commuting distances for Marbled Murrelets. It is reasonable to assume that it is less stressful and risky to deliver food to nests closer rather than further from feeding areas. However, for the most substantial available data set, that from 121 nests at Desolation Sound, B.C., successful nests were located further from feeding areas than unsuccessful nests (Bradley 2002, Zharikov et al. *submitted*), using samples that incorporate and add to those analyzed by (Hull et al. 2001a). This counter-intuitive result points out the difficulties in drawing conclusions from any observational study, and on basing conclusions on univariate analyses. In this sample, birds nesting further from the ocean also nested earlier in the season, and date in the season is the best predictor of nesting success in univariate and multivariate analyses of this data set (Zharikov et al. *submitted*). One interpretation is that those birds nesting earlier in the season are more experienced. They may have, perhaps through repeated nesting attempts, located safer nest sites further inland. Safety for the nestling could offset the increased survivorship risks for adults or young from flying further over the forest. This pattern is predicted if birds follow a "fail–move" rule as hypothesized in Section 4.1.2.

5.4.3   Adult survivorship with respect to forest structure

Despite the emphasis in the previous section on nesting success, small differences in adult survivorship have stronger influences on population growth rate than do moderately large differences in nesting success (Beissinger 1995; Boulanger et al. 1996; Cam et al. 2003).

The most direct effect would occur if altering nesting locations or flight paths made adult Marbled Murrelets more or less vulnerable to capture. Several radio-tagged birds in the Desolation Sound study were taken by bald eagles *Haliaeetus leucocephalus* (Centre for Wildlife Ecology, unpub. data), and peregrines killed 7 murrelets in central California study (Peery et al. 2003c, unpublished report). The crepuscular flight times of murrelets (e.g., Cooper et al. 2001) between terrestrial and marine habitats suggests that predation by diurnal raptors during flights can be an important source of adult mortality. We might assume that if Marbled Murrelets make longer flights to reach safer nest sites, their mortality rates may increase, but no data are available to test this.

Marbled Murrelets are too widely dispersed, and spend too little time in the forest to support specialist predators on eggs, nestlings, or adults. The principal effect of changing forest structure may be through altering the local populations of raptors (Zharikov et al. *submitted*), just as has been argued with respect to nest success. However, in contrast to corvid populations, fragmentation may decrease, rather than increase raptor populations and densities (see Sanchez-Zapata & Calvo 1999 for an European example).

6 Conclusion

The information available for making management decisions affecting Marbled Murrelets with respect to forestry activity is substantially better than that available when the species was listed in 1992, and since the summary volume on ecology and management published in 1995 (Ralph et al. 1995). Techniques for capturing murrelets, finding nests, studying nest predator distributions, and demographic techniques have advanced. Some previous speculations can now be supported or refuted with data, albeit still scanty data in many respects. Monitoring and research efforts now in place have real potential to further provide a sound scientific basis for future decision-making.

7 Acknowledgements

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